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Lukas Bögge

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Université Paris Cité

École doctorale Cognition, Comportements, Conduites Humaines (ED 261)

Laboratoire Mémoire, Cerveau et Cognition (LMC², URP 7536)

Connecting and Stimulating Body and Mind
through Heart Rate Variability Biofeedback:
Effects on Cognitive Control and Self-Referential
Processes in Memory and Thinking

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Thèse de doctorat de Neurosciences Cognitives

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Declaration of Authorship

I hereby declare that I am the sole author of my thesis, prepared in accordance with the guidelines of the Université Paris Cité. To the best of my knowledge this thesis contains no material previously published by any other person except where due acknowledgement has been made.

I also hereby declare that my thesis has not been prepared for another examination or assignment, either in its entirety or excerpts thereof.

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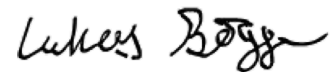
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Keywords, Title, and Abstract – English

Keywords

Heart rate variability, biofeedback, mind-body connection, heart-brain axis, long-term episodic memory, future thinking, cognitive control, self-referential processing, virtual reality, cognitive enhancement

Title

**“Connecting and Stimulating Body and Mind
through Heart Rate Variability Biofeedback:
Effects on Cognitive Control and Self-
Referential Processes in Memory and Thinking”**

Abstract

Body and mind are interwoven, as physical states influence cognition while cognitive demands drive physiological regulation. Heart rate variability (HRV), which is the naturally occurring fluctuation of the heart rate, reflects such regulatory processes that are controlled by the autonomic nervous system’s sympathetic and parasympathetic branches. HRV is a crucial biomarker of autonomic activity and brain-heart interactions and is also connected with cognitive functions underlying self-regulation. There is a proposed linkage between parasympathetic (vagally) mediated HRV and cognition, driven by shared cortical and subcortical brain regions, primarily the prefrontal cortex that regulate autonomic and behavioral responses. Such a connection has been convincingly established for cognitive control, which supports goal-directed behavior. Nevertheless, the associations were founded on relatively simple measures (global correlation with HRV measured during rest) and have not been systematically expanded to cognitive functions beyond cognitive or affective control. A number of cognitive processes engage brain hubs that are also involved in autonomic control, notably, self-referential processing, which consists in relating information to oneself (e.g., one’s name or thoughts). Yet previous research has paid little to no attention to higher-level cognitive functions related to cognitive control and self-referential processing, such as long-term memory and future-oriented thinking. Preliminary results indicate that the use of HRV biofeedback, a self-regulation training technique that enhances vagally mediated HRV, can lead to an improvement in cognitive control. However, there is limited evidence supporting the notion that an increase in vagally

mediated HRV produces the desired effects. Based on the neurovisceral theory of autonomic control and cognition and the insufficient number of studies examining the biofeedback effect on higher-level cognitive functions and its correlation to changes in HRV, this thesis aims to explore the cognitive benefits of HRV biofeedback and to investigate the body-mind interaction of the autonomic nervous system with memory and future thinking through cognitive control and self-reference processes. Biofeedback and cognitive assessments were implemented in immersive virtual reality to increase experimental robustness and control. Three randomized and placebo-controlled experiments were conducted among healthy young adults. A longitudinal study first explored the HRV biofeedback effect on cognitive control and self-referential episodic memory, revealing benefits which persisted beyond the training period and which were associated with the degree of HRV stimulation during training. In the second and third studies, HRV biofeedback was integrated for the first time with cognitive tasks in a single session to investigate how HRV stimulation during cognitive processing influences long-term declarative memory and past and future thinking. True-false memory discrimination performance and thought properties of episodic (autobiographical) memory and episodic future thinking were examined to evaluate self-referential processing and cognitive control over memory and thought. In summary, the study's results validate the neurovisceral integration model and vagal tank theory, presenting additional understanding of how autonomic control affects (higher-level) cognitive functions and how HRV biofeedback can enhance them. They add new insight how improved cardiac vagal control through HRV biofeedback can promote adaptive thinking even in healthy individuals. Future research is required to substantiate the interaction between autonomic, executive, emotional, and self-referential processes, and the utility of HRV biofeedback for preventive mental health care.

Keywords, Title, and Abstract – French

Mots-clés

Variabilité de la fréquence cardiaque, biofeedback, connexion corps-esprit, axe cœur-cerveau, mémoire épisodique à long terme, pensée future, contrôle cognitif, processus de référence à soi, réalité virtuelle, renforcement cognitif

Titre

« Connecter et stimuler le corps et l'esprit par le biofeedback de la variabilité de la fréquence cardiaque : Effets sur le contrôle cognitif et les processus liés à soi dans la mémoire et la pensée »

Résumé

Le corps et l'esprit sont intimement liés. En effet, les états physiques influencent la cognition tandis que les efforts cognitifs entraînent une régulation physiologique. La variabilité de la fréquence cardiaque (VRC ou HRV en anglais) est la fluctuation naturelle de la fréquence cardiaque qui reflète ces processus de régulation contrôlés par les branches sympathiques et parasympathiques du système nerveux autonome. La HRV est un biomarqueur essentiel de l'activité autonome et des interactions entre le cerveau et le cœur, et elle est également liée aux fonctions cognitives qui sous-tendent le processus d'autorégulation. Il existe un lien supposé entre la HRV à médiation parasympathique (vagale) et la cognition, par l'activation de régions corticales et sous-corticales du cerveau, principalement le cortex préfrontal, qui régulent les réponses autonomes et comportementales. Un tel lien a été établi de manière convaincante pour le contrôle cognitif, qui permet le comportement orienté vers un but. Néanmoins, ces liens ont été fondés sur des mesures relativement simples (corrélation globale avec la HRV mesurée au repos) et n'ont pas été systématiquement étendues à des fonctions cognitives autres que le contrôle cognitif ou émotionnel. Un certain nombre de ces processus cognitifs font appel à des régions cérébrales qui sont également impliquées dans le contrôle autonome, notamment le traitement de l'information en référence à soi, qui consiste à relier des informations à soi-même (par exemple, son nom ou ses pensées). Pourtant, les recherches antérieures ont accordé peu ou pas d'attention aux fonctions cognitives de haut niveau liées au contrôle cognitif et au traitement de

l'information en référence à soi, comme la mémoire à long terme et les pensées dirigées vers le futur. Des résultats préliminaires suggèrent que l'utilisation du biofeedback de la HRV, une technique d'entraînement à l'autorégulation qui améliore la HRV, peut conduire à une amélioration du contrôle cognitif. Cependant, il existe encore peu de preuves pour étayer l'idée qu'une augmentation de la HRV à médiation vagale produit ces améliorations souhaitées. Basé sur la théorie neuroviscérale du contrôle autonome et de la cognition et un nombre insuffisant d'études examinant l'effet du biofeedback sur les fonctions cognitives de haut niveau et sa corrélation avec les changements de HRV, cette thèse vise à explorer les avantages cognitifs du biofeedback de la HRV et à étudier l'interaction corps-esprit du système nerveux autonome avec la mémoire et la pensée orientée vers le passé ou le futur par le biais du contrôle cognitif et des processus de référence à soi. L'entraînement par biofeedback et des évaluations cognitives ont été implémentés en réalité virtuelle immersive afin d'accroître la robustesse et le contrôle de l'expérience. Trois expériences randomisées et contrôlées par placebo ont été menées auprès de jeunes adultes en bonne santé. Une première étude longitudinale a exploré l'effet du biofeedback de la HRV sur le contrôle cognitif et la mémoire épisodique en référence à soi, démontrant un bénéfice qui a persisté au-delà de la période d'entraînement et a été associé au degré de stimulation HRV pendant l'entraînement. Dans la deuxième et la troisième étude, le biofeedback de la HRV a été intégré pour la première fois à des tâches cognitives en une seule session afin d'étudier comment la stimulation HRV pendant le traitement cognitif influence la mémoire déclarative à long terme et la pensée orientée vers le passé ou le futur. Les performances de discrimination mnésique (« Vrai / Faux ») et les propriétés de la mémoire épisodique (autobiographique) et de la pensée future épisodique ont été examinées pour évaluer le traitement en référence à soi et le contrôle cognitif de la mémoire et de la pensée. En résumé, les résultats de l'étude valident le modèle d'intégration neuroviscérale et la théorie du réservoir vagal, ce qui permet de mieux comprendre comment le contrôle autonome affecte les fonctions cognitives (de haut niveau) et comment le biofeedback de la HRV peut les améliorer.

Keywords, Title, and Abstract – German

Schlüsselwörter

Herzfrequenzvariabilität, Biofeedback, Geist-Körper-Verbindung, Herz-Hirn-Achse, episodisches Langzeitgedächtnis, Zukunftsdenken, kognitive Kontrolle, selbstreferentielle Verarbeitung, virtuelle Realität, kognitive Steigerung

Titel

**„Verbindung und Stimulation von Körper und Geist
durch Biofeedback der Herzfrequenzvariabilität:
Auswirkungen auf die kognitive Kontrolle und die
selbstreferentiellen Gedächtnis- und Denkprozesse“**

Abstrakt

Körper und Geist sind miteinander verwoben, da körperliche Zustände die Kognition beeinflussen und kognitive Anforderungen die physiologische Regulation vorantreiben. Die Herzfrequenzvariabilität (HRV), d.h. die natürlich auftretende Schwankung der Herzfrequenz, spiegelt diese Regulationsprozesse wider, die von den sympathischen und parasympathischen Zweigen des autonomen Nervensystems gesteuert werden. Die HRV ist ein wichtiger Biomarker für die autonome Aktivität und die Interaktionen zwischen Gehirn und Herz und steht auch in Verbindung mit kognitiven Funktionen, die der Selbstregulation zugrunde liegen. Es wird ein Zusammenhang zwischen parasympathisch (vagal) vermittelter HRV und Kognition vermutet, da gemeinsame kortikale und subkortikale Hirnregionen, insbesondere der präfrontale Kortex, die autonomen und verhaltensbezogenen Reaktionen regulieren. Ein solcher Zusammenhang konnte für die kognitive Kontrolle, die zielgerichtetes Verhalten unterstützt, deutlich nachgewiesen werden. Die Assoziationen basierten jedoch auf einfachen Messungen (globale Korrelation mit der in Ruhe gemessenen HRV) und wurden nicht systematisch auf kognitive Funktionen jenseits der kognitiven oder emotionellen Kontrolle ausgedehnt. An einer Reihe kognitiver Prozesse sind Gehirnzentren beteiligt, die auch bei der autonomen Kontrolle eine Rolle spielen. Dies betrifft insbesondere die selbstreferenzielle Verarbeitung, die darin besteht, Informationen auf sich selbst zu beziehen (z. B. den eigenen Namen oder die eigenen Gedanken). Dennoch wurden in der bisherigen Forschung kognitive Funktionen auf

höherer Ebene, die mit der kognitiven Kontrolle und der selbstreferenziellen Verarbeitung zusammenhängen, wie das Langzeitgedächtnis und zukunftsorientiertes Denken, wenig bis gar nicht berücksichtigt. Vorläufige Ergebnisse deuten darauf hin, dass die Anwendung von HRV-Biofeedback, einer Selbstregulationstechnik, die die vagal vermittelte HRV erhöht, zu einer Verbesserung der kognitiven Kontrolle führen kann. Es gibt jedoch nur wenige Belege für die Annahme, dass die gewünschten Auswirkungen durch die Stimulation der vagal vermittelten HRV verursacht werden. Basierend auf der neuroviszeralen Theorie von autonomer Kontrolle und Kognition sowie der unzureichenden Anzahl von Studien, die den Biofeedback-Effekt auf höhere kognitive Funktionen und seine Korrelation mit Veränderungen der HRV untersuchen, zielt diese Arbeit darauf ab, den kognitiven Nutzen von HRV-Biofeedback sowie die Körper-Geist-Interaktion des autonomen Nervensystems mit dem Gedächtnis und Zukunftsdenken durch kognitive Kontrolle und Selbstreferenzprozesse zu erforschen. Biofeedback und kognitive Bewertungen wurden in einer immersiven virtuellen Realität durchgeführt, um die experimentelle Robustheit und Kontrolle zu erhöhen. Drei randomisierte und placebokontrollierte Experimente wurden mit gesunden jungen Erwachsenen durchgeführt. Eine Längsschnittstudie untersuchte zuerst die Wirkung von HRV-Biofeedback auf die kognitive Kontrolle und das selbstreferentielle episodische Gedächtnis, der über die Trainingsperiode hinaus anhielt und mit dem Grad der HRV-Stimulation während des Trainings assoziiert war. In der zweiten und dritten Studie wurde das HRV-Biofeedback zum ersten Mal mit kognitiven Aufgaben in einer einzigen Sitzung kombiniert, um zu untersuchen, wie die HRV-Stimulation während der kognitiven Verarbeitung das deklarative Langzeitgedächtnis und Zukunftsdenken beeinflusst. Die Unterscheidungsfähigkeit von wahren und falschen Erinnerungen sowie die Gedankeneigenschaften des episodischen (autobiographischen) Gedächtnisses und des episodischen Zukunftsdenkens wurden untersucht, um die selbstreferentielle Verarbeitung und die kognitive Kontrolle beim Denken zu bewerten. Zusammenfassend lässt sich sagen, dass die Ergebnisse der Studie das Modell der neuroviszeralen Integration und die Theorie des vagalen Tanks validieren und zusätzliche Einblicke liefern, wie die autonome Kontrolle (höhere) kognitive Funktionen beeinflusst und wie HRV-Biofeedback diese verbessern kann.

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How was it again, the beginning and the end are some of the bits we remember the best? Well, that is of no surprise to me considering my very first day as a fresh intern, when I met Monsieur Philippe Blondé, early as always in an empty lab. Straight in posture, sleek in his black costume, gaze leveled at the horizon, he seemed to me a professor and the wanderer above the sea of fog alike. "Monsieur, pouvez-vous m'ouvrir une porte » I asked in my broken French. Well, it turned out Philippe would be my neighboring PhD companion for the next two years. On the left flanked by Napoleon and on the right by Friedrich der Große, you never failed to amaze me with your unique quirks, historical anecdotes, and profound passion for many aspects of life. Thank you not only for tirelessly correcting my French but also for making this PhD so delightful. With sharp intellect mantled by emotional intelligence you showed greatest care for those around you. I could not have wished for more.

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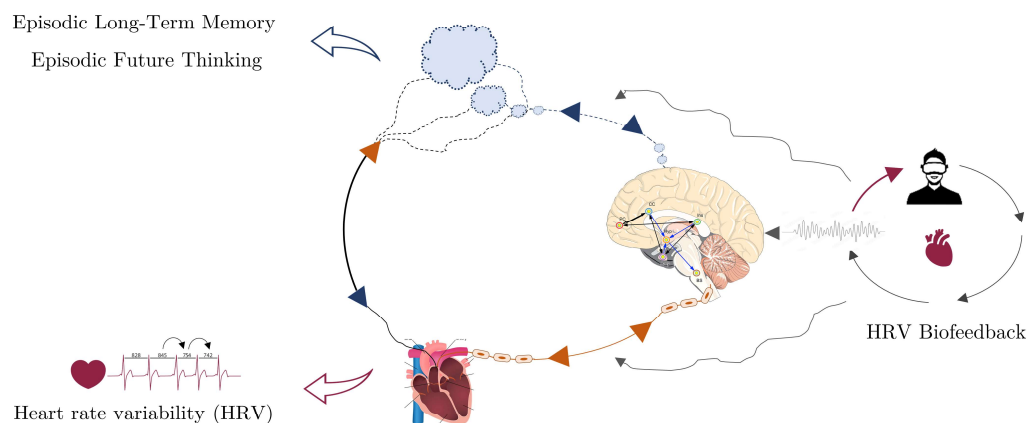
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Abbreviations

ACC	Anterior Cingulate Cortex
ANS	Autonomic Nervous System
CAN	Central Autonomic Network
DMN	Default Mode Network
ECG	Electrocardiogram
EEG	Electroencephalogram
fMRI	functional Magnetic Resonance Imaging
HRV	Heart Rate Variability
PFC	Prefrontal Cortex
PNS	Parasympathetic Nervous System
RMSSD	Root Mean Square Successive Difference in heart period series
RSA	Respiratory Sinus Arrhythmia
SNS	Sympathetic Nervous System
vmHRV	vagally mediated Heart Rate Variability
VR	Virtual Reality

Global Summary – English



When looking down, you see what everyone else would also see: your own body. To that body belongs your mind. A complicated topic regarding the different philosophical schools that argue the mind is to the body an independent substance (Descartes, 1998) or an indiscernible entity (Spinoza, 2004), or simply all that exists because the outer world is an illusion (Guyer & Horstmann, 2015). Therefore, it might suffice if we consider from a cognitive perspective that the mind refers to a set of mental processes and faculties that allow us to perceive and interact with the world. Such “mind stuff” includes the capability and process of memorizing new information, recalling them, or pondering about the future. Human cognition, thus, crucially shapes how we experience our world and live our lives. When one says “oh, my memory is bad” one might directly associate this misfortune with the brain. The latter has long been considered the main source of cognition and is the central subject of cognitive neuroscience. But what about the rest of the body? The brain makes up only 2% of our body mass (Dekaban & Sadowsky, 1978) but is highly interconnected with the periphery through nerve fibers, hormonal, and biochemical pathways. The brain is embedded in the central nervous system that runs down the spinal cord. It is interwoven with the autonomic nervous system that spans the whole organism connecting nerve fibers to organs and regulating body functions. Especially, the heart is an interesting study topic, which has already been shown to communicate with the brain via the autonomic nervous system 150 years ago by Claude Bernard. Since then, numerous studies have confirmed the existence of a heart-brain-axis (Tahsili-Fahadan & Geocadin, 2017). The heart is considered a “little

brain” itself due to its intrinsic nervous system (Armour, 1991) that encodes information from numerous inputs. So, it seems that both brain and heart are susceptible to the bodily internal and external environment, and that one influences the other. It follows the question: Do mind and heart also interact?

We all may have experienced when being excited our heartbeat increases and our thoughts start racing, for example when giving a public talk. Such arousal effects are commonly known to affect cardiac regulation and our mental state alike through activation of the autonomous nervous system (Critchley, 2005; Critchley et al., 2013). This system is divided into the sympathetic branch, responsible for fight-and-flight responses (increased heart rate), and the parasympathetic branch, active during rest. What you may not feel, however, is how your autonomic nervous system causes your heart rate to continuously move up and down, especially during resting periods. The autonomic nervous system regulates the heart rate in dynamic fashion so that heart rhythm changes from beat to beat. This phenomenon is also known as *heart rate variability* (HRV). Thus, measuring the beat-to-beat variations in the heart rate allows to assess autonomic nervous system functioning. Of probably greatest significance for cardiac control is the vagal nerve, which is the main conduit of parasympathetic drive. It functions as a brake to suppress the effects of pacemaker cells in the heart that dictate a rhythm of around 110 beats per minute. Activating and releasing this vagal brake leads to rapid fluctuations in the heart period which will be notable in measures of vagally mediated HRV. Many different measures of HRV exist, however, this thesis focuses on those that index parasympathetic regulation.

The Central Autonomic Network (Benarroch, 1993) functions as an anatomical interface between the central and autonomic nervous systems. It includes brainstem centers, from where the vagal nerve originates, as well as multiple structures in the mid- and forebrain that are also involved in cognitive functions. The neurovisceral integration model (Thayer & Lane, 2000, 2009), based on the Central Autonomic Network, provides a framework that connects vagal control of the heart, and thus HRV, with cognitive and emotional processes. The neurovisceral integration theory has been of profound significance in psychophysiological research as well as for clinical applications, as it gave rise to numerous studies that linked cardiac vagal control with cognitive faculties. Of paramount importance in this model are inhibitory feedback

loops that mediate suppression effects in physiological regulation (activating and deactivating the vagal brake) as well as in self-regulation.

Self-regulation describes the goal-directed control of behavior and thought which is strongly dependent on such inhibitory control. For example, to recall a memory or make plans, one must suppress ongoing distractions and irrelevant information we are continuously confronted with (e.g., suppress unwanted thoughts and other perceptions of the inner and outer world). This process also involves attention control which allows to orient and maintain focus and resolve internal conflicts. These cognitive processes have been grouped under the term *cognitive* or *executive* control. Cognitive control aids in resolving interference that arises when, for example, during information selection other similar or prepotent information are competing for cognitive resources. One may struggle recalling a certain memory because of another interfering memory that is recalled instead. Such erroneous retrieval is also referred to as false memory, assessing which provides a proxy of cognitive control. Moreover, thought control is deeply intertwined with emotions as executive processes allow them to be effectively regulated. Imagine you have a recurring negative thought that causes you great distress: cognitive control would engage in downregulating this emotion and shifting your attention to something more agreeable. Evolutionary, this has great benefits for the organism as it mitigates stress responses that are detrimental to physical and mental health.

Cognitive control strongly relies on the prefrontal cortex in forebrain and emotional processing on the amygdala in limbic system, both regions that play a crucial role in autonomic regulation. Thayer and Lane (2000, 2009) proposed in their model that HRV, due to the neural inhibitory circuits, interrelates with prefrontal activity and thus cognitive control. Indeed, HRV has been demonstrated as a prominent biomarker of cognitive and emotional regulation capacities and predictive of mental health outcomes and thought control. It therefore becomes clear; mind and body are connected through an intrinsically wired physiological system spanning brain and body. This system, in turn, is tasked with physiological, cognitive, and emotional regulation to promote health and adaptive behavior. Importantly, the activity of this system can be indexed by HRV with higher levels indicating better regulatory capacities. While HRV crystallizes as an important measure to assess the mind-body connection, it remains

unclear how it relates to higher-level cognitive functions such as long-term memory and future thinking.

Long-term memory is the continuing memory storage holding information over lengthy periods. Important memory stages are the encoding of new information, the consolidation of its trace, and its subsequent retrieval when the memory is brought back to consciousness. It can contain abstract and general knowledge about the world encompassing facts and concepts, what is referred to as *semantic* memory. Conversely, when memory involves an event-specific context including aspects of space, time, and phenomenological details, we talk of *episodic* memory. It is strongly connected to the memory of knowledge and experience of ourselves, the *autobiographical* memory, as we encode information from a self-perspective. Episodic autobiographical memory is characterized by autothetic consciousness, which is the capability to place oneself mentally in the past and future, known as *mental time travel*. It thus also constitutes the ability to simulate future events, known as episodic future thinking. For example, one may remember catching a sunburn on the sunny beach the second day of the last Spain vacation or picture oneself dog sledding in the outskirts of Tromsø, Norway next Winter. Mental time travel is a particularly interesting cognitive ability to study due to its relevance for human behavior and detail-rich mental context. Mentally re-experiencing and pre-experiencing events is an elaborative cognitive process that involves a multitude which involves a multitude of diversified processes. Besides mnemonic, emotional, and executive processes that support scene construction, mental time travel strongly involves self-referential processes. These are active when information is linked to the self (e.g., hearing one's name or thinking about a personal relevant goal or memory). Self-referential processing recruits the ventromedial prefrontal cortex, a hub of the Central Autonomic Network and engaged in emotion regulation. Surprisingly, no research, to the best of our knowledge, has directly investigated the relationship between mental self-referential processing with HRV, although the two share a common neural basis. Also cognitively, according to the Self-Memory System model (Conway, 2005), HRV-related executive processes are interconnected with self-referential processes and the long-term memory system. Conclusively, it seems very promising to investigate the association between HRV and self-referential processing as well as its

interaction with emotional and executive processes within mental time travel to elucidate the mind-body connection.

A major limitation of previous studies is that they primarily assessed HRV during a resting phase separated from the cognitive task. While global correlations showed predictive value, they tell little about the directionality of the effect (does HRV affect cognition or other way around?) and psychophysiological interactions during cognitive activity. The Vagal Tank Theory (Laborde et al., 2018) provided a conceptual framework confronting this problem. It is hypothesized that by measuring changes in tonic HRV (at one time point) from a resting baseline phase to task (reactivity) and from task to a post-task baseline phase (recovery), patterns in HRV will provide additional insight into the psychophysiological relationship. Such phasic HRV (changes between tonic levels of HRV) is assumed to sensitively index self-regulatory efficacy and thus executive processes. Research based on phasic HRV is still in its infancy but may provide essential contribution to psychophysiological domain. Therefore, one goal of this thesis was to assess tonic and phasic HRV during personal past and future thought.

If greater cardiac vagal control is beneficial for cognition, what promise does increasing this control hold for the body and mind? A prominent, non-invasive technique to effectively increase cardiac vagal control is HRV biofeedback. This technique involves the real-time display of the cardiac activity, based on which the user up-regulates HRV. Such self-regulation training mainly involves adapting slow breathing which evokes physiological resonance effects due to respiratory effects on blood pressure and cardio-respiratory reflexes (baroreflex and respiratory sinus arrhythmia). Consequently, this leads to a large-amplitude and sin-like heart rate pattern, indicative of increased cardiac vagal control. Moreover, resonance produces coherence effects by harmonizing and cross-coupling cardiac oscillations with other physiological oscillatory systems (respiration, blood pressure). Subsequent increases in cardiac vagal control have been hypothesized to affect through changes in afferent parasympathetic outflow the brain. However, other pathways have been defined (Mather & Thayer, 2018), such as changes in cerebral blood flow and sensory inputs from heart to brain due to large-amplitude cardiac oscillations. HRV biofeedback has been demonstrated to effectively improve cardiovascular status, physical, and mental health (Lehrer et al., 2020). Importantly,

it also showed to influence mental disorder like anxiety (Goessl et al., 2017) and depression (Pizzoli et al., 2021), which are related to the cognitive functions of interest in this thesis. Nonetheless, it remains unclear how HRV biofeedback specifically affects cognitive functions. Especially, the healthy population remains understudied, though, HRV biofeedback bears great potential to improve peak performance and prevent cognitive impairment. Preliminary evidence exposed promising improvements in executive and attentional control (Prinsloo et al., 2013; Sutarto et al., 2012, 2013) but the underlying mechanisms remain unclarified. A compelling avenue would be exploration of the interplay in cardiac vagal control and cognitive changes induced by HRV biofeedback. Such stimulation has the potential to elucidate putative mediating pathways in the mind-body complex.

In summary, the Neurovisceral Integration Model (Thayer & Lane, 2000, 2009) and Vagal Tank Theory (Laborde et al., 2018), form the bedrock of the connection between cardiac vagal control and cognition which could be studied through HRV stimulation. The present thesis aims to establish an association between HRV and different cognitive processes (self-referential, emotional, executive) in memory and thought in healthy adults. Moreover, HRV biofeedback, as a mind-body technique, is applied to investigate whether changes in HRV mediate cognitive alterations.

The thesis therefore begins with a definition of HRV, and a description of the underlying neurophysiological mechanisms that govern cardiac and respiratory regulation, including principles of allostasis, baroreflex, and respiratory sinus arrhythmia. In specific, the role of the vagal nerve in connection to the brain and the influence of slow breathing to increase parasympathetic activity is illustrated. In the second part, HRV biofeedback and its most prominent training modalities, the resonance frequency training and coherence training, are presented and compared. In addition, the utility of biofeedback for self-regulation training is outlined. The following chapter introduces the human long-term memory system with a special emphasize on episodic memory and its various components, whether shared with other types of memory (encoding, storage, retrieval) or specific to episodic memory (phenomenology associated with retrieval, contextual memory). Furthermore, the different modes of episodic future thinking, based on the taxonomy of Szpunar et al. (2014), are shortly depicted. The chapter concludes with the description of the neural basis of the self and

the Self-Memory System (Conway, 2005), interconnecting the different cognitive processes. The fourth chapter will define cognitive (executive) control and its fundamental elements (central executive of working memory and attentional control). This is followed by an elaboration on the connection of executive processes with episodic memory and future thinking. Lastly, we provide an overview of the triple brain network model as a neural basis of cognition which subserves the integrative view on body and mind in the following chapter. We commence with an extensive description of embodied and psychophysiological theory, most notably the Neurovisceral Integration Model (Thayer & Lane, 2000, 2009) and Vagal Tank Theory (Laborde et al., 2018), before detailing the neuroanatomical basis in the brain and its various components (e.g., ventromedial prefrontal cortex, anterior cingulate cortex, amygdala) that crucially connect the bodily and cognitive processes. A demonstration of empirical evidence underscores the linkage of HRV with cognition. Finally, we look at the physiological mechanisms of HRV biofeedback and first results that have been derived in the last years. Once the main theoretical concepts underlining the utility of virtual reality have been presented, we will describe four methodological highlights of this thesis: the development of a novel virtual reality system that integrates HRV biofeedback and cognitive assessment in a controlled environment, the implementation of active placebo control groups in each experiment, the use of semi-automatized signal processing and correction procedures, as well as the application of statistically robust linear mixed effect models.

The various works carried out during this thesis will then be included one by one, according to the order they were conducted: An article published in *Frontiers in Neuroscience* for the first study (Bögge et al., 2022), a manuscript reviewed in *Psychophysiology*, but not yet modified, for the second study (Bögge et al., *in review*), and a manuscript in preparation and nearly ready for submission to *Psychophysiology* for the last study (Bögge et al., *in prep*).

In our first, longitudinal study (Bögge et al., 2022), 1-week persistent effects of HRV on various facets of cognitive control as well as self-referential episodic memory were explored. The aim was to test with a small sample of young, healthy adults which parameters would be most sensitive to HRV biofeedback manipulation, and how these relate to respiratory-coupled cardiac oscillations during training. HRV was found to

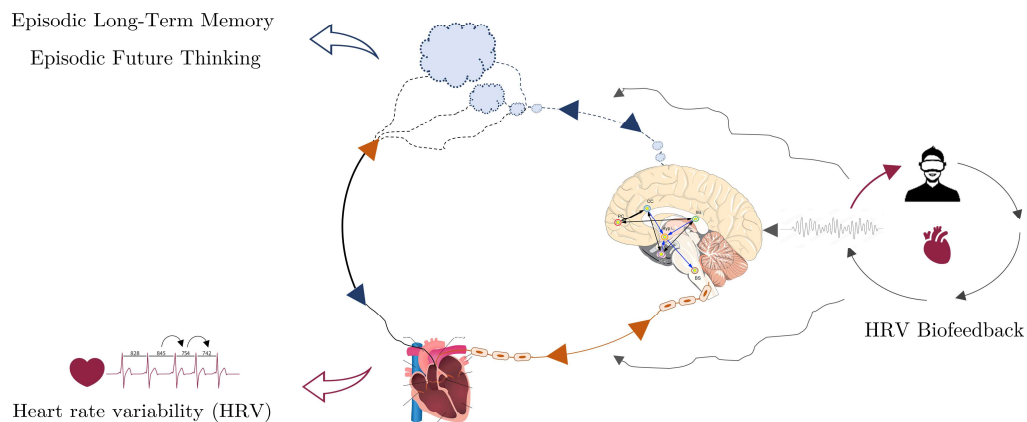
have remarkable effects on a positive-self bias in episodic memory and accuracy in interference (executive) control involved in discrimination of low-distinctive stimuli. These effects were related to cardiac oscillatory stimulation.

Departing from results of the previous investigation, the second study (Bögge et al., *in review*) focused on interference control over long-term memory, assessed as the production of false memories. The design of a new virtual reality setup, integrating cognitive assessment and HRV biofeedback in a single session, allowed for the assessment of simultaneous effects of HRV biofeedback on task-related HRV and cognitive outcomes. HRV biofeedback had no immediate effect on HRV during encoding or retrieval and on memory control. Fatigue was found to moderate psychophysiological associations. Exploratory analyses revealed that phasic HRV during retrieval predicts memory control when controlled for phasic heart rate.

In our last experiment (Bögge et al., *in prep*), the different cognitive processes (executive, emotional, self-referential, thought) were brought together in a comprehensive investigation by assessing phenomenological properties of past and future mental time travel. Like the previous study, immediate HRV biofeedback effects were tested in an integrated virtual reality environment, but the design was adapted to reduce fatigue effects. We found that phasic HRV was associated with executive control involved in event construction during positive future thinking, while tonic HRV predicted a decrease in negative self-referential processing during episodic (autobiographical) memory recollection.

The final chapter of this dissertation synthesizes all the results obtained in these three experimental studies to compare them and gain an overall perspective on the contributions of this thesis. We will then describe their implication for existing psychophysiological and cognitive theories and propose a new integrative model. Finally, several untested avenues are described to explore the link between cardiac vagal control and thought as well as the HRV biofeedback effect on mind and body.

Global Summary – French



En regardant vers le sol, on voit ce que tout le monde verrait aussi : son propre corps. C'est à ce corps qu'appartient votre esprit. Il s'agit là d'un sujet complexe étudié par différentes écoles philosophiques. Certaines considèrent que l'esprit est pour le corps une substance indépendante (Descartes, 1998), d'autres une entité indiscernable (Spinoza, 2004), ou simplement tout ce qui existe parce que le monde extérieur n'est qu'une illusion (Guyer & Horstmann, 2015). Par conséquent, il pourrait suffire de considérer, que l'esprit correspond à un ensemble de facultés et de processus mentaux qui nous permettent de percevoir le monde et d'interagir avec lui. Cette « matière grise » comprend la capacité et le processus de mémorisation de nouvelles informations, leur rappel ou la réflexion sur l'avenir. La cognition humaine façonne donc de manière cruciale la façon dont nous percevons notre monde et vivons notre vie. Lorsque l'on dit « oh, j'ai une mauvaise mémoire », on associe cela spontanément au fonctionnement du cerveau. Ce dernier est depuis longtemps considéré comme la principale source de la cognition et constitue le sujet central des neurosciences cognitives. Mais qu'en est-il du reste du corps ? Le cerveau ne représente que 2 % de la masse corporelle (Dekaban & Sadowsky, 1978), mais il est fortement interconnecté avec les systèmes périphériques par des fibres nerveuses et des voies hormonales et biochimiques. Le cerveau fait partie du système nerveux central qui descend le long de la moelle épinière. Il est imbriqué dans le système nerveux autonome qui s'étend à l'ensemble de l'organisme, reliant les fibres nerveuses aux organes et régulant les fonctions corporelles. Le cœur, en

particulier, semble être un sujet d'étude particulièrement intéressant. Claude Bernard, il y a déjà 150 ans, a démontré que le cœur communique avec le cerveau par l'intermédiaire du système nerveux autonome. Depuis, de nombreuses études ont confirmé l'existence d'un axe cœur-cerveau (Tahsili-Fahadan & Geocadin, 2017). Le cœur est lui-même considéré comme un « petit cerveau » grâce à son système nerveux intrinsèque (Armour, 1991) qui encode des informations provenant de nombreuses sources. Il semble donc que le cerveau et le cœur soient tous deux sensibles à l'environnement corporel interne et externe, et que les deux sont connectés. Il s'ensuit la question suivante : l'esprit et le cœur interagissent-ils également ?

Il nous est certainement déjà tous arrivé, lorsque nous sommes excités, nous sentons que notre rythme cardiaque et nos pensées s'accélèrent, par exemple lors d'un discours public. Ces effets d'éveil sont généralement connus pour affecter la régulation cardiaque et notre état mental par l'activation du système nerveux autonome (Critchley, 2005; Critchley et al., 2013). Ce système se divise en deux parties : la branche sympathique, responsable des réactions de lutte et de fuite (augmentation du rythme cardiaque), et la branche parasympathique, actif au repos. Ce que vous ne sentez peut-être pas, en revanche, c'est la façon dont votre système nerveux autonome fait monter et descendre votre rythme cardiaque en permanence, en particulier au repos. Le système nerveux autonome la régule de manière dynamique, de sorte que le rythme cardiaque change d'un battement à l'autre. Ce phénomène est également connu sous le nom de variabilité de fréquence cardiaque (VRC ou HRV en anglais). La mesure des variations de la fréquence cardiaque permet d'évaluer le fonctionnement du système nerveux autonome. Le nerf vagal, qui est le conducteur principal de la commande parasympathique, est crucial pour le contrôle cardiaque. Il sert de frein pour supprimer les effets des cellules *pacemaker* du cœur, qui dictent un rythme d'environ 110 battements par minute. L'activation et la libération de ce frein vagal entraînent des fluctuations rapides de la période cardiaque, impactant la HRV à médiation vagale. Il existe de nombreuses mesures différentes de la HRV, mais cette thèse se concentre sur celles qui indexent la régulation parasympathique.

Le réseau autonome central (Benarroch, 1993) fonctionne comme une interface anatomique entre le système nerveux central et le système nerveux autonome. Il comprend les centres du tronc cérébral, d'où part le nerf vagal, ainsi que de multiples

structures du mésencéphale et du cerveau antérieur qui sont également impliquées dans les fonctions cognitives. Le modèle d'intégration neuroviscérale (Thayer & Lane, 2000a, 2009), basé sur le réseau autonome central, fournit un cadre qui relie le contrôle vagal du cœur, et donc la HRV, aux processus cognitifs et émotionnels. La théorie de l'intégration neuroviscérale a été d'une grande importance pour la recherche psychophysologique ainsi que pour les applications cliniques, car elle a donné lieu à de nombreuses études établissant un lien entre le contrôle vagal cardiaque et les facultés cognitives. Dans ce modèle, les boucles de rétroaction inhibitrices qui médient les effets de suppression dans la régulation physiologique (activation et désactivation du frein vagal) ainsi que dans l'autorégulation sont d'une importance capitale.

L'autorégulation décrit le contrôle du comportement et de la pensée, orienté vers un objectif, qui dépend fortement de ce contrôle inhibiteur. Par exemple, pour se remémorer un souvenir ou faire des projets d'avenir, il faut supprimer les distractions et les informations non pertinentes auxquelles nous sommes continuellement confrontés (par exemple, supprimer les pensées indésirables et les autres perceptions du monde intérieur et extérieur). Ce processus implique également le contrôle de l'attention, qui permet d'orienter et de maintenir la concentration et de résoudre les conflits internes. Ces processus cognitifs ont été regroupés sous le terme de contrôle *cognitif* ou *exécutif*. Le contrôle cognitif aide à résoudre les interférences qui surviennent lorsque, par exemple, au cours de la sélection des informations, d'autres informations similaires ou prépondérantes sont en concurrence pour les ressources cognitives. On peut avoir du mal à se rappeler un certain souvenir à cause d'un autre souvenir interférent qui est rappelé à sa place. Cette récupération erronée est également appelée « faux souvenir », une évaluation qui fournit une approximation du contrôle cognitif. En outre, le contrôle de la pensée est profondément lié aux émotions, car les processus exécutifs permettent les réguler efficacement. Imaginez que vous ayez une pensée négative récurrente qui vous cause une grande détresse : le contrôle cognitif s'engage à réguler cette émotion et à déplacer votre attention vers quelque chose de plus agréable. Sur le plan de l'évolution, cela présente de grands avantages pour l'organisme, car cela atténue les réactions de stress qui sont préjudiciables à la santé physique et mentale.

Le contrôle cognitif repose fortement sur le cortex préfrontal du cerveau antérieur et le traitement des émotions sur l'amygdale du système limbique, deux régions qui jouent

un rôle crucial dans la régulation autonome. Thayer et Lane (2000, 2009) ont proposé dans leur modèle que la HRV, due aux circuits neuronaux inhibiteurs, soit liée à l'activité préfrontale et donc au contrôle cognitif. En effet, il a été démontré que la HRV est un biomarqueur important des capacités de régulation cognitive et émotionnelle et qu'elle permet de prédire les résultats en matière de santé mentale et de contrôle de la pensée. Il devient donc évident que l'esprit et le corps sont liés par un système physiologique intrinsèquement interconnecté qui englobe le cerveau et le corps. Ce système est chargé de la régulation physiologique, cognitive et émotionnelle afin de promouvoir la santé et un comportement adaptatif. Il est important de noter que l'activité de ce système peut être indexée par la HRV, des niveaux plus élevés indiquant de meilleures capacités de régulation. Alors que la HRV représente une mesure importante des rapports entre le corps et l'esprit, son lien avec les fonctions cognitives de haut niveau, telles que la mémoire à long terme et la réflexion sur l'avenir, n'est pas encore clairement établi.

La mémoire à long terme assure le stockage continu d'informations sur de longues périodes. Les étapes importantes de la mémoire sont l'encodage de nouvelles informations, la consolidation de leur trace et leur récupération ultérieure lorsque la mémoire est ramenée à la conscience. La mémoire peut contenir des connaissances abstraites et générales sur le monde, englobant des faits et des concepts, ce que l'on appelle la mémoire *sémantique*. À l'inverse, lorsque la mémoire s'inscrit dans un contexte événementiel incluant des aspects spatiaux, temporels et phénoménologiques, on parle de mémoire *épisode*. Elle est fortement liée à la mémoire de la connaissance et de l'expérience de soi et à la mémoire *autobiographique*, car nous encodons des informations à partir d'une perspective personnelle. La mémoire autobiographique épisodique se caractérise par la conscience autoérotique, c'est-à-dire la capacité de se placer mentalement dans le passé et le futur, ce que l'on appelle le *voyage mental dans le temps*. Par exemple, on peut se souvenir d'avoir attrapé un coup de soleil sur une plage ensoleillée le deuxième jour des dernières vacances en Espagne ou s'imaginer en train de faire du traîneau à chiens dans les environs de Tromsø, en Norvège, l'hiver prochain. Elle constitue donc également la capacité de simuler des événements futurs, ce qu'on nomme la pensée épisodique du futur. Le voyage mental dans le temps subjectif est une capacité cognitive particulièrement intéressante à étudier en raison de son

importance pour le comportement humain et de son contexte mental riche en détails. Ré-expérimenter et pré-expérimenter mentalement des événements est une fonction cognitive élaborée qui implique une multitude de processus diversifiés. Outre les processus mnésiques, émotionnels et exécutifs qui soutiennent la construction de la scène, le voyage mental dans le temps implique fortement les processus de référence à soi. Ceux-ci sont actifs lorsque l'information est liée au soi (par exemple, étendre son nom ou en pensant à un objectif ou à un souvenir personnel pertinent). Le traitement de la référence à soi nécessite l'activation du cortex préfrontal ventromédian, une plaque tournante du réseau autonome central et impliqué dans la régulation des émotions. De manière surprenante, aucune étude à notre connaissance ne s'est directement intéressée à la relation entre le traitement mental de la référence à soi et la HRV, bien que les deux partagent certaines bases neuronales. Sur le plan cognitif également, le modèle du système du mémoire de soi (*Self Memory System*, M. A. Conway, 2005) relie les processus exécutifs liés à la HRV au traitement de la référence à soi et au système de mémoire à long terme. En conclusion, il semble très prometteur d'étudier l'association entre la HRV et le traitement autoréférentiel, ainsi que son interaction avec les processus émotionnels et exécutifs dans le cadre du voyage dans le temps mental, afin d'élucider le lien entre le corps et l'esprit.

L'une des principales limites des études précédentes est qu'elles ont principalement évalué la HRV pendant une phase de repos séparée de la tâche cognitive. Si les corrélations globales ont montré une valeur prédictive, elles en disent peu sur la direction de l'effet (la HRV a-t-elle un effet sur la cognition ou l'inverse ?) et sur les interactions psychophysiologiques pendant l'activité cognitive.

La théorie du réservoir vagal (Laborde et al., 2018) a fourni un cadre conceptuel pour faire face à ce problème. L'hypothèse est qu'en mesurant les changements dans la HRV tonique (à un moment donné) d'une phase de référence au repos à une tâche (réactivité) et d'une tâche à une phase de référence post-tâche (récupération), les profils de HRV fourniront un aperçu supplémentaire de la relation psychophysiologique. Cette HRV phasique (changements entre les niveaux toniques de la HRV) est supposée indexer de manière sensible l'efficacité de l'autorégulation et donc les processus exécutifs. La recherche basée sur la variabilité phasique de la fréquence cardiaque en est encore à ses débuts, mais elle peut apporter une contribution essentielle au domaine

psychophysiologique. Par conséquent, l'un des objectifs de cette thèse était d'évaluer la variabilité tonique et phasique de la fréquence cardiaque pendant des pensées personnelles tournées vers le passé et futur.

Si un contrôle vagal cardiaque plus important est bénéfique pour la cognition, quelles sont les perspectives d'amélioration de ce contrôle pour le corps et l'esprit ? Le biofeedback de la HRV est une technique non invasive de premier plan qui permet d'accroître efficacement le contrôle vagal cardiaque. Cette technique implique l'affichage en temps réel de l'activité cardiaque, sur la base de laquelle l'utilisateur augmente la HRV. Cet entraînement à l'autorégulation implique principalement l'adoption d'une respiration lente qui évoque des effets de résonance physiologique dus aux effets respiratoires sur la pression artérielle et les réflexes cardiorespiratoires (baroréflexe et arythmie sinusale respiratoire). Il en résulte un rythme cardiaque de grande amplitude et de type sinusoïdal, qui témoigne d'un contrôle vagal cardiaque accru. En outre, la résonance entraîne des effets de cohérence en harmonisant et en couplant les oscillations cardiaques avec d'autres systèmes oscillatoires physiologiques (respiration, pression artérielle). On a émis l'hypothèse que les augmentations ultérieures du contrôle vagal cardiaque affectent le cerveau par l'activité parasympathique afférente. Cependant, d'autres voies ont été définies (Mather & Thayer, 2018), telles que les changements dans le flux sanguin cérébral et les entrées sensorielles du cœur au cerveau en raison des oscillations cardiaques de grande amplitude. Il a été démontré que le biofeedback de la HRV améliore efficacement l'état cardiovasculaire et la santé physique et mentale (Lehrer et al., 2020) et qu'il améliorerait les troubles mentaux tels que l'anxiété (Goessl et al., 2017) et la dépression (Pizzoli et al., 2021), liés aux fonctions cognitives qui nous intéressent dans le cadre de cette thèse. Néanmoins, la façon dont le biofeedback de la HRV affecte spécifiquement les fonctions cognitives n'est toujours pas claire. En particulier, la population en bonne santé reste peu étudiée, bien que le biofeedback HRV présente un grand potentiel pour améliorer les performances de pointe et prévenir les troubles cognitifs. Des preuves préliminaires ont révélé des améliorations prometteuses dans le contrôle exécutif et attentionnel (Prinsloo et al., 2013 ; Sutarto et al., 2012, 2013), mais les mécanismes sous-jacents restent non clarifiés. Une piste intéressante serait d'explorer l'interaction entre le contrôle vagal cardiaque et les changements cognitifs induits par le biofeedback de la

HRV. Une telle stimulation a en effet le potentiel d'élucider les voies médiatrices dans le complexe corps-esprit.

La thèse commence donc par une définition de la HRV et une description des mécanismes neurophysiologiques sous-jacents qui régissent la régulation cardiaque et respiratoire, y compris les principes de l'allostasie, du baroréflexe et de l'arythmie sinusale respiratoire. En particulier, le rôle du nerf vagal dans la connexion au cerveau et l'influence de la respiration lente pour augmenter l'activité parasympathique sont illustrés. Dans la deuxième partie, le biofeedback de HRV et ses principales modalités d'entraînement, l'entraînement à la fréquence de résonance et l'entraînement à la cohérence, sont présentés et comparés. En outre, l'utilité du biofeedback pour la formation à l'autorégulation est décrite. Le chapitre suivant présente le système de mémoire à long terme de l'homme en mettant l'accent sur la mémoire épisodique et ses différentes composantes, qu'elles soient partagées avec d'autres types de mémoire (encodage, stockage, récupération) ou spécifiques à la mémoire épisodique (phénoménologie associée à la récupération, mémoire contextuelle). En outre, les différents modes de pensée future épisodique, basés sur la taxonomie de Szpunar et al. (2014), sont brièvement décrits. Le chapitre se termine par la description de la base neuronale du soi et du système de mémoire du soi (Conway, 2005), qui relie les différents processus cognitifs. Le quatrième chapitre définit le contrôle cognitif (exécutif) et ses éléments fondamentaux (exécutif central de la mémoire de travail et contrôle attentionnel), avant d'élaborer sur la connexion de ces éléments avec la mémoire épisodique et la pensée future. Enfin, nous donnons un aperçu du modèle du triple réseau cérébral en tant que base neuronale de la cognition, qui sous-tend la vision intégrative du corps et de l'esprit dans le chapitre suivant. Nous commençons par une description détaillée de la théorie incarnée et psychophysiologique, notamment le modèle d'intégration neuroviscérale (Thayer & Lane, 2000, 2009) et la théorie du réservoir vagal (Laborde et al., 2018), avant de détailler la base neuroanatomique du cerveau et ses différents composants (par exemple, le cortex préfrontal ventromédian, le cortex cingulaire antérieur, l'amygdale) qui relie de manière cruciale les processus corporels et cognitifs. Une démonstration empirique souligne le lien entre la HRV et la cognition. Enfin, nous examinons les mécanismes physiologiques du biofeedback de la HRV et les premiers résultats obtenus ces dernières années. Après avoir présenté les

principaux concepts théoriques qui soulignent l'utilité de la réalité virtuelle, nous décrirons quatre points forts méthodologiques de cette thèse : le développement d'un nouveau système de réalité virtuelle qui intègre le biofeedback de la HRV et l'évaluation cognitive dans un environnement contrôlé, la mise en œuvre de groupes de contrôle actifs dans chaque expérience, le traitement et la correction semi-automatisés des signaux et l'utilisation de modèles linéaires robustes à effets mixtes.

Les différents travaux réalisés au cours de cette thèse seront ensuite repris un par un, selon l'ordre dans lequel ils ont été menés : Un article publié dans *Frontiers in Neuroscience* pour la première étude (Bögge et al., 2022), un manuscrit revu dans *Psychophysiology*, mais pas encore modifié, pour la seconde étude (Bögge et al., *in review*), et un manuscrit en préparation et presque prêt à être soumis à *Psychophysiology* pour la dernière étude (Bögge et al., *in prep*).

Dans notre première étude longitudinale (Bögge et al., 2022), nous avons étudié les effets persistants à un délai d'une semaine de la HRV sur diverses facettes du contrôle cognitif ainsi que sur la mémoire épisodique autoréférentielle. L'objectif était de tester, sur un petit échantillon de jeunes adultes en bonne santé, quels paramètres seraient les plus sensibles à la manipulation du biofeedback de la HRV, et comment ces paramètres sont liés aux oscillations cardiaques couplées à la respiration pendant l'entraînement. La HRV s'est avérée avoir des effets remarquables sur un biais de soi positif dans la mémoire épisodique et sur le contrôle de l'interférence (exécutif) impliqué dans la discrimination de stimuli peu distinctifs. Ces effets étaient liés à la stimulation oscillatoire cardiaque.

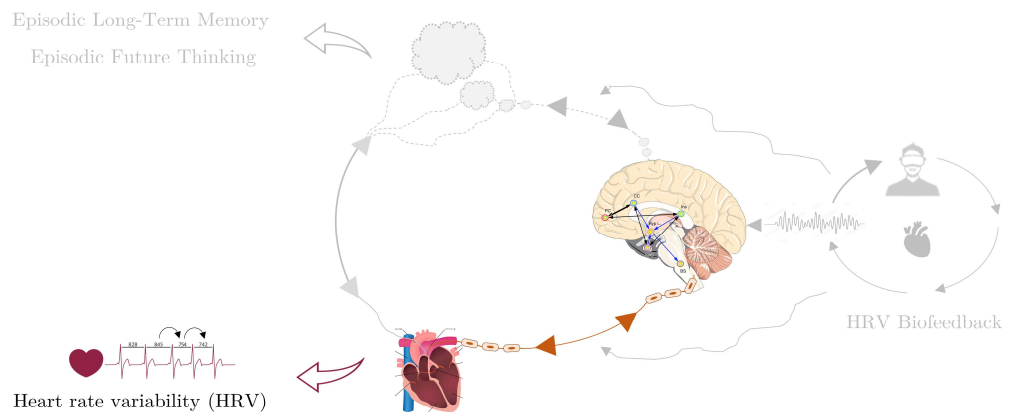
S'écartant des résultats de l'étude précédente, la deuxième étude (Bögge et al., *in review*) s'est concentrée sur le contrôle de l'interférence sur la mémoire à long terme, évalué comme la production de faux souvenirs. La conception d'une nouvelle configuration de réalité virtuelle, intégrant l'évaluation cognitive et le biofeedback HRV en une seule session, a permis d'évaluer les effets simultanés du biofeedback HRV sur la HRV liée à la tâche et les résultats cognitifs. Le biofeedback HRV n'a pas eu d'effet immédiat sur la HRV pendant l'encodage ou la récupération et sur le contrôle de la mémoire. La fatigue a modéré les associations psychophysologiques. Des analyses

exploratoires ont révélé que le HRV phasique pendant la récupération prédit le contrôle de la mémoire lorsqu'il est contrôlé par la fréquence cardiaque phasique.

Dans notre dernière expérience (Bögge et al., *in prep*), les différents processus cognitifs ont été réunis dans une étude complète en évaluant les propriétés phénoménologiques du voyage mental dans le temps passé et futur. Comme dans l'étude précédente, les effets immédiats du biofeedback sur la HRV ont été testés dans un environnement de réalité virtuelle intégré, mais la conception a été adaptée pour réduire les effets de la fatigue. Nous avons constaté que la variabilité phasique de la fréquence cardiaque était associée au contrôle exécutif impliqué dans la construction d'événements pendant la pensée future positive, tandis que la variabilité tonique de la fréquence cardiaque prédisait une diminution du traitement autoréférentiel négatif pendant la remémoration de la mémoire épisodique (autobiographique).

Le dernier chapitre de cette thèse synthétise l'ensemble des résultats obtenus dans ces trois études expérimentales afin de les comparer et d'obtenir une perspective globale sur les contributions de cette thèse. Nous décrirons ensuite leurs implications pour les théories psychophysologiques et cognitives existantes et proposerons un nouveau modèle intégratif. Enfin, plusieurs pistes non testées sont décrites pour explorer le lien entre le contrôle vagal cardiaque et la pensée ainsi que l'effet du biofeedback de la HRV sur le corps et l'esprit.

1 Chapter 1 – Heart Rate Variability



1.1 Physiology of the Heart

The muscular heart is vital for body functioning beating on average 100,000 times a day to pump 7500 liters of blood through 100,000 km of blood vessels. It consists of two interconnected chambers on each side of the heart: an atrium and a ventricle on the left and right sides ([Figure 1A](#)). Venous blood enters the atria, flows into the lower ventricles, and is pumped into the lungs and arteries. The right atrium receives deoxygenated blood which is pushed by ventricular contraction to the lungs where metabolic waste is removed. Re-oxygenated blood from the pulmonary veins enters the left side and is ejected to the arterial system to provide other organs with oxygen and nutrients (Marieb & Hoehn, 2013; Tortora & Derrickson, 2014). The cardiac cycle is the muscular activity of the heart from the beginning of one heartbeat to the beginning of the next. It is divided into a period of ventricular relaxation, called diastole, followed by ventricular contraction, called systole. During diastole, blood flows into the heart, whereas during systole blood is ejected causing blood pressure to decrease and rise, respectively. In the electrical recording of the heart, the electrocardiogram (ECG), the cycle (see [Figure 1B](#)) is described by the P wave (depolarization and contraction of atria) followed by the QRS complex (depolarization and contraction of the ventricles) and the T wave (ventricular repolarization).

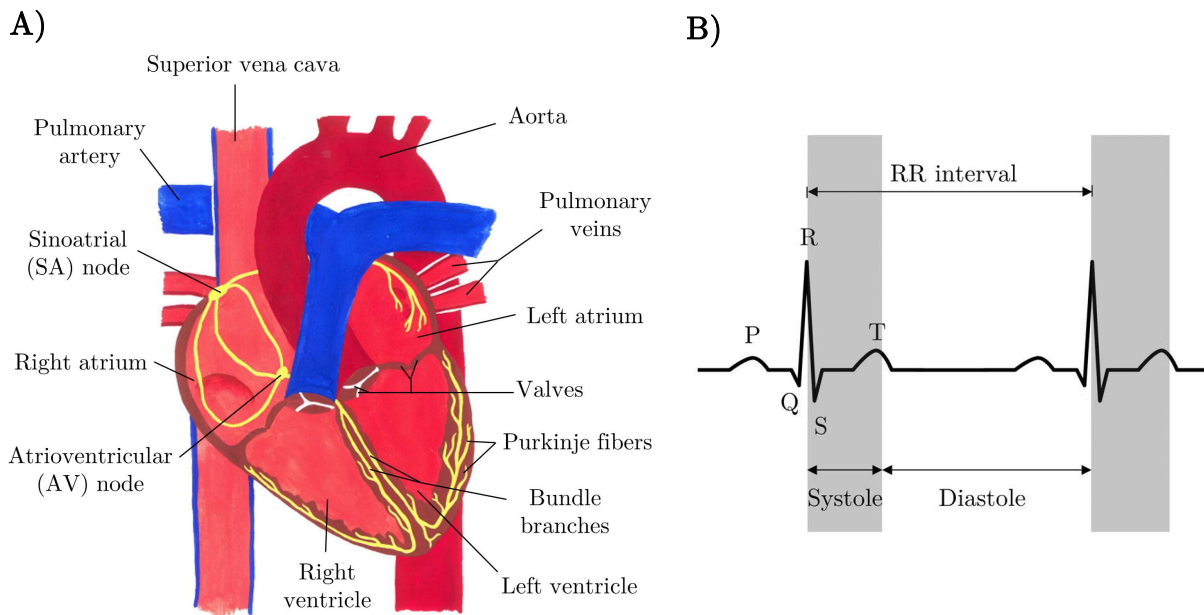


Figure 1 – Anatomy and Cycle of the Heart

Note. **A)** Efferent nerve fibers connect to the sinoatrial node initiating the spread of cardiac action potentials along the myocardium (yellow fibers) that lead to the contraction of the heart. **B)** Distinct patterns in the electrocardiogram (P wave, T wave, QRS complex) denote the de- and repolarization of the atria and ventricles involved in one heart cycle. Each cycle is marked by a phase of ventricular diastole and systole, when blood flows in and out, respectively. The heart period or heart rate for beat-to-beat analysis is determined as the time period between successive R peaks (ventricular depolarization and contraction). Art design by Dora van Duijvendijk ©.

Heart contractions are initiated spontaneously by autorhythmic pacemaker cells in the sinoatrial node in the upper part of the right atrium. These cells trigger cardiac action potentials that spread to nearby cells down to the atrioventricular node and septum where right and left bundle branches and Purkinje fibers cause the depolarization and contraction of the ventricles (QRS). The heart period corresponds to the time interval between successive R-peaks ([Figure 1B](#)). The beat-specific heart rate is then determined from the RR interval referred to hereinafter (in contrast to mean heart rate calculated over multiple intervals). Pacemaker cells fire in the absence of external innervation and hormonal influences at a rhythm of around 110 beats per minute, referred to as the intrinsic heart rate. Their firing speed, and thus the heart rate, is regulated by the innervation of the heart through the autonomic nervous system.

1.2 Visceral Regulation through the Autonomic Nervous System

1.2.1 The autonomic nervous system

The autonomic nervous system (ANS) refers to the parts of the nervous system outside the brain and spinal cord that regulate involuntary physiological processes such as the heart rate, blood pressure, and respiration. It is a self-governing system that integrates biomechanical, biochemical, and thermal afferent (ascending) signals to ensure the steady state of physiological processes required for healthy functioning. This is achieved through homeostasis (steady state) and allostasis (predictive regulation to satisfy a need before it arises), which seek to maintain or move body physiology towards the condition of optimal functioning. Besides the enteric system, the ANS is divided into the sympathetic nervous system (SNS) and parasympathetic nervous system (PNS). The SNS is responsible for increasing overall activity and initiating the “fight and flight” (sympathoadrenal) response in the face of stressful situations, which leads to an increase in blood pressure, heart rate, and force contraction of the myocardium. Contrary, the PNS promotes “rest and digest” activities that occur primarily at rest when the body is relaxing, which has a lowering effect on blood pressure and heart rate. In concert, both systems react in response to changes in the internal (e.g., thinking) and external processes (e.g., cold weather) to match the physiological and metabolically needs via control through a neural network spanning the whole body.

Efferent (descending) pathways that affect organs, blood vessels, and the skin are formed by two sets of neurons ([Figure 2](#)). Preganglionic neurons originate from the brainstem and spinal cord in the central nervous system and connect to postganglionic neurons in the periphery that innervate the target tissue. In the SNS, nuclei in the hypothalamus connect to preganglionic neurons in the intermediolateral columns and lateral horns from where presynaptic fibers leave the spinal cord at segments between T1 and L2. These connect to paravertebral and prevertebral ganglia from where postganglionic sympathetic efferents extend to the target tissues. In regard to the cardiovascular system, heart ganglia in the thoracic cavity link to the heart and control blood vessel constriction (sympathetic activation) throughout the body. Afferent fibers sending back sensory information pass through the same nerves that carry efferent fibers to the dorsal root ganglion just before entering the dorsal horn and synapsing with the spinal cord. In the PNS, the heart is linked with the vagal complex in the

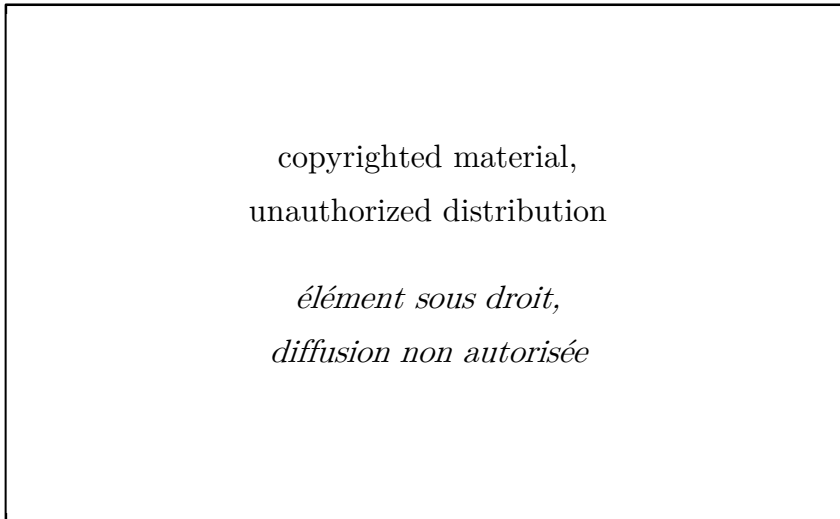


Figure 2 – Cardiovascular Brain Circuits

Note. The autonomic nervous system connects to the brain with heart via pre- and post-ganglionic fibers. The heart has its own intrinsic cardiac nervous system (ICN) that receives efferent inputs and transmits afferent information back to the brain. RA = right atrium; LA = left atrium. Image from Mohanta et al. (2023).

brainstem through the vagal nerve (or vagus nerve). It is the tenth cranial nerve that derives from the medulla oblongata and contains approximately 85% afferent and 15% efferent nerves, respectively (Berthoud & Neuhuber, 2000). From there long preganglionic efferent fibers connect to short postganglionic fibers within the heart or vascular tissue (Klabunde, 2021).

1.2.2 Homeostasis and allostasis

The concept of homeostasis presents a framework for the regulation of physiological processes (Cannon, 1929). The primary goal of this model is to maintain relatively stable conditions within the body's internal environment. This entails keeping internal parameters close to a designated “setpoint” or within a relatively narrow range around it. Numerous autonomic processes align with this homeostatic model, effectively regulating factors like core body temperature and water content (Cannon, 1939). However, the principles of homeostasis sometimes reveal shortcomings, prompting the emergence of the idea of allostasis (McEwen, 1998; Sterling, 2012). Allostasis embodies the notion of “stability through change,” characterizing the behavior of fluctuating physiological parameters that do not center around a single setpoint. The core concept here is that these parameter levels oscillate to help individuals adapt to ever-changing circumstances. This dynamic process establishes a link between external conditions and the body's capacity to effectively respond to imposed demands, a regulation orchestrated by the brain, as we will explore later. These quantifiable physiological systems proactively anticipate demands, possessing numerous stable states that activate in response to the ongoing shifts in the environment, whether real or perceived.

1.2.3 Cardiac control

The heart rate, also called chronotropy, is regulated by the PNS and SNS through the movement of electrolytes, especially at the sinoatrial node of the heart evoked by the postganglionic fibers. Sympathetic nerves release the neurotransmitter norepinephrine (or noradrenaline) for docking at beta-adrenergic receptors, which increases the excitability of the pacemaker cells, causing them to fire at a higher rate, which in turn raises heart rate. Contrary, parasympathetic nerves release acetylcholine to G-protein coupled muscarinic receptors that reduce firing speed and with such heart rate. Consequently, the chronotropic state results from the net effect of the neural output of the PNS and SNS, and changes in either system will change the heart rate. Upon initiation of a sympathetic stimulus, it takes 2-3 and up to 5 seconds until the heart rate increases due to slow metabotropic cascades initiated by norepinephrine binding (Kleiger et al., 2005; Nunan et al., 2010). The much faster vagus nerve (<1s), however, almost directly affects heart rate due to a high neurotransmitter discharge frequency caused by rapid elimination in the synaptic cleft (Picciotto et al., 2012). Though parasympathetic control is faster, sympathetic inputs have a more long-lasting effect on the cardiac cycle. While parasympathetic activity after its onset influences only one or two heartbeats (Draghici & Taylor, 2016; Shaffer et al., 2014), sympathetic inputs alter heart rate for 5-10 seconds (Mark & Herlitz, 2000; Saul, 1990).

The heart is part of feedback-regulated closed loops rather than being controlled by the central nervous system. The heart possesses its own intrinsic neural network (Verkerk et al., 2012), which communicates with other regional networks to regulate autonomic functions, including heart rate, blood pressure, or respiration (Ardell et al., 2016; Shivkumar et al., 2016). Moreover, peripheral nerves send feedback information back up to the brainstem and higher centers in the central nervous system ([Figure 4](#), see following section). Respiratory, cardiovascular, and gastrointestinal information from proprioceptors, chemoreceptors, and mechanoreceptors are integrated at the nucleus of the solitary tract, which informs the brain and modulates SNS and PNS outflow via other regulatory structures in the medulla (PNS: nucleus ambiguus from which arises the vagal nerve, SNS: rostral ventrolateral medulla). Hence, SNS and PNS are linked at the brainstem level. Traditionally, the PNS and SNS have been regarded together as reciprocal acting systems: as sympathetic activity increases, parasympathetic activity decreases, and vice versa. However, the autonomic space model (Berntson et al., 1991, 1993a, 1994) proposes that the activity of both branches may concurrently increase (coactivation), decrease (coinhibition) or be uncoupled

([Figure 3](#)). Consequently, a change in heart rate may result from vagal or sympathetic (de-)activation, or both.

Autonomic regulation is dynamic. Different neurophysiological processes at the brain stem and upper centers modulate autonomic activity. It involves a time-variant mixture of vagal and sympathetic inhibition and activation causing complex fluctuations in the heart rate. These dynamic processes are quantifiable by assessing the beat-to-beat changes in the heart period, termed heart rate variability (HRV).

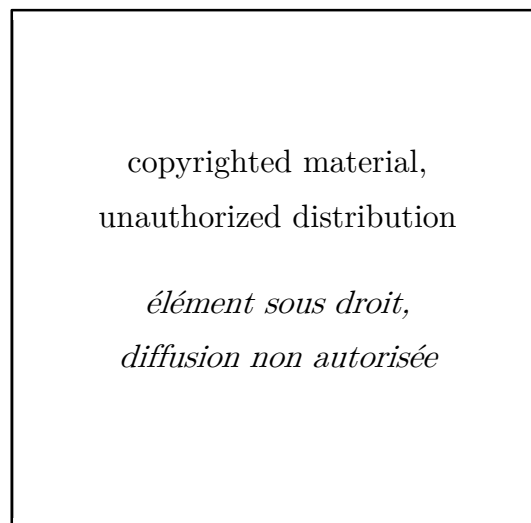


Figure 3 – Two-Dimensional Representation of Autonomic Space

Note. Axes units are expressed as a proportional activation of the sympathetic and parasympathetic branches. On the diagonal of reciprocity, increased activity in one autonomic division is associated with decreases in the other. On the diagonal of coactivity, activities in the autonomic branches concurrently increase (coactivation) or decrease (coinhibition). The arrows along the axes depict uncoupled changes in the single ANS divisions. The arrows, and vectors parallel to them, illustrate the major modes of autonomic control. Figure and caption retrieved from Berntson et al. (1994).

1.2.4 Interaction between the central and autonomic nervous systems

The ANS is connected to a large brain network called the Central Autonomic Network (CAN) (Benarroch, 1993, 1997). It contains reciprocally connected structures in cortical regions of the forebrain, the limbic system, the brain stem, and spinal cord, including the prefrontal cortex (PFC, most notably the ventromedial part), basal forebrain, cingulate cortex, insular cortex, amygdala, hypothalamus, periaqueductal gray, locus coeruleus, nucleus of the solitary tract, and ventrolateral medulla ([Figure 4](#)). There is

a constant bidirectional exchange of information between the peripheral system and the central nervous system, which arrives via the brainstem to sub-cortical structures and the cerebral cortex and is sent back down from there. Thus, the interaction between the central and autonomic nervous systems is governed by upstream (bottom-up) and downstream (top-down) neural traffic, with the information streams being processed at different brain levels. Viscerosensory inputs containing biomechanical, biochemical, and thermal signals arrive at the nucleus of the solitary tract, where medullary reflexes are initiated for cardiovascular and respiratory regulation through control of sympathetic and parasympathetic pre-ganglionic motoneurons (as described above). Furthermore, inputs are relayed to the remaining parts of the CAN. Further up in the brainstem, the periaqueductal gray integrates autonomic control with behavioral responses to

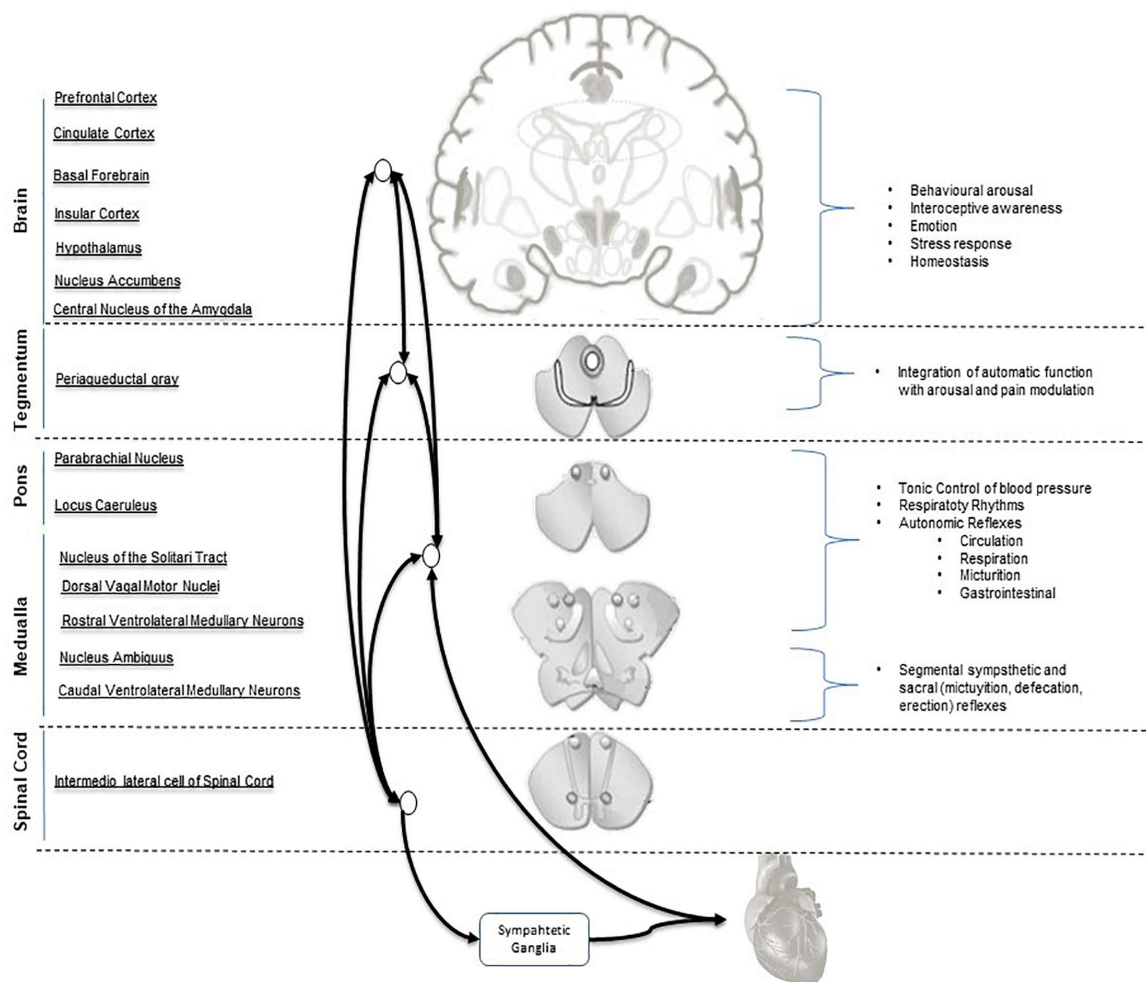


Figure 4 – Central Autonomic Network Hierarchical Organization and Interconnections

Note. Parasympathetic output is mediated mainly by the nucleus of the vagus and nucleus ambiguus. Sympathetic output is mainly mediated by the intermediolateral column cell. Reproduced from Riganello et al. (2019, CC-BY 4.0).

stress, sleep, and pain. At the hypothalamus, autonomic and endocrine functions are linked. Cortical and subcortical structures, including the ventromedial PFC, amygdala, insular cortex, and anterior cingulate cortex (ACC), mediate high-order autonomic control by integrating bodily sensation with emotional and goal-related autonomic responses (Benarroch, 2014; Thayer et al., 2012). Finally, top-down control originating from the PFC is exercised to adapt cardiac and other autonomic functions to the needs of the organism. Measures of HRV assess this efferent activity arriving at the sinus node influencing heartbeat. Much of the bottom-up traffic to inform the brain about control decisions is mediated by the vagal nerve. As mentioned above, most of its fibers carry afferent neural traffic, which influence brain centers that are involved in cognitive and emotional processing. Hence, the dynamic of the cardiac cycle is crucial for brain function. Besides, mechanical and chemical factors stemming from various body functions like respiration modulate the input at the brain level but also affect intrinsic cardiac neural circuits (Armour & Kember, 2004). In sum, the heart and brain are in complex interaction such that changes in brain's activity affect the heart and vice versa ([Figure 3](#) p. 23).

1.2.5 Baroreflex

Cardiac output, which is the blood flow through the circulatory system, depends on the force with which blood is pushed through the vessels. This is accomplished by constriction and relaxation of vascular smooth muscle, which causes blood pressure to rise and fall. A special role in cardiac control can be ascribed to the baroreflex system ([Figure 5](#)) that regulates blood pressure to maintain homeostasis. Mechanosensitive baroreceptors in the carotid sinuses and aortic arch sense changes in blood pressure so that an increase evokes, through neural traffic passing the brainstem, a decrease in heart rate (parasympathetic activation and sympathetic inhibition) and vice versa. In addition, total peripheral resistance is adjusted through vasodilation (sympathetic inhibition) and constriction (sympathetic activation). Therefore, the baroreflex acts as a negative feedback system that counteracts disturbances in blood pressure. The baroreflex sensitivity (i.e., magnitude of the variation in heart rate) of the system is determined by the blood pressure level (e.g., the higher the blood pressure the greater the subsequent drop in heart rate). Moreover, due to the inertia of the blood flow, these negative feedback responses take a delay of around 5 seconds to affect the heart rate (Vaschillo et al., 2006). Due to the delay and the property of the system to regulate itself (allostasis), blood pressure constantly fluctuates. Consequently, when stimulated, the baroreflex evokes ongoing variations in the heart rate that are reflected in HRV.

Such stimulation is produced by Mayer waves, which are sympathetically evoked oscillations of arterial blood pressure with a frequency of 0.1 Hz. To buffer the Mayer waves, the baroreflex evokes vagally mediated heart rate oscillations at the same frequency. Another inherent characteristic of such regulatory systems is resonance: baroreflex sensitivity increases as heart rate and blood pressure functions become more aligned with a phase shift of 180° . This means oscillations are strongest when heart rate and blood pressure are antiphasic. Such an increase in the baroreflex sensitivity is also referred to as baroreflex gain and is measured as the variation in heart rate per unit of change in systolic blood pressure. The resonance frequency of the baroreflex, also called *baroreflex resonance*, depends on the aforementioned 5 seconds delay (inertia). Thus, in adults, the baroreflex resonance is about 0.1 Hz (10 s per cycle: 5 s increase, 5 s decrease).

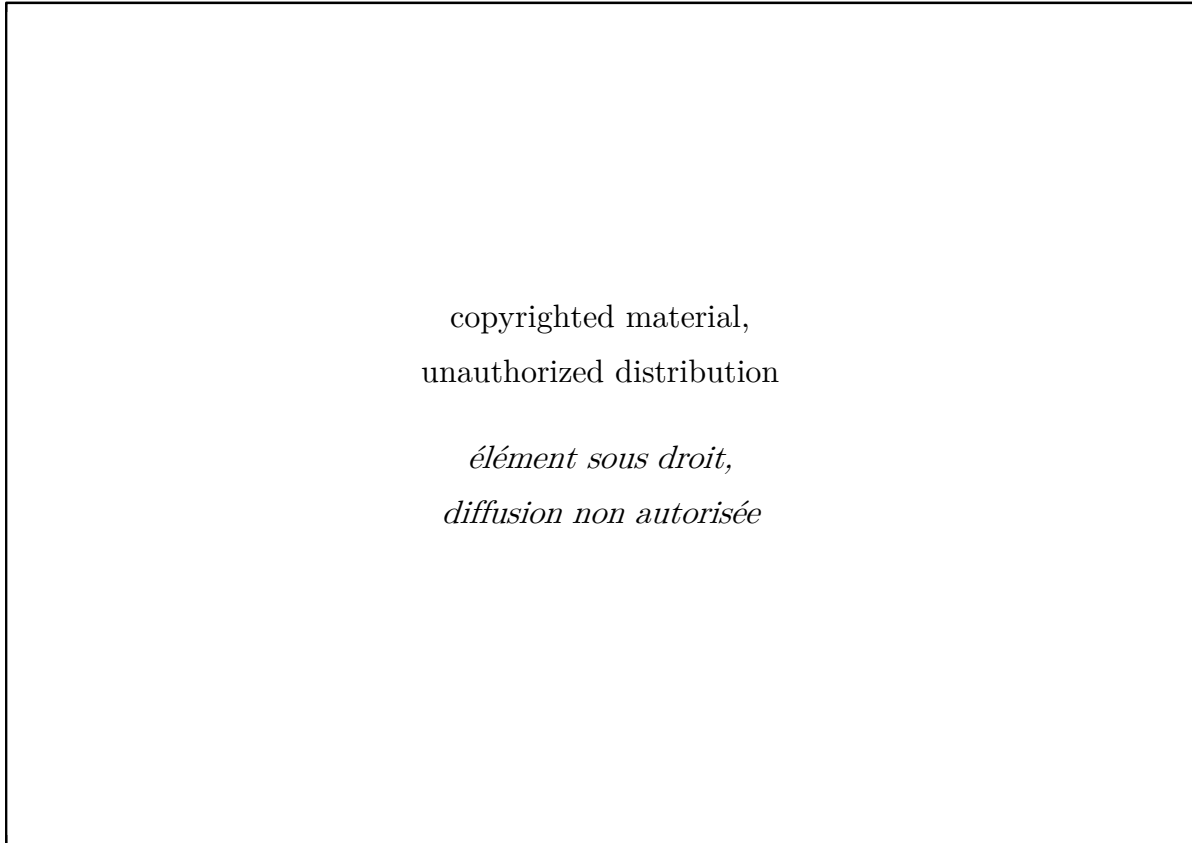


Figure 5 – Organizational Arrangements and Influences on Baroreflex

Note. (A) Schematic illustration of viscerosensory brain centers and connectivity involved in baroreflex. Rostrolateral medulla (RVLM), caudolateral medulla (CVLM), area postrema (AP), hypothalamus (HPT), and nucleus of solitary tract (NTS).

(B) Illustration of aortic arch and carotid showing location of arterial baroreceptors and cranial nerves (GN, glossopharyngeal nerve; VN, vagus nerve) carrying baroreceptor afferent signal to NTS.

(C) Overview of baroreflex and influences. Baroreceptor firing signals the timing and strength of each heartbeat. Increases in blood pressure to elicit a slowing of subsequent heartbeat through dorsal motor nucleus of vagus, increase parasympathetic drive to sinoatrial node, and engender vasodilatation in muscle vascular beds through inhibition of muscle sympathetic nerve traffic via CVLM inhibition of RVLM influence on preganglionic sympathetic neurons in intermediolateral column of spinal cord. Anterior cingulate, insula, amygdala, and periaqueductal gray (PAG) activity is associated with top-down suppression of baroreflex induced by stress challenge (Gianaros et al., 2012). Figure and caption reproduced from Critchley & Harrison (2013).

1.2.6 Respiratory sinus arrhythmia

Respiratory sinus arrhythmia (RSA) is the variation of the heart period in phase relationship to the respiration, by which the RR interval shortens during inspiration and lengthens during expiration (Berntson et al., 1993b). RSA therefore represents a form of respiration-driven HRV. RSA is believed to increase the efficiency of pulmonary gas exchange by matching alveolar ventilation and its perfusion (i.e., blood volume flow). Gas exchange is dependent on the ratio of ventilation to perfusion. During inspiration, when the heart rate speeds up, more gas can be exchanged in the alveoli as more blood flows through its capillaries, reducing physiological dead space. It is further hypothesized that RSA minimizes energy expenditure by suppressing unnecessary heartbeats during expiration (Giardino et al., 2003; Hayano et al., 1996; Hayano & Yasuma, 2003). RSA arises from the complex interaction of factors linked to chemoreceptor and mechanoreceptor activity, arterial baroreflex, pulmonary stretch and cardiopulmonary reflexes, as well as mechanical and metabolic processes. However, nonneural determinants are negligible in the face of neural control (Berntson et al., 1993b). RSA has been proposed to be mainly of vagal origin and to index cardiac vagal control (Berntson et al., 1993b; Shaffer & Ginsberg, 2017). Just like HRV, it is determined by tonic and phasic (frequency) processes. In this context, RSA is induced by the principle of vagal gating (Eckberg, 2003b) by which respiratory activity alters the responsiveness of parasympathetic motor neurons. Tonic vagal outflow arrives the brainstem where its subject to phasic modulation by cardiorespiratory coupling and the baroreflex, along other neurophysiological sources (Berntson et al., 1993b). During inhalation central respiratory neurons inhibit vagal motor neurons which causes vagal input to the sinoatrial node and thus the heart rate to fluctuate synchronously (0°) with the respiratory cycle. In fact, respiratory-induced changes in blood pressures, and thus heart rate oscillations, stem mostly from mechanical factors (Montano et al., 2000). During each inspiration, intrathoracic pressure changes and associated venous blood return to the right ventricle decrease arterial pressure (Verhoeff & Mitchell, 2017). The resulting blood pressure oscillations are called Traube-Hering waves (Billman, 2011). These are antiphase (180°) to respiratory flow and consequently in phase (0°) with cardiac oscillations due to the tonic compensatory activity of the baroreflex (parasympathetic and sympathetic drive). However, respiratory and cardiac oscillations are shifted, due to the delay in the baroreflex system. Consequently, oscillatory neural inputs to the heart by the central respiratory network (instant) and

Traube-Hering waves (baroreflex delay) are shifted, minimizing RSA and causing heart rate to rise or fall a few seconds after inspiration/expiration onset.

Though RSA has an important effect on vagal activity, its modulation changes only a small part of the total parasympathetic influence on the heart (Craft & Schwartz, 1995; Eckberg, 2003a). Sympathetic activity is also altered by respiration, however, its effect on HRV is negligible for high-frequency modulations of sympathetic nerves that are induced by normal or fast breathing. The reason is that the slow bio-cellular-conditioned translation of the sympathetic stimulation onset to the heart rate rise acts as a low-pass filter that diminishes high-frequency sympathetic fluctuations. Therefore, breathing patterns are usually too fast to induce sympathetic fluctuations that affect HRV or RSA. Different pathways linking RSA and HRV have been discussed, but greatest importance has been given to the stimulation of the homeostasis in the baroreceptor (Lehrer & Gevirtz, 2014). Conclusively, RSA represents the systemic effort to optimize physiological processes through vagal adaption of the heart rate in accordance with the respiratory cycle.

1.3 The Importance of the Vagal Nerve

As we have seen, the heart is controlled via tonic and phasic activity of the vagal and sympathetic nerves that are in turn regulated by different neurophysiological circuits. Pacemaker cells dictate the intrinsic heart rate so that a slowing below this level requires parasympathetic activation. At rest, the heart rate of an adult approximates 75 beats per minute and typically ranges, according to the American Heart Association (2023), between 60 and 100 beats per minute. Hence, the resting heart rate is well below the intrinsic heart rate, indicating vagal dominance that reduces spontaneous pacemaker firing. Consequently, the system's main response to increase heart rate above the resting level is to withdraw vagal activity (Bernardi et al., 1996; De Ferrari, 2014). As the mean heart rate rises and vagal activity drops, sympathetic nerve conduction steadily increases. Thus, an increase in heart rate above the natural firing rate of the sinus node is mainly due to increased sympathetic activity (Hainsworth, 1995). In fact, it has been proposed that cardiac control for heart rates below 140 beats per minute is mainly vagally driven (Gourine & Ackland, 2019). Moreover, fast modulations in the heart period, as for the RSA, are due to the slowness of the sympathetic system almost entirely mediated by the vagal nerve. Therefore, it can be credited with the main role in cardiac control due to its ability to initiate rapid and potent cardiovascular regulation (Goldberger et al., 2001; Hainsworth, 1995).

Measuring the natural fluctuations in the heart rate, specifically those mediated by the vagal nerve, thus provides an index of cardiovascular adaption, that is the capacity to adjust the cardiac rhythm in response to environmental constraints exercised on the organism (McCraty & Shaffer, 2015).

The vagal nerve reaches down from the head down to the abdomen and innervates besides the heart also the eyes, lungs, as well as reproductive and gastro-intestinal organs (Câmara & Griessenauer, 2015). This *wandering* (that is that *vagus* means in Latin) property highlights its important role in the regulation of diverse parts of the organism including the reciprocal communication of the gut-brain-axis (Carabotti et al., 2015). It becomes therefore clear that HRV indicates activity in a large neurophysiological system that aims to efficiently regulate bodily functions. For instance, vagal withdrawal has been proposed as a regulator of energy expenditure in face of a task (Duschek et al., 2009). Moreover, HRV is seen as an index of the efficiency of the neural network implicated in the autonomic regulation and of the nervous system itself (Thayer et al., 2012). The vagal nerve, through its afferent activity, is able to influence large brain networks engaged in body regulation, emotion, and cognition, and this activity is reflected in HRV. The latter is now recognized as an indicator of a person's physiological and behavioral regulatory capacities underlying physical and psychological resilience (Andreassi, 2010; Holzman & Bridgett, 2017; Thayer & Lane, 2000). Moreover, increased levels of HRV have been associated with beneficial effects for health (Gevirtz, 2013; Lehrer et al., 2020; McCraty & Shaffer, 2015) cognitive performance (Forte et al., 2019; Hansen et al., 2004; McCraty, 2003, 2016; Thayer & Lane, 2009). In Chapter 5, we will revisit the specific role of cardiac vagal control in brain functioning and cognition.

1.4 Measurements of Heart Rate Variability

The quantification of HRV is not based on the variability in the heart rate, but in the heart period. Hence, *heart period variability* or *RR variability* would be the more fitting term. However, to avoid confusion, we will here refer to HRV, as its commonly done in literature, as the measure of variability in the heart period. HRV provides a measurable mean of the various patterns and degree of stability of the cardiac rhythm that encodes the information exchanged between autonomic and nervous systems (McCraty et al., 2009). It thus permits a glimpse into the complex interaction between heart and brain.

The most commonly used HRV statistics are defined by the guidelines of the Task Force of The European Society of Cardiology and The North American Society of Pacing and Electrophysiology (Camm et al., 1996) and were described more in detail by Shaffer & Ginsberg (2017). HRV indices are calculated from the time series of RR intervals derived from an ECG ([Figure 1B](#) p. 19). These are also sometimes referred to as NN intervals. This simply indicates that only intervals between normal beats were used, neglecting R peaks that might have been distorted or missing due to artefacts or recording issues. They are categorized by the length of the ECG recording used for the computation into 24h, short-term (≈ 5 min), and ultra-short-term (< 5 min) recordings. Furthermore, measures are divided into a temporal (time) and spectral (frequency) domain. Since 24h recordings are a rarity in psychophysiological research and are not considered in this work, we will focus only on metrics related to short-term and ultra-short-term recordings. A brief overview of the measures described is given in [Table 1](#).

Importantly, it is to note that the different measures of HRV can either be tonic or phasic. Tonic HRV is assessed at a one-time point and is commonly measured as *resting HRV* recorded a moment of quiescence. In contrast, phasic HRV indexes relative changes between tonic measures to evaluate the system's response. These are frequently indexed by reactivity and recovery (Laborde et al., 2018), (see Chapter 5.2.5 for more details). Most of the presented studies here investigated tonic resting HRV. However, the focus in this work will be on tonic and phasic (reactivity) HRV during cognitive activity.

Measure	Unit	Autonomic origin during rest	Autonomic origin of change during slow breathing (< 9 cpm)	Minimal recording length (s)
Temporal domain				
RMSSD	ms	PNS	PNS	60, 120
SDNN	ms	PNS	PNS	60, 180
pNN50	%	PNS	PNS	60, 60
P2T-RSA	ms	PNS	PNS	-, -
Frequency domain				
Spectral power				
Very low frequency (VLF) (0.0033 to 0.04 Hz)	ms ²	SNS PNS	SNS PNS	180, 240
Low frequency (LF) (0.04 to 0.15 Hz)	ms ²	Baroreflex PNS, SNS	Baroreflex PNS	90, 180
High frequency (HF) (0.15 to 0.4 Hz)	ms ²	PNS	Unspecified	120, 150
Total power (TP)	ms ²	Baroreflex PNS, SNS	Baroreflex PNS, SNS	-, 210
Deviates of spectral power				
Normalized LF (LFn)	nu	SNS (ambiguous)	PNS	120, 150
Normalized HF (HF _n)	nu	PNS (ambiguous)	PNS ^a	120, 150
LF/HF ratio	nu	Sympatho-vagal balance (ambiguous)	PNS	-, 150

Table 1 – Heart Rate Variability Measures

Note. The table provides a summary of the main HRV measures used in psychophysiological research. Furthermore, it lists the autonomic activity each variable primarily reflects during resting-state and during slow-breathing at a rhythm of 6 cycles per minute. The indicated autonomic activity is positively associated with the respective measure, if not stated otherwise. The first value of each measure for the minimal recording length corresponds to cutoffs derived from (Shaffer et al., 2016), who assessed 38 undergraduate students. The second value corresponds to the cutoff derived from (Baek et al., 2015), who assessed 127 young adults (20-29 years). ^a During slow breathing HF_n decreases primarily due to an increase in LF_n.

1.4.1 Time domain analysis

Time-domain measures indicate the total variability based on simple statistical computation. They are the most commonly reported HRV indices, but appear to capture similar neurophysiological processes, as evidenced by the high degree of correlation between measurements (Rajendra Acharya et al., 2006). A selection of the most important indices believed to assess cardiac vagal control of the heart is presented below (Shaffer et al., 2014).

1.4.1.1 RMSSD

RMSSD (root mean square of successive differences) is calculated by applying the square root to the mean of the squared differences between adjacent RR intervals. It has been proposed as the primary measure of cardiac vagal control (McCraty & Shaffer, 2015), and it shows greater robustness against reductions in ECG recording lengths below 5 min compared to spectral measures ([Table 1](#)). However, RMSSD can be influenced by the sympathetic system and is biased by mean heart rate (Berntson et al., 2005). Furthermore, it is relatively unaffected by respiration (Hill et al., 2009; Penttilä et al., 2001). In this line, slow breathing has a much smaller effect on RMSSD than on spectral measures (Laborde et al., 2021 for a review) or measures of RSA. Parasympathetic reactivity evoked by deep breathing is not sensitively captured by RMSSD (Ali et al., 2023).

1.4.1.2 SDNN

SDNN is calculated as the standard deviation of NN intervals. It is mainly mediated by respiratory-linked vagal activity. Therefore, it is specifically affected during slow and deep breathing and closely related to RSA. SDNN has a history of being used as a clinical indicator, especially in ambulatory long-term recordings. It shows different mechanisms when derived from 24h or short-term recordings because SNS has a higher contribution in longer recordings (Kuusela, 2012; Umetani et al., 1998). Hence, great care should be taken when comparing SDNN measures of short-term with 24h recordings.

1.4.1.3 pNN50

pNN50 is the proportion of number of pairs of successive NNs that differ by more than 50 ms. It is related to parasympathetic activity and correlates with RMSSD and high-frequency power (Umetani et al., 1998). Generally, RMSSD better assesses RSA and is preferred over pNN50 (Otzenberger et al., 1998).

1.4.2 Frequency domain analysis

Frequency-domain variables are determined from the power spectral density of different frequency ranges. These are divided into three main bands: very low frequency (VLF) from 0.003 to 0.04 Hz, low frequency (LF) from 0.04 to 0.15 Hz, and high frequency (HF) from 0.15 to 0.4 Hz. Spectral indices are often calculated along temporal measures to better understand distinct aspects of cardiovascular status and nervous system activity. However, they also exhibit large interindividual variability (Laborde et al., 2017; Quintana & Heathers, 2014) and lower reliability when respiratory patterns are manipulated (Kuss et al., 2008; Penttilä et al., 2001).

1.4.2.1 Very low frequency (VLF)

The VLF band (0.003 - 0.04 Hz) encompasses rhythms with periods between 25 and 300 s and requires a recording length of at least 5 minutes. Low VLF-HRV has been linked to arrhythmic death (Bigger et al., 1992), an increased risk of developing post-traumatic stress (Shah et al., 2013), and high levels of inflammation (Carney et al., 2007; Lampert et al., 2008). Some other studies suppose PNS activity to be the primary source of variation, however, the underlying neurophysiological mechanisms remain poorly understood (Taylor et al., 1998). McCraty & Shaffer (2015) suggested that VLF-HRV is generated by the intrinsic neural network of the heart and is associated with sympathetic activation or reduced parasympathetic inhibition.

1.4.2.2 Low frequency (LF)

The LF band (0.04–0.15 Hz) spans rhythms with periods between 7 and 25 s and may reflect sympathetic, parasympathetic, and baroreflex activity (Akselrod et al., 1981; Berntson et al., 2007; Camm et al., 1996; Lehrer, 2007). Oscillations stemming from the baroreflex resonance occur at a frequency of around 0.1 Hz (Vaschillo et al., 2002, 2006) and are thus captured by the LF region. The PNS appears to affect frequency down to 0.05 Hz, while the SNS does not seem to generate a frequency much higher than 0.1 Hz (Shaffer et al., 2014). It has therefore been suggested that during rest the LF component primarily indicates PNS and baroreflex activity (Eckberg, 1983; Lehrer et al., 2003; McCraty & Shaffer, 2015), giving it the name *baroreceptor range*. Reducing breathing rhythm entrains heart period rhythms also to oscillate in lower frequency. Therefore, during slow-paced breathing, especially when breathing rhythms are below 9 cycles per minute, oscillations shift from the HF-HRV into the LF band.

1.4.2.3 High frequency (HF)

The HF band (0.15–0.40 Hz) covers rhythms with periods between 2.5 and 7 s and is strongly influenced by parasympathetically mediated heart period oscillations induced by breathing from 9 to 24 cycles per minute. This span envelopes the normal respiratory rate of 12 to 20 cycles per minute for resting adults (Chourpiliadis & Bhardwaj, 2023), which is why the HF band is also called the *respiratory band*. HF-HRV power is therefore closely related to RSA and correlates with RMSSD and pNN50 (Kleiger et al., 2005). However, it must be noted during moments of slow breathing (< 9 cycles per minute), HF-HRV does not or only poorly reflects respiratory-linked cardiac vagal control due to the crossover of the power into the LF band. Moreover, HF (and LF) has been criticized to properly reflect autonomic regulation, due to non-vagal HRV components such sinoatrial instability (Hayano & Yuda, 2019).

1.4.2.4 Normalized power (LFn and HFn)

Normalized HRV values of LF (LFn) and HF (HFn) are obtained by calculating the ratio of the respective band to the total frequency power ($TF = LF + HF$ or sometimes $TF = VLF + LF + HF$). Often LFn and HFn are interpreted as sympathetic and parasympathetic indicator, respectively. However, there is an intrinsic statistical problem in interpreting normalized HRV units (Burr, 2007). The authors demonstrated that LFn and HFn are characterized by a perfect linear association when VLF is discounted. Hence, they are exchangeable measures reflecting the same neurophysiological processes, and their ratio is algebraically redundant with LF/HF. Redundancy is not given any more when VLF is included in TF. However, the new information that discriminates LFn from HFn derives solely from VLF, which provides no clear interpretation of autonomic regulation. Moreover, normalized measures disregard total power changes as power ratios remain relatively stable, for example, when surges in LF and HF power occur congruently. Therefore, interpretations of normalized values are ambiguous, and they should not be preferred over total power values.

1.4.2.5 LF/HF ratio (LF/HF)

LF/HF is calculated as the ratio of total LF to total HF power. It is a popular clinical indicator to estimate the balance between SNS and PNS activity. The idea is that LF-HRV reflects sympathetic while HF-HRV is generated by parasympathetic activity, so that an increase in LF/HF is equivalent to a sympathetic shift. However, LF/HF has been heavily disputed as a measure of sympatho-vagal balance (Billman et al., 2015;

McCraty & Shaffer, 2015; Shaffer & Ginsberg, 2017). Firstly, as illustrated in the automatic space model (Berntson et al., 1994), the relationship between SNS and PNS is not necessarily reciprocal. Secondly, LF reflects both sympathetic and parasympathetic influences and varies strongly with experimental conditions. Thirdly, the respiration rate confounds the interpretation of the LF and HF bands. For instance, slow breathing at 6 cycles per minute strongly stimulates via parasympathetic pathways LF-HRV (Laborde, Allen, Borges, Dosseville, et al., 2022), consequently increasing LF/HF. On the other hand, higher LF/HF at rest might indicate arousal-related sympathetic activation. Thus, great care should be taken when interpreting LF/HF, specifically in regard to testing conditions.

1.4.2.6 Peak-to-Trough Respiratory Sinus Arrhythmia (P2T-RSA)

RSA calculated by the peak-to-trough method (P2T-RSA) corresponds to the heart period variations related to the respiratory cycle. It is computed by first subtracting the shortest heart period during inspiration from the longest heart period during expiration in any given respiratory cycle and then averaging all subtractions. Hence, P2T-RSA is determined in line with the theory of vagal gating so that the magnitude of both heart rate acceleration during inhalation (cardio-respiratory inhibition of vagal outflow) and heart deceleration during expiration (restoration of vagal outflow) are positive contributors. Consequently, P2T-RSA foremost assesses cardiac vagal control linked to respiration. Moreover, it indicates a rise in homeostatic activity and adaptability (Berntson et al., 1997). P2T-RSA correlates strongly with HF-HRV when the respiratory rate is between 9 and 24 cycles per minute and with LF-HRV when respirations are between 2.4 and 9 cycles per minute.

1.4.3 Further measures of HRV

1.4.3.1 Coherence

Another critical measure derived from the frequency domain is the heart coherence (named also cardiac coherence or resonance; McCraty & Shaffer, 2015). “Coherence is assessed by identifying the maximum peak in the 0.04 Hz to 0.26 Hz range of the HRV power spectrum, calculating the integral in a window 0.030 Hz wide, centered on the highest peak in that region, and then calculating the total power of the entire spectrum.” (McCraty & Shaffer, 2015). Therefore, high coherence is characterized by a stable, highly auto-correlated, and harmonic heart period signal that is defined by a narrow, high-amplitude in the LF band. Inversely, low coherence would arise from chaotic signals with flat power distribution or with major power peaks in the VLF or

HF bands. The authors posit that coherence implies stability in oscillating systems like the heart which is required for efficient and optimal physiological and cognitive functioning.

Beyond temporal and spectral measures, analytical approaches based on entropy and fractal analysis have been developed to disentangle the complex non-linear dynamics of HRV, which conclusively might provide a more in-depth insight into neurophysiological and cardiovascular processes (see Pham et al., 2021 for a review).

1.4.3.2 Non-linear indices

Non-linear indices represent features derived from the Poincaré plot. The latter is a diagram in which each NN interval is plotted against its preceding NN interval. It is used to assess the non-linear dynamics of HRV by quantifying the correlation between successive NN intervals. Typical features are the SD1 which is the standard deviation of the Poincaré plot perpendicular to the line of identity and SD2 which represents the standard deviation along the identity line. SD1 is an index of short-term variability of RR intervals and corresponds to RMSSD, and thus cardiac vagal control, whereas SD2 reflects long-term variability. Moreover, often the ratio of SD1 to SD2 as the ratio of short-term to long-term variability in HRV is reported.

1.4.3.3 Heart rate asymmetry

Heart rate asymmetry is characterized by the asymmetry features of Poincaré plot (Yan, 2017). For example, SD1d and SD1a measure the partitioning of the contribution to short-term variance (SD1) to cardiac decelerations (prolonged heart period) and deacceleration (shortened heart period), respectively (Piskorski & Guzik, 2011).

1.4.3.4 Heart Rate Fragmentation

Heart rate fragmentation (Costa et al., 2017) is a new method to assess vagally mediated short-term HRV, by assessing sudden changes in the sign of heart rate acceleration. Measures, for example might help discriminating individuals suffering of coronary artery disease from healthy patients.

1.4.3.5 Complexity and fractal measures

The complexity is often calculated as a measure for the *chaos* or the information content of a signal as entropy (e.g., Shannon entropy). A popular fractal approach is the monofractal detrended fluctuation analysis of the HR signal which provides an index

of short-term or long-term correlations. Complexity and fractal measures can describe the clinical significance of the ANS.

1.4.4 Validity of ultra-short-term recordings

Though short-term recordings have been established as the gold standard in psychophysiological research, there is an interest in reducing recording lengths, for example, due to experimental constraints. For instance, when repeated HRV measures are required over a single experimental session, protocols might quickly and unnecessarily grow in length. Moreover, reducing the segments' length is especially important when cognitive processing phases need to be matched with the ECG recording time, for example, when the cardiac regulation during a task is investigated. Many cognitive processes, for example imagining an event in the future or recollecting it from the past, typically last around 1 min. In addition, chaining repeated cognitive actions, e.g., memorizing a stimulus, over a span of 5 min might engender fatigue effects or attentional decoupling biasing the cognitive outcome.

To assess the validity of ultra-short-term recordings, several researchers have examined the correlation between 5 min recordings with segments of different lengths (i.e., 10–270 s; see (Shaffer & Ginsberg, 2017) for an overview). In this context Shaffer et al., (2016) proposed the following minimal recording lengths when a conservative criterion of $r > 0.9$ explaining at least 81% of the variance is applied: 10s for mean heart rate, 60 s for RMSSD, SDNN, and pNN50, 90 s for LF, 120 s for HF, LFn, and HFn, and 180 s for VLF. In another study, correlations were determined based on 467 subjects for different age groups (Baek et al., 2015). The authors reported for a criterion of $r > 0.9$ in young adults (< 30 years) the following minimal segment lengths: 10 s for mean heart rate, 60 s for pNN50, 120 s for RMSSD, 150 s for HF-HRV, LFn, HFn, LF/HF, 180 s for SDNN, LF, 210 s for TF, and 240 s for VLF. Conclusively, recording time can be reduced while maintaining measurement validity to approximately 150 s for the main spectral measures (i.e., HF, LF) and even down to 60 s for the main temporal measure of cardiac vagal control (i.e., RMSSD). Some researchers demonstrated that RMSSD can even be reliably reduced to 30s (Salahuddin et al., 2007) or 10 s (Munoz et al., 2015) and requires no longer periods than 120s. Yet, when 10 s are taken it is preferable to average multiple segments. These may not necessarily be in succession but can be spread over the experiment.

1.4.5 Main measures of cardiac vagal control

It can be noted from the sections above that HRV measures are particularly sensitive to capture the activity the PNS exerts to control the heart, also referred to as vagally mediated HRV (vmHRV). In summary, the central indices of vmHRV for short-term or ultra-short-term recordings are RMSSD, HF-HRV, and P2T-RSA (de Geus et al., 2019; Laborde et al., 2017; Shaffer & Ginsberg, 2017). It must be noted though that HF-HRV and P2T-RSA are largely driven by respiration. In addition, HF does not reflect vmHRV during slow breathing and is more biased than RMSSD in ultra-short-term recordings. Therefore, when recordings are very short (< 2 min) or contain large variation in the breathing rhythm, RMSSD may be the preferable choice to assess cardiac vagal control.

1.4.6 Influencing factors

There are a variety of demographic, physiological, and behavioral factors that influence HRV indices. Laborde et al. (2017) and Shaffer et al. (2017) list important factors in their recommendations for assessing and evaluating HRV in psychophysiological research, such as health status, sleep, and smoking habit. Since the subject of this thesis is the study of cardiac vagal control, in the following the term HRV refers mainly to vmHRV.

1.4.6.1 Respiration

Respiration can have strong effects on HRV by changes in the respiratory rhythm (T. E. Brown et al., 1993; Houtveen et al., 2002), respiratory depth (Hirsch & Bishop, 1981), and central respiratory drive (Houtveen et al., 2002). Inter- and intra-individual differences in breathing affect HRV indices differently and can significantly reduce the reliability of spectral measures (Hill et al., 2009; Kuss et al., 2008; Penttilä et al., 2001). Statistically controlling for respiration is problematic and is not recommended (Laborde et al., 2017). Nonetheless, it is important to monitor respiration to understand the autonomic source of neurobiological processes underlying HRV. The effect of breathing on HRV is further discussed in the following chapter.

1.4.6.2 Cardiac chronotropic state

The cardiac chronotropic state, the mean heart rate or mean heart period over a defined time interval, reflects the net effect of efferent influences of the PNS and SNS. All conventional measures of HRV depend on the cardiac chronotropic state (de Geus et al., 2019; Shaffer & Ginsberg, 2017). In this line, higher heart rates decrease HRV, and

lower heart rates increase HRV; an effect known as the cycle length dependence (McCraty & Shaffer, 2015). Alterations in both HRV and the chronotropic state are predominantly mediated by vagal influences when heart rates are below 140 beats per minute, as proposed by (Gourine & Ackland, 2019). Consequently, these measures have been suggested as closely interconnected (Boyett, 2017; Boyett et al., 2017). However, it is important to note that sympathetic activity also impacts the chronotropic state, and the potential existence of a non-vagal influence of the chronotropic state on HRV cannot be dismissed. For instance, part of the cycle length dependence may be inferred from the intrinsic property of the heart that the period between sinoatrial myocyte firing is a nonlinear function of neurotransmitter concentration. In this line, the same level of phasic vagal activity elicits at greater heart rates (shorter heart periods) reduced shortening and prolongation of RR intervals and thus a lower HRV (Melenovsky et al., 2005; Rocchetti et al., 2000; Zaza & Lombardi, 2001). Accordingly, the chronotropic state would also interfere with the association between HRV and other (psychological) parameters. This led to the suggestion to systematically control or even correct HRV for heart rate (de Geus et al., 2019; Sacha, 2014).

The difference between heart rate and heart period is important because the transfer function from heart period to heart rate is hyperbolic (heart rate [in beats per minute] = 60 / heart period [in seconds]). That means both measures are not proportional, which is specifically critical when HRV measures are adjusted for mean heart rate. Measurements of HRV show high linearity to heart period but not to heart rate. Therefore, to avoid biases due to non-linearity and differences in measurement units (temporal measures are mostly like the heart period measured in milliseconds) it is preferable to adjust HRV by the heart period (de Geus et al., 2019).

1.4.6.3 Health Status, Lifestyle, and Other Stable Factors

HRV is affected by a variety of stable factors including age, gender but also mental and physical disorders such anxiety, depression, cardiac disease, asthma, diabetes etc. Also, the intake of various medicaments such as treatment against thyroid dysfunction or the use of contraception can influence HRV. In addition, lifestyle habits such as smoking, drinking alcohol, insufficient food intake (bulimia nervosa), regular physical activity and aerobic fitness play a crucial role.

1.4.6.4 Transient Factors

Cardiovascular function is also influenced by transient effects including substance intake (caffeine, nicotine, psychoactive drugs), sleep deprivation, fatigue, circadian rhythm, sickness, physical and digestive activity that can last for many hours or days. Generally, physical and mental stressors as well as poor health have a reducing effect on HRV (stable or transient), However, elevated HRV can also be indicative of abnormalities in the cardiovascular system, such as atrial fibrillation (Stein et al., 2005).

Changing body postures also shifts cardiovascular functioning mainly due to changes in systemic vascular resistance. Equally, the seating position is important because it can change the respiration rate and tidal volume (Burns et al., 1994), as well as autonomic cardiovascular regulation (Kubota et al., 2013) that influences RSA. For example, slightly flexing the upper torso, as in the Fowler's position, changes respiratory function and increases vagal activity in young adults (Kubota et al., 2013).

1.4.6.5 Sampling

HRV measures can substantially differ if recordings lengths are too short (see above) or largely vary between measurement points. As a best practice, HRV recordings should be calculated and compared between segments of the same length. In addition, a minimum sample frequency of 500 Hz is recommended to ensure the validity of non-linear and frequency indices (Merri et al., 1990)

For a more precise description of HRV factors please consult previously proposed guidelines (Laborde et al., 2017; Shaffer & Ginsberg, 2017) or and the extensive screening procedure used in another recent HRV study (Magnon et al., 2021).

1.5 Effects of Slow-Paced Breathing

1.5.1 Resonance Frequency Model

Resonance describes the phenomenon when an oscillating system (e.g., a pendulum) is stimulated at (roughly) the same frequency (e.g., pushing the pendulum every time it passes the midpoint), causing an increase in amplitude. Research on the so-called *Resonance Frequency* found that slow and deep breathing evokes heart period oscillations to increase in amplitude and to align with the respiratory and baroreflex cycle ([Figure 6](#); Lehrer et al., 2000, 2003; Lehrer & Gevirtz, 2014; Vaschillo et al., 2002, 2006). Lehrer, Vaschillo, and colleagues argued that the origin of the phenomenon is

rooted in the combined effect of RSA and baroreflex. On the one hand, RSA regulates heart rate, such that it increases during inhalation and decreases during exhalation (respiratory induced heart rate oscillations, see Chapter 1.2.6). On the other hand, the baroreflex triggers changes in heart rate following the drop and rise in blood pressure (blood pressure induced heart rate oscillation, e.g., Traube-Hering waves), whose sensitivity is affected by the phase relationship between heart rate and blood pressure. Hence, RSA and baroreflex represent two stimulators that evoke resonance when aligned with the heart rate oscillations. Consequently, during moments when the heart rate is synchronous (0° phase relationship) with the respiratory cycle and antiphase (180° phase relationship) to the blood pressure, both RSA (positive feedback) and the baroreflex (negative feedback) will produce maximal variations in the heart rate and maximal baroreflex gain. Such phase relationship is given when the breathing rhythm is aligned with the baroreceptor resonance frequency of approximately 0.1 Hz (1 cycle per 10 seconds or 6 cycles per minute). In respect to the previous discussion (Chapter 1.2.5 and 1.2.6), resonance arises from alignment of influences by central respiratory neurons and baroreflex responses to Traube-Hering and Mayer waves (always at 0.1 Hz).

The exact resonance frequency, however, slightly differs between individuals due to variations in the length of the baroreflex feedback delay (inertia). Inertia values range for adults between 4 and 6.5 s, and the frequency accordingly between 0.075 and 0.125 Hz (i.e., 4.5 and 7.5 cycles per minute), (Vaschillo et al., 2006). The authors conjecture that resonance frequency is a variable of blood volume. Indeed, they found that inertia and resonance frequency depend on height and gender (lower values for small people and women) but not on age or weight. Hence, it has been proposed that the individual resonance frequency should be determined, evoking maximal heart rate oscillations and, therefore, fluctuations in the vagal output (Lehrer et al., 2000; Shaffer & Meehan, 2020). At the beginning of the so-called Resonance Frequency Training, maximal fluctuation is identified by instructing participants to breathe at rhythms of 4.5, 5.0, 5.5, 6.0, and 6.5 cycles per minute, 2 minutes for each frequency, and by evaluating respectively multiple HRV indices including P2T-RSA, LF-HRV, and the amplitude of the LF spectral peak (Fisher & Lehrer, 2022; Lehrer et al., 2000, 2013). For the remainder of the training, participants continue breathing at the specified resonance frequency. It has to be noted, though, that while maximal heart swings occur in younger adults at a phase relationship of 0° , the phase approaches 90° in the elderly population, such that inhalation should be initiated at the middle of each heart rate acceleration

phase (Lehrer et al., 2020). Moreover, HRV and its increase at resonance frequency decreases with age in adults, which might have important psychophysiological implications. The reason might be that cardiovascular responsivity is reduced in aging, but this still needs to be clarified (Lehrer, 2022). In short, resonance frequency is the individually specified rhythm of around 0.1 Hz or 1 cycle every 10 seconds at which breathing evokes the greatest improvements in parasympathetically mediated RSA and baroreflex gain.

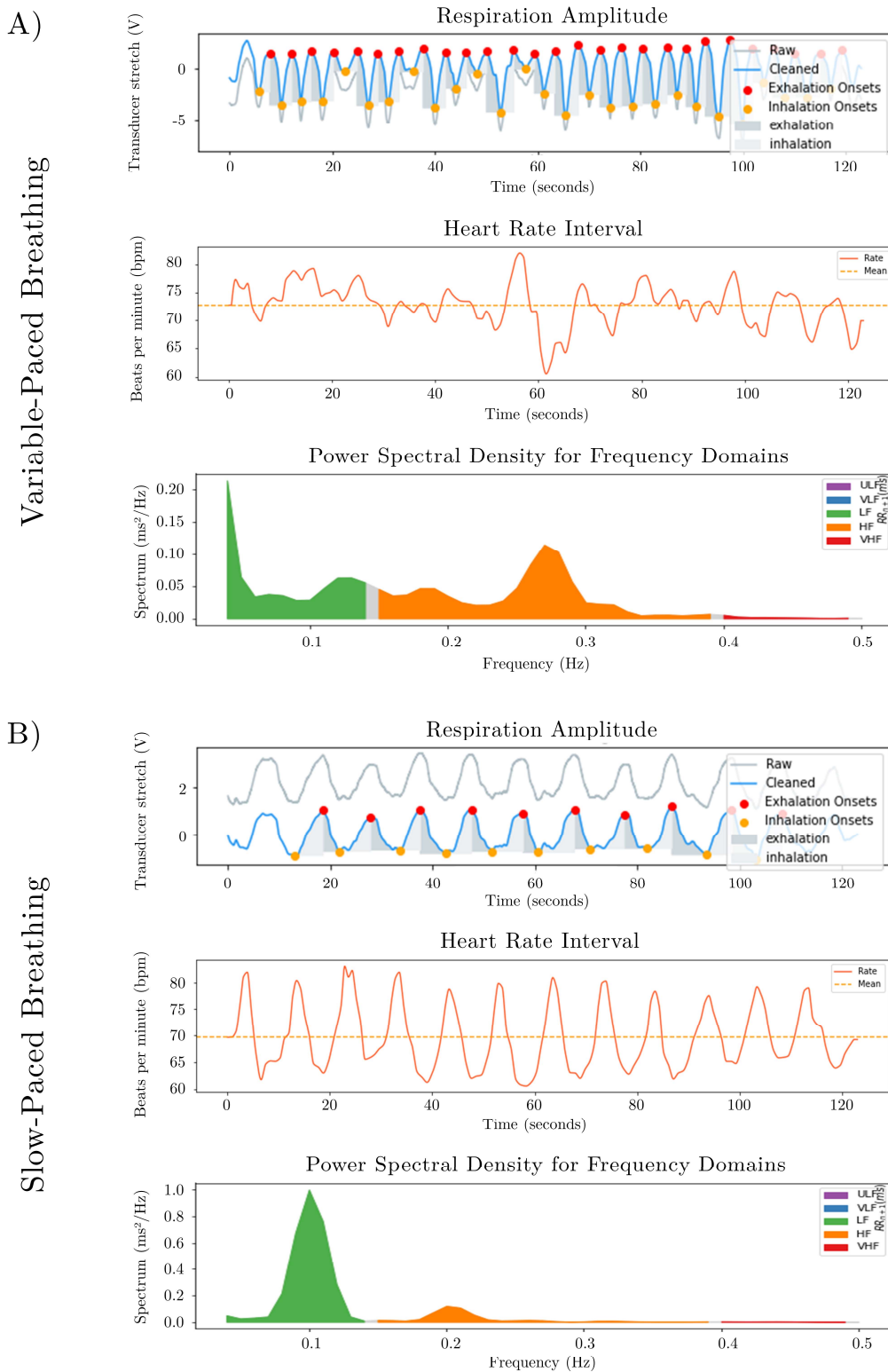


Figure 6 – Physiological Responses to Paced Breathing

Note. Example graphs present real data from study 3 during paced breathing following **(A)** a variable pacer (mean = 14 cycle per minute) and **(B)** a constant pacer at 6 cycles per minute. Slow breathing evokes a coherent large-amplitude heart rate wave at a central peak power at 0.1 Hz.

1.5.2 Breathing at 6 cycles per minute

If the resonance frequency is closely around 0.1 Hz, the question arises whether slow-paced breathing at 6 cycles per minute without determining the exact resonance frequency would evoke equal physiological effects. Specifying the resonance frequency adds additional constraints to the protocol, because it requires a physiological monitoring device and different frequencies need to be evaluated and carefully analyzed before the actual training can start. Therefore, benefits must be weighed against costs to determine whether resonance frequency is superior to slow-paced breathing at 6 cycles per minute. An additional problem is, that estimates of resonance frequencies were found not to be reliable in the first session due to relaxation effects (Lehrer et al., 2013). This is especially troublesome for single-session protocols. However, even if multiple sessions are planned, resonance frequencies might not be reliable, because they are unstable over time (Capdevila et al., 2021; G. Lin et al., 2012). Capdevila et al. (2021) demonstrated that in two third of a small sample of adults ($n = 21$) the resonance frequency changed over a span of only 1 week. In addition, they showed that the mean resonance frequency across participants was 6 cycles per minute and that breathing at a fixed pace of 6 cycles per minute produced only slightly lower levels of RMSSD compared to resonance breathing. Consequently, it seems that the resonance frequency needs to be determined before each training session, adding extra cost to the intervention. Moreover, it demonstrates that simply breathing at a rhythm of 6 cycles per minute could have the same effectiveness as Resonance Frequency Training. Indeed, there is evidence that slow-paced breathing at 6 cycles per minute maximizes RSA and baroreflex sensitivity (Russo et al., 2017; Zaccaro et al., 2018). Moreover, it has been shown that breathing at resonance frequency does not generate better HRV outcomes than breathing at 6 cycles per minute (Shaffer & Meehan, 2020) nor does it produce clinically relevant differences (Lehrer et al., 2020).

1.5.3 Influence of the breathing pattern

Breathing patterns other than the frequency may affect HRV, for example, the ratio of inhalation time period to exhalation time period or pauses in the breathing cycle (i.e., blocking breathing). Numerous studies have shown that maintaining an equal or lower inspiratory/expiratory time ratio, which emphasizes a longer exhalation, at a constant breathing rhythm, enhances HRV when compared to a higher ratio (Bae et al., 2021; De Couck et al., 2019; Edmonds et al., 2009; Jafari et al., 2020; Laborde et al., 2021; Sevoz-Couche & Laborde, 2022; Van Diest et al., 2014). For example, Laborde et al.

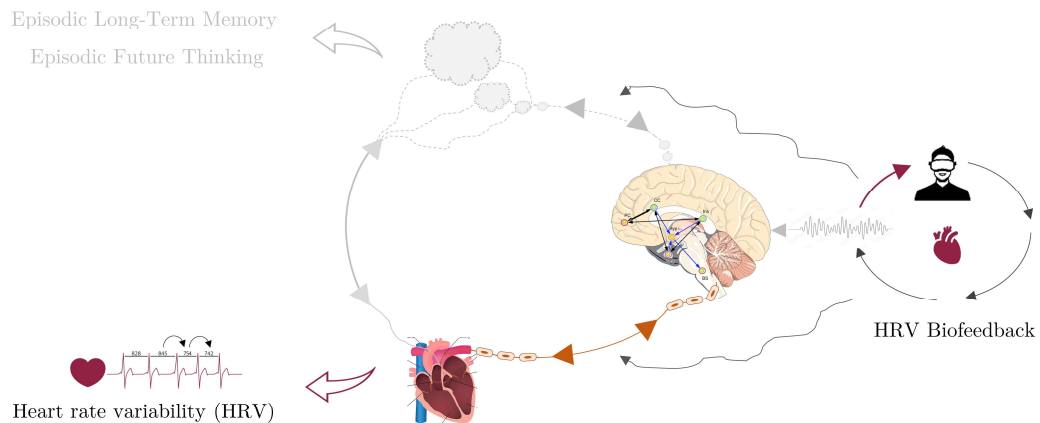
(2021) investigated the effect of inhalation-to-exhalation ratio during slow-paced breathing at 6 cycles per minute. They found that longer exhalation (ratio = 0.8) compared to longer inhalation (ratio = 1.2), or an equal inhalation-to-exhalation increases RMSSD. Also, during resonance frequency assessment, lower ratios have been found to increase RSA, presumably due to vagal activation. However, other HRV metrics (e.g., pNN50, RMSSD, SDNN, and LF power) remained unaffected (see for a review, Shaffer & Meehan, 2020). Similarly, a pause during slow-paced breathing between inspiration and expiration of > 1 s could increase RSA (Edmonds et al., 2009; Russell et al., 2017), while a pause of 0.4 s did not further increase RMSSD (Laborde et al., 2021). Hence, whether HRV increases depends on pause duration and the parameter assessed (RSA or RMSSD).

In summary, it seems adventurous to increase exhalation times to increase vmHRV. In addition, short pauses in breathing between cycles may further increase RMSSD. The effects may depend on individual differences and HRV parameters recorded. Therefore, determining individual breathing patterns may maximize HRV.

1.6 Chapter Summary

- The heart and the brain are bidirectionally connected by an intricate neural and biochemical system.
- This integrative system spans the autonomic nervous system connecting to further body functions in the periphery and neural circuits in the brainstem and upper brain regions, involved in cognition and emotion.
- Efferent inputs from the autonomic nervous system to the heart deriving from the brainstem regulate the heart rate.
- Heart rate variability (HRV) arises from complex interactions between the nervous systems and indicates sympathetic and parasympathetic regulation.
- Thus, HRV encodes efferent as well as afferent information streams associated with different physiological systems.
- The main purpose of the integrated control of body functions, including the heart, is to promote adaptive functioning through homeostasis and allostasis.
- Regulation by respiratory drive and the baroreflex (negative feedback loops) strongly influence HRV.
- Respiratory Sinus Arrhythmia (RSA) arises as the respiratory-coupled HRV to optimize body functioning.
- Parasympathetic activity via the vagal nerve is paramount to cardiac control.
- Main HRV measures indicating cardiac vagal control are RMSSD, HF-HRV, and P2T-RSA. The latter is specifically sensitive to respiratory effects.
- Breathing at or near the individual resonance frequency (≈ 0.1 Hz) evokes a phasic alignment of physiological oscillators (respiration, blood-pressure, heart rate) at 0.1 Hz mainly through RSA and the baroreflex system evoking large-amplitude and coherent heart rate oscillations and thus an increase in baroreflex sensitivity and vagally mediated HRV.
- Individual adaptation of breathing patterns, e.g., increasing exhalation-to-inhalation period or including pauses between cycles can further increase HRV.

2 Chapter 2 – Heart Rate Variability Biofeedback



2.1 Introduction to Biofeedback

Biofeedback is the biological signal (“bio”) that is taken from a person’s body through technical recording and displayed back to the person (“feedback”). In this looping process, biological functions are made observable, that otherwise may go unnoticed, allowing the person to regulate these functions through behavioral adaptation. The term biofeedback may also refer to the technological system involved in the recording and display, or the training technique applied for self-regulation. Biofeedback signals are typically presented in real-time through the visualization on a screen, through auditory or vibrotactile outputs, or a combination of these. Hence, biofeedback provides a means to increase state awareness of endogenous bodily parameters and to drive voluntary physiological changes. Typically, biofeedback applications aim to evoke physical and psychological short- and long-term change during and beyond the training or to master self-regulatory skills that can also be applied without biofeedback.

Biofeedback is categorized by the biological source or physiological process the signal describes. For instance, the subcategory neurofeedback refers to biofeedback based on brain signals usually derived from an electroencephalogram (EEG) or functional magnetic resonance imaging (fMRI) to directly alter brain functioning. Besides, many other forms of biofeedback have been developed, including the following common modalities (Khazan, 2013):

Respiratory – Measurement of the breathing rate and pattern or the level of carbon dioxide levels in the blood using a respiratory belt transducer or capnograph. Breathing biofeedback is applied to learn how to maintain adequate respiratory chemistry (e.g., oxygen and carbon dioxide levels) that otherwise might be disbalanced due to respiratory dysfunction or hyperventilation.

Cardiovascular – Measurement of the heart rate, HRV, RSA, or blood volume pulse using ECG sensors or photoplethysmography. HRV or RSA biofeedback is usually used to increase parasympathetic activity. Intended training goals are often the reduction of arousal and the increase of relaxation, physical performance, or the ability to regulate behavior.

Neuromuscular – Measurement of muscle tension using surface electromyography (EMG). EMG biofeedback is applied to learn how to relax and control muscles. It is typically used to release muscle pain, decrease arousal, or rehabilitate muscle control.

Skin conductance – Measurement of eccrine sweat gland activity using electrodermal activity (EDA) sensors. EDA reflects sympathetic activity linked to arousal, affective, and motivational processes. Hence, EDA biofeedback is applied to reduce levels of sympathetic tone and reactivity, supporting emotional responsiveness and stress-related responses.

Peripheral skin temperature – Measurement of finger, hand, or toe temperature using a thermistor. Skin temperature changes as a function of vasoconstriction controlled by the sympathetic system. Thermal biofeedback is applied to reduce stress and tension, especially in the context of functional vascular disease or circulatory problems, diabetes, and migraine headaches.

Biofeedback is a body-mind intervention because volitional control is mediated by changes in the autonomic and central nervous systems, affecting physiological and psychological components. Biofeedback has its origin for broader use in health, psychological, and wellbeing applications in the early 70s (B. B. Brown, 1975; Karlins & Andrews, 1973). Since then, it has gained momentum on the transhumanist agenda for human performance enhancement (Hansell & Grassie, 2011) and medical purposes. For example, a high level of confidence in positive effects has been found on the headache, as well as urinary and fecal incontinence (Kondo et al., 2019). Moreover,

biofeedback has been classified as efficacious (level 4 out of 5; Yucha et al., 2008) for various physical and psychiatric health issues, including anxiety, attention deficit hyperactivity disorder, headache, and chronic pain (Frank et al., 2010; Schoenberg & David, 2014).

In the domain of psychophysiological research, probably the largest interest was given to neurofeedback due to its ability to directly control brain correlates involved in cognition and emotion. Previous studies confirmed its beneficial effect on cognitive performances in young (Dessy et al., 2018) as well as in elderly adults (Angelakis et al., 2007; Becerra et al., 2012; Dessy et al., 2018; Lecomte & Juhel, 2011). The inherent problem, however, with neurofeedback is that it is very specific to the physiological signal it targets. In addition, it requires many sessions to produce observable effects that are not long-lasting, and its efficacy is in many cases inconclusive (Dessy et al., 2018; Gruzelier, 2014; Luctkar-Flude & Groll, 2015; Marzbani et al., 2016; Renton et al., 2017; Trambaiolli et al., 2021). In parallel, the last two decades have witnessed a growing interest in HRV biofeedback for psychological and psychiatric purposes due to the involvement of cardiac vagal control in functional brain activity associated with cognitive functions (Critchley, 2005; Critchley et al., 2013; Thayer et al., 2012; Thayer & Lane, 2000). Interest in HRV biofeedback might have been propelled by its cost-effectiveness and ease of use. In comparison to neurofeedback, it is generally cheaper, easier and faster to setup, easier to learn, and less prone to training-induced fatigue (Dessy et al., 2018; Marzbani et al., 2016; McCraty & Tomasino, 2004; Vernon, 2005).

2.2 Training Modalities

HRV biofeedback is a training technique that seeks to modify the naturally occurring periodic change and regularity of the cardiac rhythm. To this end, the heart period signal is derived in real-time from an ongoing ECG or photoplethysmography recording, transformed into an interpretable metric, and presented to the user. Sometimes, the target is to directly increase RSA, which is why the term RSA biofeedback is occasionally used. Generally, the goal of HRV biofeedback training is to evoke a harmonic, large-amplitude heart rate signal indicating increased vmHRV and therefore cardiac vagal control. The precise indicator of HRV and the way it is presented varies greatly between protocols. In most cases, a computer screen displays running graphs of the heart rate and a calculated metric (e.g., coherence or RMSSD) that may be accompanied by numerical or graphical demonstrations of further HRV indices (e.g., power spectral density). Biofeedback may also take forms in auditory or, less

commonly, in tactile signals. Many HRV biofeedback applications targeting enhanced HRV rely on voluntary slow-paced breathing as a behavioral modulator of HRV.

2.2.1 Resonance breathing

Lehrer's proposed Resonance Frequency Training (Lehrer et al., 2000) is a form of HRV biofeedback (Chapter 1.5.1) since it involves communicating body-own physiological information to the subject. In this line, maximal RSA and baroreflex sensitivity are assessed through multiple HRV indices during the step-wise decrease in breathing frequency (Shaffer & Meehan, 2020), the latter determining the individual resonance frequency. The resonance approach seems to be particularly interesting due to fast and stable effects, irrespective of age, after only four to six training sessions (Lehrer et al., 2003; Lehrer & Vaschillo, 2004; Vaschillo et al., 2006). Indeed, many HRV biofeedback systems are based on the principles of resonance frequency in that they instruct participants to breathe near resonance frequency, generally at 6 cycles per minute. However, they do not necessarily determine individual frequencies. As described in Chapter 1.5.2, the usefulness of specifying the resonance frequency is doubtful because it imposes additional constraints (e.g., assessment) without adding significant value. A possibility to provide individualized HRV biofeedback while circumventing a lengthy assessment procedure is to apply more specific real-time biofeedback. By keeping participants informed about cardiac activity and their success to increase heart rate oscillations (e.g., via running graphs of the heart period, respiration, RSA, or spectral power), they can dynamically adapt their breathing pattern towards the resonance frequency. For example, participants may be instructed to follow a breathing pacer running at 6 cycles per minute and adapt their breathing patterns from there (e.g., reducing or increasing respiratory frequency). Though the assessment of online HRV parameters would not be as detailed as in resonance frequency HRV biofeedback, the design of the setup would be much simpler (no assessment, resting pauses, and extraction of multiple spectral measures). Moreover, it would allow for adaptive learning, because subjects can more dynamically regulate their behavior; a component that is crucial for motivation (see Chapter 2.3). Consequently, such a simpler and more adaptive approach is especially useful when conducting high-volume single-session experiments, where its duration is important. For this reason, several protocols based on slow breathing near resonance frequency have emerged, all aimed at increasing vmHRV or RSA.

2.2.2 Coherence training

Another important training approach that is less centralized on breathing has been developed by the HeartMath® Institute (Childre et al., 1999; Childre & Rozman, 2003, 2005). The goal of the Coherence Training is to optimize dynamic structures and interplay of physiological rhythms reflected in higher levels of cardiac coherence (i.e., stability and consistency in the heart period signal, see Chapter 1.4.3.1 for calculation) and vmHRV. Training may be based on different techniques (Heart-Focused Breathing, Freeze Frame, Inner-Ease, Quick Coherence, Heart Lock-In, Prep, Shift and Reset, Getting In Sync, and Coherent Communication) primarily focusing on cognitive reappraisal. Participants are instructed to self-induce positive or calming emotions while slowing their breathing. HRV biofeedback typically supports the training to indicate whether the heart is coherent or not. Training success, and thus a high coherence level, is reflected by a large amplitude sin-like waveform with a single power peak around 0.1 Hz in the frequency spectrum (see [Figure 6](#) p. 44 for an example on paced-breathing HRV biofeedback). Besides the strong auto-correlation in the heart period, coherence also refers to cross-coupling with other physiological oscillatory systems like the respiratory and blood pressure cycle. High (cross-)coherence implies a strong degree of synchronization also between these systems. Furthermore, it has been argued that coherence training increases vagal outflow, causing cerebral synchronization, which optimizes cognitive functioning and emotion processing (McCraty et al., 2009; McCraty & Childre, 2010; McCraty & Zayas, 2014).

2.2.3 Similarities and differences

Coherence training shares many similarities with resonance frequency training. An obvious commonality is that both are self-regulation approaches that are best used with HRV biofeedback. Moreover, both focus on a stable alignment of cardiac, respiratory and blood pressure cycles driven by parasympathetic influences that produce auto-coherent (sinusoidal) heart rate waveforms around 0.1 Hz in the LF band. This, in turn, produces higher HRV and RSA amplitudes that are linked to increased efferent and afferent vagal traffic. The difference is that while the Resonance Frequency Training focuses purely on respiratory control, the Coherence Training emphasizes the self-activation of positive emotions. Though the Coherence Training also involves slow breathing instructions, the main focus of conscious attention rests on the positive emotions. McCraty & Zayas (2014) argue that coherence training sustains high coherence and thus vmHRV for a longer period than slow-paced breathing due to the

enjoyment of subjectively perceived affective changes (e.g., feeling more positive or less stressed). However, they also admit that positive activation may fail in the face of strong emotions or when the subject is not practiced enough. Thus, the Coherence Training crucially relies on the self-regulatory capacities and self-awareness of emotions to increase vmHRV, which may develop first with the ongoing training. On the contrary, HRV biofeedback based on resonance breathing is easy to learn and can induce large physiological changes within a minute or less (Lehrer et al., 2003). In sum, both resonance and coherence training are based on the same autonomic processes to increase parasympathetic activity. While resonance breathing relies on slow breathing, coherence training focuses on positive affectivity. Resonant breathing may be simpler to accomplish, especially if the number of sessions is small, because breathing can easily be controlled at will.

2.2.4 Combining mindfulness with biofeedback

Beyond those training techniques, it has been proposed to combine biofeedback with mindfulness approaches (Khazan, 2013). Mindfulness is the mental quality or state of being conscious of something, while calmly accepting feelings, thoughts, and sensations. The idea is to implement elements that can also be found in mindfulness-based cognitive behavioral therapy to let go of the struggle and thoughts related to unsuccessful physiological or behavioral control. In this line, biofeedback and mindfulness form a balance between goal-directed and unfettering forceful behavior that is blocking training progress. The use of mindfulness in HRV biofeedback (Khazan, 2013) may therefore contribute positively to psychological outcomes by reducing exercise-induced stress and instilling positive coping strategies. Mindfulness fosters the perception of internal and external states. It can be applied to direct focus on the internal perception of externally presented biofeedback (e.g., feeling the heartbeat). Biofeedback, in combination with mindfulness, might thus promote the recognition of inner body signals and thus bodily self-awareness.

2.3 Why Biofeedback?

When looking at the previously detailed modalities of HRV biofeedback, one might wonder why biofeedback may be relevant to increase vmHRV. Or, why could participants not simply follow a breathing pacer fixed at a frequency near resonance of 0.1 Hz? Below, we highlight the cognitive mechanisms underlying biofeedback and briefly review why biofeedback is important for slow-paced breathing.

2.3.1 Cognitive mechanisms underlying biofeedback

To understand the usefulness of biofeedback, it is crucial to consider the neurocognitive mechanisms underlying feedback learning. Biofeedback enables the target individual (agent) to engage in a continuous adaptation process, where behavior is modified to attain a goal (e.g., high HRV); a process that is based on learning. Feedback learning is an important aspect of biofeedback training success, which has led to the emergence of comprehensive models that elucidate the underlying mechanisms (Gaume et al., 2016). In principle, biofeedback strongly draws upon principles of reinforcement learning and operation conditioning (Sherlin et al., 2010; Skinner, 1938). According to the theories, behavior is reinforced by reward and repressed (negative reinforcement) by punishment since the agent naturally seeks to obtain rewards and avoid punishment. With respect to biofeedback, reinforcement is the success or failure to alter the feedback signal. For reinforcement to occur, the biosignal needs to be explicit, i.e., the participant is aware of how changes in behavior are related to changes in the signal. Inversely, implicit signals are subtle changes in the system that agents are not directly aware of, and that may operate through motivational variables (e.g., the biosignal changes implicitly the game difficulty). HRV biofeedback usually returns explicit signals which, through reinforcement, prompt the agent to take actions towards the achievement of the intended goal. Hence, the participants exercise self-regulation by learning to adapt their behavior that shifts the biofeedback signal into the intended direction (usually increasing vmHRV).

Learning leads to skill acquisition until it becomes automatized and neuronally imprinted in the connections of the nervous system (Brener, 2007). This would lead to spontaneous and automated behavior (e.g., adapting breathing that increases vmHRV unconsciously). In addition, biofeedback increases awareness of the biological variable, which may facilitate the exact perception of its internal representation even in the absence of the biofeedback. The processing of such internal representations of afferent bodily signals is known as interoception (e.g., feeling one's heartbeat, Critchley & Garfinkel, 2017). Consequently, increased interoception would function as a surrogate, internal biofeedback that could be used for self-regulation without a HRV biofeedback system (e.g., maximizing RSA just by feeling how the heartbeat rises and falls in relation to the breathing) and thus volitional control over autonomic mechanisms. It has to be noted that to date, the effect of biofeedback on interoception is disputed (Meyerholz et al., 2019; Rominger et al., 2021), however, only short protocols (20 min)

were used. Moreover, there is evidence that interoception is associated with the level of HRV in healthy subjects (Lischke et al., 2021; Owens et al., 2018).

Two skills that are central to self-regulation are discrimination and maintenance (Epstein & Blanchard, 1977). Discrimination is the ability to acquire or augment the internal perception of the physiological function related to biofeedback (e.g., feeling one's heartbeat), and is therefore closely tied to interoceptive skills. Self-maintenance is the aptitude to modify this physiological function towards the desired state (e.g., increasing heart rate during inspiration). For the acquisition of these skills and the success of HRV biofeedback, reward and motivation are central elements. Punishment can sometimes be motivating, but what drives people the most are rewards (Guitart-Masip et al., 2014). Motivation, in turn, ensures that the user stays on task in the face of challenges, e.g., when the user needs to maintain HRV for a long time but is tired. Intrinsic motivators that are based on self-motivation are most important to achieve long-term effects (Gaume et al., 2016). In game theory, for example, intrinsic factors are a major reason people are so attracted to gaming. The self-determination theory (Ryan & Deci, 2000) identified three intrinsic motivation factors that are the psychological needs of mastery, autonomy, and relatedness, which have been shown in game research to lead to states of flow, hyper-focused attention, being pleasantly and completely absorbed (Olson, 2010; Swanson & Whittinghill, 2015). Moreover, they are related to “fun” and associated with biological rewards with dopamine release (Lorenz et al., 2015). HRV biofeedback as a learning process towards mastery of HRV self-regulation (i.e., improving discrimination and maintenance) is such an intrinsic factor. However, for biofeedback to be motivating, there must be a balance between the difficulty of the task and the user's ability to make the task a feasible challenge. Moreover, the biosignal needs to be perceived as a reward. This depends on motivational state (e.g., interest in body physiology) because not all rewards are motivating. In summary, biofeedback enables skill acquisition through feedback learning and provides intrinsic motivation in this process, which helps to maximize task success (high vmHRV). Self-regulatory capacities might be applied even when no technical biofeedback is delivered.

2.3.2 Learning and motivation

As described in the previous section, learning and motivation are central elements of biofeedback. Paced breathing is also a form of self-regulation, where the feedback is the perceptual difference between interoceptive signals of the breathing cycle (am I

breathing in or out?) and the breathing pacer. Negative reinforcement would be a mismatch of the actual and pacer cycle (e.g., breathing in while the pacer indicates breathing out) and positive reinforcement synchronicity. However, the feedback is not the direct target of the training, which is to maximize HRV. The lack of external cardiac biofeedback thus gives no possibility of learning how to adjust the ANS. Inversely, biofeedback allows for behavior adjustment, such as finding the resonance frequency or fine tuning other respiratory patterns. For example, a certain inhalation-to-exhalation ratio, or pattern, including pauses, may increase vmHRV in one person but not another (see Chapter 1.5.3). Biofeedback thus enables individualized training to achieve a more optimal state than slow breathing alone would.

This learning process itself is engaging because it is based on the intrinsic motivation to acquire skills and want to improve. In comparison, slow breathing is easy for most healthy people to achieve and can easily become a tedious task. It is neither cognitively engaging nor does it provide motivating reinforcement. Participants do not know or see if they are improving, so their intrinsic motivation is based solely on the belief that they are. Motivational factors are determinants of concentration and engagement in the task and, thus, the average HRV value. Therefore, biofeedback is useful when motivation is low or likely to diminish as training progresses. This might, for example, be the case when experimental/ training protocols are long and tiring or when subjects are pushed to participation (e.g., students who need to earn course credits or patients taking part in a longitudinal trial).

2.3.3 Agency and placebo effect

Moreover, motivation might be modulated by the sense of agency. The sense of agency, as part of embodied cognition, refers to feeling that one's own action controls an external event (S. Gallagher, 2000). Controlling the biofeedback can contribute to a sense of agency when the action is perceived to succeed (Gaume et al., 2016). In turn, the capability to generate perceptible effects through one's own actions can be motivating (Eitam et al., 2013; Karsh & Eitam, 2015). In addition, the perception of control over physiological parameters can influence subject-expectancy effects on the training outcome (Weerdmeester et al., 2020). In other words, successful biofeedback might increase positive placebo effects (i.e., treatment improvements due to belief), due to a higher sense of agency. This in turn might further stimulate motivation. It has been argued that subject-expectancy effect is a clinically important parameter known to contribute to HRV biofeedback (Khazan, 2013). Therefore, when investigating the

link between physiological stimulation and cognitive outcomes, placebo effects should be controlled.

2.3.4 Adverse effects

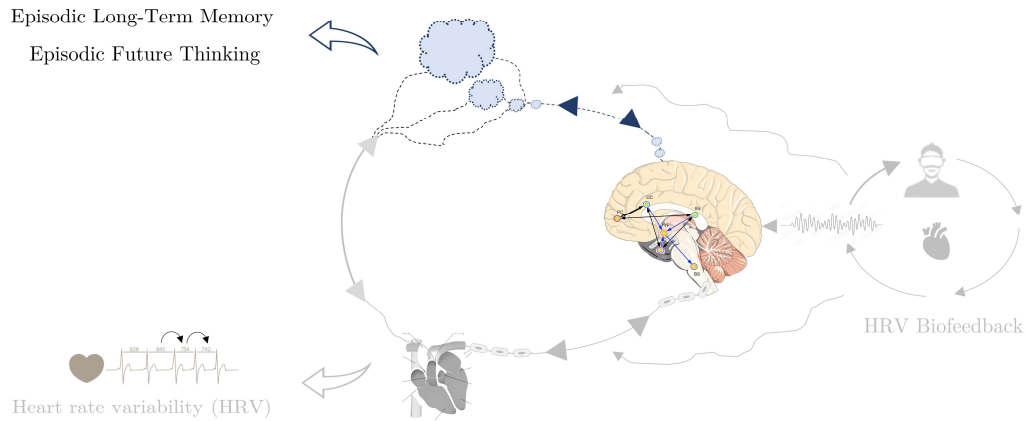
While biofeedback can be intrinsically motivating, it is important to consider adverse effects. Unsuccessful self-regulation can evoke frustration due to the lack of reward or the presence of punishment. Moreover, feedback learning is a cognitively demanding task that recruits executive brain regions and self-control networks due to the constant engagement of attention and cognitive functions that need to process the biofeedback (Gaume et al., 2016). It can lead to the depletion of such functions, also known as Ego-depletion effect (Hagger et al., 2010), which has negative effect on task performance. It is therefore helpful to implement principles of mindfulness biofeedback training (see Chapter 2.2.4) to counteract adverse effects.

2.4 Chapter Summary

- Biofeedback is mind-body self-regulation exercise that allows to manipulate physiological states at will.
- Various types of biofeedback exist, but heart rate variability (HRV) biofeedback may be the most effective and simplest-to-use to influence vagal functioning.
- Most popular techniques applied for HRV biofeedback are the Resonance Frequency Training and coherence training.
- Both techniques target an increase in vagally mediated HRV through stable alignment of physiological oscillations (respiration, heart rate, blood pressure) increasing vagal efferent and afferent flow.
- Training success shows specifically in increased LF-HRV and RSA.
- Effects are based on the resonance breathing effect detailed in Chapter 1.
- While Resonance Frequency Training is purely based on breathing, coherence training focuses on self-activation of positive emotions, which might be difficult to achieve.
- Induced changes in autonomic functioning may alter physiological functioning of the integrated system in cardiac control, which may optimize cognitive functioning and emotion processing (more in Chapter 5).
- Mindfulness approaches can contribute to HRV biofeedback outcomes.
- Biofeedback is crucial to slow-paced breathing due to components of feedback learning and motivation as well as to possibility to individualize breathing patterns. Together these maximize task success (high HRV) and may support self-regulation skill transfer.

3 Chapter 3 – Episodic Memory and Future Thinking

Thinking



The interest of this thesis was to investigate how the regulation of the heart by the brain is related to our thoughts. The latter includes many different processes. This thesis focuses on the episodic memory system and the capability to think into the future, which will be highlighted in this chapter. Moreover, the chapter will illuminate the role of the self in memory and future thinking and introduce the Self-Memory System, interlinking the different cognitive concepts.

3.1 Episodic Memory

Episodic memory is the capacity to recollect personally experienced events and their associated context, including spatial, temporal, and affective components (Tulving, 1985b, 2002). Typically, everyday life activities would not be possible without episodic memory, for instance, remembering the last work meeting or where you have put the keys. It also forms the basis for many other cognitive functions (Abram et al., 2014; Mahr & Csibra, 2018), including episodic autobiographical memory which is long-term self-relevant episodic memory (Piolino et al., 2009; Staniloiu et al., 2020), and future-oriented cognition, such as contemplating future scenarios or remembering to accomplish a previously planned action or restore a planned intention (Kliegel et al., 2002). Maintaining a good episodic memory is thus crucial for adaptive and social behaviors as well as wellbeing. Below, we will briefly review its function and processes in the context of the global human memory system.

3.1.1 Long-term memory systems

The memory system, rather than being monolithic, can be divided into various co-existing sub-systems and processes, (Figure 7 and Figure 8A). Research based on lesions studies, such as the famous case HM, have confirmed a dissociation between short-term and long-term memory (Squire, 2009). In addition, it was proposed to distinguish in long-term memory between the acquisition of implicit memory, such as skills and habits (procedural memory), and explicit memory, the former being preserved in amnesic syndrome and the latter being altered (Squire, 2009; Squire & Zola, 1996). Memory retrieval can be consciously described with language in declarative memory. In contrast, procedural (non-declarative) memory is not easily accessible by consciousness (i.e., anoetic) but expressed by the performance associated with the memory (e.g., know how to ride a bike). Tulving (1972) proposed that explicit or declarative memory can be further divided into two distinct memory concepts: *semantic* and *episodic*. Semantic memory, on the one hand, is composed of knowledge about the world, including generic classes of facts, meaning, ideas, and concepts (e.g., organ) and their specific instances (e.g., heart). Episodic memory, on the other hand, is the memory of personally experienced events associated with an affective, spatial, and temporal context. It would be specifically altered compared to semantic memory in amnesic patients (Squire &

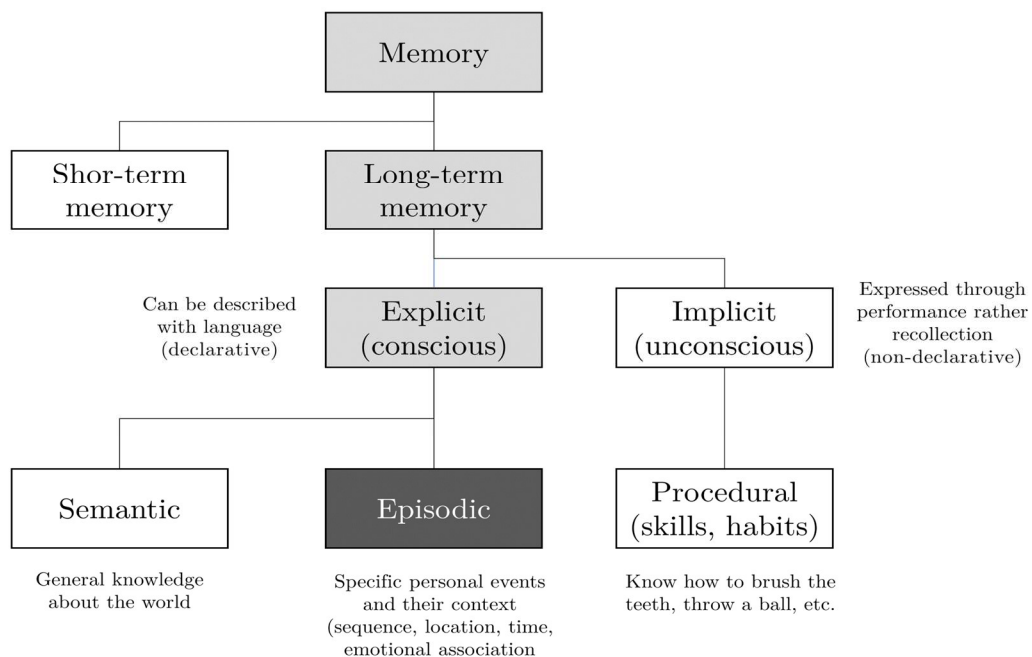


Figure 7 – Taxonomy of Memory Systems

Note. Episodic memory is a type of explicit and declarative long-term memory that is related to the retrieval of personal experienced events and their context.

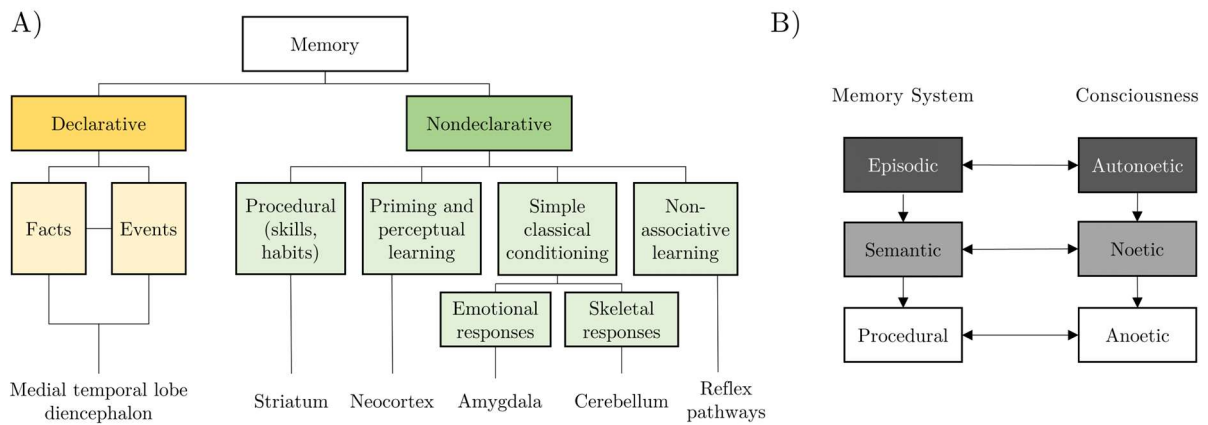


Figure 8 – Taxonomy of Long-Term Memory and Arrangement with Consciousness

Note. **A)** Taxonomy of long-term memory systems as proposed by (Squire & Zola, 1996). **B)** Schematic arrangement of long-term memory systems and kinds of consciousness as proposed by (Tulving, 1985a).

Zola, 1996). Furthermore, Tulving (1985a, 1985b) suggested a theoretical framework which consists of three hierarchical ordered subsystems according to the order of emergence in ontogeny and that links the procedural, semantic, and episodic memory system with types of consciousness (Figure 8B). It is important to note that, in the

transition from procedural to episodic memory, memory is linked to an increasing level of awareness. In contrast to procedural memory, which is anoetic, semantic memory is noetic and thus accessible to consciousness. However, any context at encoding remains dissociated from the memory (e.g., “riding the bicycle requires keeping balance, but I do not remember how I learned it”). Episodic memory includes such context from remembered events of the personal past. These memories are characterized by a reliving of their context of acquisition and a strong mental imagery. They are called *auto-noetic* (“auto” is Latin and means self) because they are not only accessible to consciousness, but also enable us to become aware of one’s own identity, through the mental experience of one’s past, as well as through projection into the future.

Accordingly, the episodic memory system is responsible for recording events experienced by the self, which can be consciously recollected through auto-noetic consciousness or mentally traveling in time. Such retrieval of episodic memories is based on re-experiencing phenomenal details and context, which also involves the subject (“the traveler”), and its subjectivity. We constantly experience our world from the first-person perspective which defines the egocentric reference frame that is

fundamental for episodic memory (Bergouignan et al., 2014; Hommel, 2004). It is a characteristic of the minimal self (self-consciousness before reflection on the experience) that initiates the pre-reflective sense of being a subject of experience, distinct from the environment (Blanke & Metzinger, 2009; Vogeley & Fink, 2003). When recalling events, the episodic memory system allows the re-experience of a subjective first-person perspective stemming from the initial encoding context (Suddendorf & Corballis, 1997; Wheeler et al., 1997). Hence, the sense of self plays a central role in episodic memory throughout every phase of the memory process – from encoding to retrieval (see below) – enabling individuals to construct a sense of temporal continuity and personal identity.

The Serial-Parallel-Independent model (Tulving, 1985a), (Figure 9) divides the memory process into three different stages: encoding, storage, and retrieval. Encoding, which corresponds to the acquisition of information from the environment for storage, is said to be serial. In other words, encoding in the episodic memory system presupposes prior encoding in semantic memory, which in turn presupposes encoding in perceptual representation system. The storage of information, i.e., the maintenance of encoded information, is performed in parallel for each memory sub-system. This means that the associated information of each system is stored and finally retrieved independently.

Episodic memory is part of autobiographical memory which is about one’s personal history (Conway & Pleydell-Pearce, 2000). The difference is that episodic memory is specific to the recollection of unique events while autobiographical memories may also

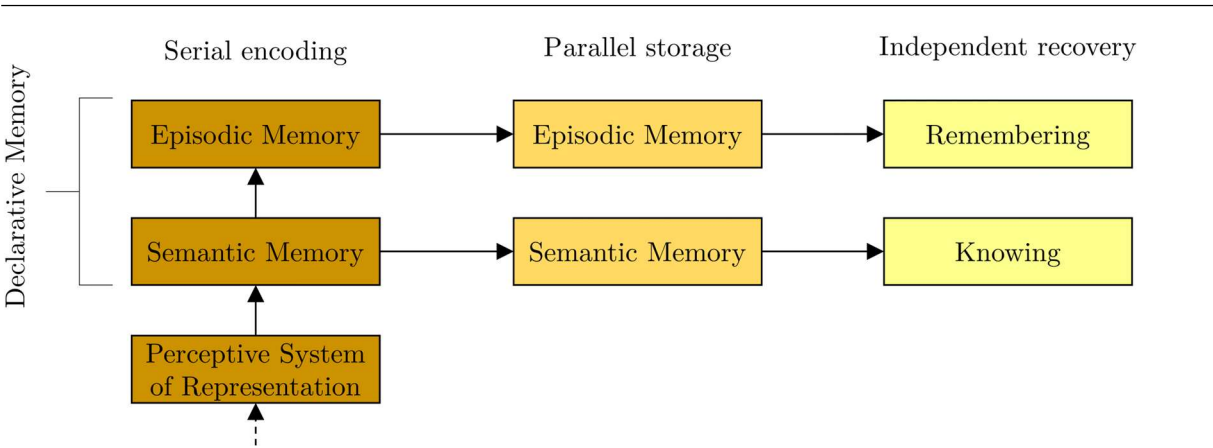


Figure 9 – Serial-Parallel-Independent Model

Note. Relations between episodic and semantic memory according to Tulving (1995a). Episodic memory relies on semantic memory which in turn relies on the perceptive system. Episodic and semantic memory are processes in parallel and independently retrieved leading to the phenomenon of “remembering” (contextual retrieval) and “knowing” (feeling of familiarity).

include generic facts. Thus, episodic memory is considered close to the notion of episodic autobiographical memory, which concerns most long-lasting, emotional, and self-relevant episodic memories, including mundane events rapidly forgotten (Piolino et al., 2009; Staniloiu et al., 2020). Hence, episodic memory is distinguished from generic autobiographical memory as well as from other types of memory by its particularly rich content. The information present in episodic memory is not encoded on its own but is associated with other contextual information characterizing both the situation in which the information was encoded, and the individual's mental state at the time of encoding. Thus, the event is associated with factual, idiosyncratic, spatial, and temporal information. When recalled, the event may be associated with high sensory vividness, thanks to mental visual imagery, which may include diverse other details (e.g., sounds, smells, touch, feelings). Event memory retrieval is thus less like a simple recall of knowledge, and more like a mental journey enabling the subjective reliving of the event. During such *mental time travel*, episodic memory involves a subjective awareness of the continuity of the self across time. This form of memory has an obvious evolutionary interest, as it enables us to remember what we have experienced and when to avoid dangerous situations. Still, episodic memory also has a less obvious function, which is to aid projection into the future. Imagining future scenes is largely based on the memories we possess. Episodic memories and episodic future thinking are temporally linked to one another and help to promote the cohesion of the self, since they are recalled or imagined as if we were there.

Although episodic memory concerns the memory of experienced events, most laboratory studies assessed episodic memory based on simple stimuli and procedures (e.g., recognizing lists of words or images). This allows for a better experimental control from encoding to retrieval stages but may access memory processes that vastly differ in real-life settings and episodic autobiographical memory tasks (Marsh & Roediger, 2013).

3.1.2 Processing stages

Episodic memory can be divided into three different information stages at which the memory is processed: encoding, storage, and retrieval.

3.1.2.1 Encoding

Encoding refers to the process of memorizing new information. For a memory to be recalled, it needs first to be encoded. This might happen either automatically or in a controlled fashion (Hasher & Zacks, 1979). Automatic encoding is incidental and occurs

spontaneously without the use of specific strategic processes. On the contrary, controlled encoding is voluntary and needs the deployment of attention resources and may involve the use of strategies (Taconnat et al., 2007, 2009). Though controlled encoding is more effortful than its automatic counterpart, it is characterized by stronger information processing, which enhances the chances of subsequent recall success (Craik & Tulving, 1975). It was noted, though in many memory experiments participants are asked to learn new items voluntarily, most encoding of personal events is spontaneous (Goetschalckx et al., 2019; Hale et al., 2020; Köster et al., 2014; Vingerhoets et al., 2005), probably due to cost minimization.

The success of an information to be encoded or not depends on how profoundly it is processed. Such encoding depth is a critical component of information processing and is determined by the type of information processed. If a word, for example, is visually presented, only structural features (form, color) may be processed (shallow encoding). On the contrary, deep encoding involves semantic meaning and further associations, such as its relationship to the self-concept or its use, e.g., “that is a very French common word”. The more attention and cognitive resources are allocated at the moment of learning, the greater the encoding depth. Moreover, deep processing implies association processes that relate the information to already encoded information. Deep encoding increases the chance that a memory trace is formed (Galli, 2014). Other important factors of encoding success are the amount of information to learn, their repetition, as well as perceptive and semantic similarity (Atkinson & Juola, 1973). For example, viewing a stimulus that is very distinct from its encoding or retrieval context (presence of similar stimuli) increases its chance of being recognized later.

Information is treated in relation to each other. Specifically, episodic memory contains information that is kept in context with additional information linked to the content (What, Where, When). Memory recollection depends on the binding (i.e., connecting memory features such as objects, persons, etc., to a whole) of such information at encoding (Diana et al., 2007; Yonelinas et al., 2019). Binding gives coherence between information and allows for complex memories. It can take place between different properties of the stimulus (e.g., form, color, lexical meaning) or between the stimulus and its context (e.g., position, feeling).

Encoding is related to brain activation depending on the nature of the information and the mental operation performed (Buckner et al., 2000). Left prefrontal structures are activated during more elaborative processing, increasing recollection success (Tulving

et al., 1994). Lesion studies showed that damage in the PFC reduces encoding probability (Wheeler et al., 1997). Encoding also involves the hippocampus and other temporo-medial structures (Eichenbaum, 2004; Eichenbaum et al., 1994; Squire & Zola-Morgan, 1991). The hippocampus within the medial temporal lobe is responsible for the integration of information and thus binding processes at encoding (Diana et al., 2007; Henke et al., 1997). Please note that a more comprehensive description of large-scale brain networks involved in cognitive processes are detailed in Chapter 4.5.

3.1.2.2 Storage

Memory needs to be stored between encoding and retrieval. The storage, however, is not infinite; some memories are relatively preserved, but others degrade over time. Consolidation largely contributes to the persistence of long-term memory. Consolidation is the stabilization of memory, increasing its resistance to temporal degradation. It is divided into two types, “synaptic consolidation”, which is rapid consolidation taking place within minutes to hours, and “system consolidation”, which stabilizes the memory trace over long-term (Nader & Einarsson, 2010). Synaptic consolidation refers to the process of stabilizing the early memory trace, still unstable just after encoding, and transforming it into a long-term trace. Memories are encoded by synapses whose strength can be changed by learning. System consolidation, on the other hand, corresponds to the cerebral reorganization of long-term memory representations promoted by the hippocampus that moves information to the neocortex, thus becoming independent of the hippocampus. Accordingly, one should suppose that once consolidated, there is a temporally stable memory trace. Yet, there is evidence that consolidation is a dynamic process and prone to changes (Nadel et al., 2012). Two types of memory storage have been proposed: active and inactive (Lewis, 1979). Inactive memory implies a relatively stable storage that is little affected after consolidation. Contrary, active memory corresponds to newly encoded memories, as well as old memories that have just been retrieved. Active memories can be modified, then consolidated again. Thus, the reactivation of an old memory would lead to its reconsolidation (Alberini & LeDoux, 2013). During reconsolidation, the memory is again fragile and susceptible to modification and distortion (Hupbach et al., 2007; Scully et al., 2017). This transient instability of the memory during its retrieval into memory allows it to be updated and consolidated again, in order to maintain its relevance (Lee, 2009; Lee et al., 2017). The changeability of this phenomenon can be illustrated by the fact that a frightening memory can be modified during its

reactivation, in order to decrease the associated feeling of fear (Agren et al., 2012; Golkar et al., 2017; Liu et al., 2014). In this example, the instability of the memory, when it is reactivated, enables it to be modified and its emotional valence to be reduced. Thus, information stored in episodic memory is far from static, and is likely to undergo transformations as time passes. It is even possible, over time, for an episodic memory to be transformed into semantic knowledge, via the process of semantization. This phenomenon is characterized by a progressive decontextualization of the memory, associated with a disengagement of the hippocampus itself, in favor of consolidation in extra-hippocampal structures (Winocur & Moscovitch, 2011). Sleep has shown to play an important role in memory consolidation, such that sleep disturbances impair memory recall of newly encoded information (Rasch & Born, 2013). Moreover, previous findings demonstrate that post-encoding memory consolidation can occur at rest (Axmacher et al., 2008; Tambini & Davachi, 2013) and when engaged in a task with high frontal related processing demands but low hippocampal related processing demands (Varma et al., 2017, 2018) underlining the importance of memory re-accessing, for example during mind wandering, on memory retrieval (Wamsley, 2022).

3.1.2.3 Retrieval

Retrieval is the mnemonic process of recalling previously encoded information. Episodic memory retrieval is typically assessed through tasks such as free recall, where the participants retrieve previously encoded information on their own, or cue recall, where an item associated with the information is presented to promote recall. Finally, recognition involves presenting previously encoded information, mixed with distractors, which the participant must distinguish by indicating which are Old or New (Old/New paradigm).

Early theories of episodic memory retrieval postulated that the recognition process obeyed the rules of signal detection theory (Green & Swets, 1966). The similarity between an item and the information contained in memory, whether corresponding to the item in question or to “noise” generated by other similar items, will determine whether an item is considered to have been previously encoded or not. This process, known as familiarity, implies that greater exposure to a stimulus will make it more familiar, and therefore more likely to be recognized later. Correct recognition of an item will then be based on a decision criterion indexed on the strength of the memory trace (Verde & Rotello, 2007). Thus, items similar to the previously encoded item will be more likely to be incorrectly judged as having been encoded, as they share similar

characteristics and will be perceived as familiar. Recognition accuracy will therefore vary according to the ratio of correct answers/false alarms.

However, a number of studies have challenged this unitary conception of memory retrieval (Gardiner & Parkin, 1990; McElree et al., 1999; Yonelinas, 1999) in favor of a retrieval model based on two distinct processes: *recollection* and *familiarity*. Recollection would correspond to a conscious recall of encoded information, associated with a feeling of reliving the encoding situation, while familiarity would be a decontextualized recall. Gardiner (1988) sees this dissociation as characterizing two modes of retrieval, episodic memory on the one hand and semantic memory on the other, corresponding to the distinction between auto-noetic and noetic consciousness in retrieval (Tulving, 1985b, 1985a). In fact, as we have seen earlier, one of the characteristics of episodic memory is the setting up of mental time travel, enabling the subjective reliving of an event, which corresponds to the initiation of a recollective process. Conversely, semantic memory corresponds to the recall of decontextualized knowledge, potentially attributable to familiarity processes. The phenomenology associated with information retrieval would, therefore, characterize both the process used to access it and the type of memory involved (Gardiner, 1988; Tulving, 1989). Jacoby (1991) proposes another form of distinction based on the level of awareness associated with information retrieval. Recollective retrieval will be conscious and controlled, while familiarity-based retrieval will be unconscious and automatic. Finally, Yonelinas (1994) suggests that the two processes operate differently. Indeed, observation of ROC (Receiver-Operating-Characteristic) curves during recognition has revealed two types of profiles associated with the level of confidence when retrieving new versus old items. One is symmetrical, characterized by a Gaussian distribution of the confidence level at recognition for both old and new items, which explains well the level of familiarity according to signal-detection theory. The second curve is skewed with a large proportion of old responses and a high degree of confidence, which corresponds to the recollective responses. Recollection would be characterized by an “all-or-nothing” process, illustrating that if old information is retrieved, this would automatically lead to the recall of associated items, thus generating a high level of confidence. Conversely, if this threshold is not reached, no associated elements can be retrieved, and information retrieval will be based on familiarity.

These different perspectives use different methods to highlight a distinction between recollection and familiarity responses. Tulving (1985b) proposes to estimate recollection

and familiarity processes explicitly, by asking whether, after retrieving a piece of information, the participant remembers it (Remember - R) or knows that it was present (Know - K). In the former case, retrieval is associated with a reliving of the encoded information, with rich contextual details, while in the second case, the information is recalled without details and context, simply on the basis of a feeling of familiarity. Later, a third option (Guess - G) was added to further delineate the distinctions between R and K responses. This option, indicating an uncertain response, helps to reduce the variance due to random responses as well as inferential processes, which could be confused with K responses (Gardiner, Java, et al., 1996; Gardiner, Kaminska, et al., 1996). Hence the name of the test: the RKG paradigm (Remember - Know - Guess; for a review, see Gardiner et al., 1998).

Proponents of the existence of two memory retrieval processes draw on a large corpus of studies showing both behavioral and cerebral differences between recollection-based and familiarity-based recall. Different properties of encoding will influence the way material is recalled, such as the level of cognitive control or self-referential processing (see Chapter 3.3 and 4). For example, the level of processing at encoding will affect the two processes differently. The propensity to recollect is increased when the material under study is processed deeply (e.g., semantically) than when it is processed superficially (e.g., graphemically), whereas the number of familiarity-based recognitions does not differ between the two conditions (Gardiner, Kaminska, et al., 1996; Gregg & Gardiner, 1994). Similarly, the presentation of familiar material (e.g., famous music or popular music) generates more recollections than unfamiliar material (Gardiner, Kaminska, et al., 1996; Java et al., 1995). Furthermore, greater elaborative learning and cognitive effort lead to more recollections than familiarity-based retrievals (Dewhurst, 1999; Gardiner et al., 1994). These results, concerning operations different from encoding, show that recollection is a mode of retrieval representing a more accomplished encoding. The memory trace associated with a recollective memory is more specific than that associated with a familiarity judgment (Dewhurst & Anderson, 1999; Dewhurst & Conway, 1994). Beyond the particularities of encoding, the distinction between two processes contributing to retrieval is reinforced by the fact that information associated with recollection is preserved longer than that associated with familiarity (Yonelinas & Levy, 2002). Interestingly, information associated with a recollective experience can, over time, be retrieved based on familiarity, illustrating the degradation of memories over time and showing that, although distinct, the two processes interact (Knowlton & Squire, 1995).

From a neuronal point of view, the involvement of different structures has been demonstrated for these two processes. In particular, the hippocampus has been shown to be mainly involved in the recollective process (Daselaar et al., 2006; Düzel et al., 2001; Ranganath et al., 2004; Wan et al., 1999). Conversely, the perirhinal cortex is responsible for creating shared representations between stimuli, on which the familiarity process is based (LaRocque et al., 2013; Staresina & Davachi, 2008). Evoked potential analysis also supports a distinction between these two processes (Friedman & Johnson Jr., 2000; Mecklinger, 2000). However, it is to note that some authors still maintain that recollection and familiarity only correspond to two different levels of a single process corresponding to the strength of the memory trace (e.g., Berry et al., 2008; Dunn, 2008).

3.1.3 Assessment

In regard to the previous section, it thus proposes to study memory by recording participants response during retrieval of previously registered items; either by assessing Old/ New responses, or for a more fine-grained assessment by using the RKG paradigm (Gardiner et al., 1998). In the case of the former, a confidence rating can be drawn which can provide conclusions whether recollective or familiarity-based processes were in progress. It provides a proxy of metamemory, i.e., consciousness of the own memory process. For the assessment, conditions during the memory processing stages are crucial. The task may, for example, include material that helps to investigate essential cognitive processes underlying memory, among other cognitive functions, such as the self-referential processing system and cognitive control (see Chapter 3.3 and 4). For instance, participants can be asked to make judgements about encoded material (e.g., trait adjectives) whether it describes themselves or reminds them of another episodic memory, while they make statements for other stimuli in reference to others. By comparing retrieval responses between these two categories this would provide conclusions about self-referential memory.

Another special type of long-term memory is false memory that is particularly useful to assess memory control (more in Chapter 4.4). It is a form of memory distortion and describes the erroneous retrieval of an event that did not occur, or that is remembered differently in contrast to the actual event (Abichou et al., 2020; Roediger et al., 1998; Schacter, 1999, 2021). These commission errors are often held in memory with a high confidence level (Dehon, 2012), making them difficult to detect or eradicate. False memory arises from memory interference when correct retrieval of stored information

is hindered because true memory competes with other memories for cognitive resources. High relatedness between competing memories favors false memory production, a circumstance that is used by the Deese-Roediger-McDermott (DRM) paradigm (Deese, 1959; Roediger & McDermott, 1995) to assess false memory. In this paradigm, participants are instructed to memorize several lists of items during an encoding phase. The items in each list may either be strong semantical associates (e.g., “sit”, “table”; associative list) of a not listed item (e.g., “chair”) or be members (e.g., “kiwi”, “orange”; categorical list) of the same category (e.g., “fruits”), excluding the most prototypical item (e.g., “apple”). During a later recognition phase, additional, previously unseen lure items are presented that are either semantically related to learned list items (i.e., critical lures, e.g., associative list: “chair”, categorical list: “fruits” or “apple”) or semantically weakly to unrelated (i.e., distractors, e.g., “car”). False recognition of distractors and critical lures can be seen as forms of false memories. However, critical lures are much more likely believed to be truly memorized than distractors and thus their false recognition will provide a more sensitive index of false memory and its underlying processes.

Different explanations for the formation of false memories have been proposed, of which some (e.g., the fuzzy trace theory; Reyna & Brainerd, 1995) bring the semantic-level similarity to the fore, arguing that false memories are a result of overreliance on gist (i.e., essential meaning) and familiarity due to a lack of episodic details and distinctiveness at retrieval (possibly from stronger encoding of gist than verbatim information) and the existence of shared features between the false memories and recently encoded information. Another model, the Activation Monitoring Theory (Gallo, 2010; Roediger et al., 2001; Roediger & McDermott, 2000), proposes that false memories derive from implicit associative activation of non-presented critical lures during the processing of list items and errors in determining the source of information (e.g., perceptual details). In this regard, activating information, for example, at encoding or retrieval, also strengthens the representation of associated items (e.g., the critical lures), facilitating their false recognition. For these activated lures to be detected as false memories, source monitoring processes must be engaged to disentangle their origin from those of true memories, i.e., the perceptual details and spatiotemporal context in which they were previously encoded (Abichou et al., 2021, 2022).

3.2 Episodic Future Thinking

3.2.1 Definition and taxonomy

Future thinking, or its more generic terms prospection and future-oriented cognition, describes the capacity to envision the possible future. This broad concept envelopes a wide variety of cognitive functions which led to the development of a taxonomy to disentangle the conceptually different constructs (Szpunar et al., 2014). In this framework, future thinking is divided into episodic and semantic forms, analogous to the concept of long-term memory (see [Figure 7](#) p. 60), and into four different interacting modes: simulation, prediction, intention, and planning. Based on prior conceptual frameworks, it focused on relating memory to future thinking (Atance & O’Neill, 2001; Suddendorf & Corballis, 2007), and treats episodic and semantic forms equivalent to the previously described episodic and semantic forms of memory. Consequently, episodic future thinking relates to processes in relation to a specific autobiographical event possibly taking place in the future, whereas semantic future thinking refers to general and abstract states of the world or personal life in the future. In the following, we will put a focus on episodic future thinking, but it is to note that this taxonomy treats the difference between semantic and episodic forms not according to a strict categorical memory classification but as a continuum between most episodic and most semantic. In general models of autobiographical memory, research considers memories as a ratio of episodic and semantic details (Conway, 2005; Levine et al., 2002; Piolino et al., 2009) or a continuum with personal semantic memories ranging in the mid-field (Renoult et al., 2012). Hence, many, if not all, different instances of future thinking may constitute episodic and semantic components. Indeed, there is a stronger relationship between episodic and semantic memory during prospection (Duval et al., 2012), as semantic knowledge subserves episodic future thinking in organizing event details.

3.2.2 Episodic simulation

“Episodic simulation is the construction of a detailed mental representation of a specific autobiographical future event” (Szpunar et al., 2014). For example, before a trip to Paris, one might simulate possible events that might happen during the visit (e.g., eating a fresh croissant, being drawn by a street artist in Montmartre, or visiting a cabaret show in the evening). This process is closely related to the simulation of episodic past events, and likewise engages the hippocampus and other medial temporal lobe regions. Damage to these regions impairs episodic simulation, while semantic simulation

may still be possible (Addis & Schacter, 2012; Buckner, 2010). Semantic simulation, like semantic memory, subserves the thinking processes with prior knowledge but does not involve self-projection or the phenomenological experience of mental time travel. Episodic simulations may not necessarily be directed into the future, though they often are. For instance, simulations can be counterfactual (how situations might have turned out differently). Specifically younger adults generate more episodic details compared to older adults, likely due to the fragility of the episodic memory system and prefrontal cognitive decline in aging. Thus, assessing younger adults seems particularly interesting to study properties of episodic future thinking. Lastly, episodic simulations are crucial also for other future thinking modes. In this line Szpunar et al. (2014) proposes that creating episodic mental representations improves the effectiveness of prediction, intention, and planning.

3.2.3 Episodic prediction

“Episodic prediction is the estimation of the likelihood of and/or one’s reaction to a specific autobiographical future event” (Szpunar et al., 2014). For example, in anticipation of the trip to Paris, one may dither in determining whether one may succeed in ordering a croissant in a *boulangerie* and which sentiment talking in French may evoke. Predictions concern the outcome of the event, including anticipated feelings, rewards, or potential threats. While pondering about Paris might be pleasant, prediction of reoccurring traumatic event can be detrimental for one’s wellbeing. Research has shown that humans generally exaggerate predictions. They commonly expect that a future event will make them feel better or worse than they finally do (Wilson & Gilbert, 2005). One potential reason for such prediction errors is faulty episodic simulations (e.g., simulating an event more negative than it will be), whose repetitions will enforce the perceived likelihood (e.g., ruminative thinking about having an accident). Contrary, the same is also true for positive events and outcomes, what makes future simulations crucial for positive self-projection. Importantly, forming an expectation is associated with the attainment of personal goals (Oettingen & Mayer, 2002) whereas projections without predictions (e.g., during passive mind-wandering) decreases success (Oettingen, 2012).

3.2.4 Episodic intention

“Episodic intention is the mental act of setting a goal in relation to a specific autobiographical future event” (Szpunar et al., 2014). For example, before ending the trip in Paris, one may wish to get a little present for his/her loved one and thus sets

the goal of buying some aged *Comté* cheese shortly before setting off home. Forming such intends is an important aspect for the early-stage process of prospective memory which includes setting an intention and executing a task in the near future (Kliegel et al., 2007). The simulations of contextual information around the stated goals enhances prospective memory and facilitates goal-attainment.

3.2.5 Episodic planning

“Episodic planning is the identification and organization of steps needed to arrive at a specific autobiographical future event or outcome” (Szpunar et al., 2014). For example, before the trip to Paris, one devises a detailed plan about what places should be visited at what time and which steps needs to be taken (e.g., checking the weather, making a reservation for the cabaret, look up for a cheese store not far from the hotel). Specifically, the frontal lobe, which we will later see is strongly involved in executive control, plays an essential role in planning. Planning is a cognitively, were taxing processes that involves all previous future thinking modes. Consequently, those elements, for example how we simulate our future, will influence how we plan our life.

3.2.6 Assessment

Different approaches have been proposed to assess mental time travel or episodic future thinking in specific. A popular method is the “future fluency task” which consists in generating as many future events as possible within one minute (Coste et al., 2015; MacLeod & Byrne, 1996; MacLeod & Conway, 2007). This task mainly assesses the capability to retrieve generic future-related information, such as abstract goals and plans or repeated events. However, other tasks exist that allow a more fine-grained assessment of episodic detail and thus components of cognitive control and self-referential processing. A popular method, for example, is to evaluate the ability to construct mental representation of specific future episodes (Abram et al., 2014; J. M. G. Williams et al., 1996) or to generate episodic details once a specific event has been found (e.g., imagining precise sensory and contextual details, like who is the scene, where are they placed, or what one might feel during the situation; Hassabis et al., 2007). Specific future episodes in this context refer to unique events that take place in particular place (e.g., in the *patisserie* Cyril Lignac in Paris) at a specific time (e.g., at a cold December morning before going to work) that last a few minutes or hours, but no more than a day (e.g., buying a croissant and conversing with the bakery salesperson). Following such mental simulations, their phenomenological characteristics can be assessed using rating scales. For example, subjects can be asked to rate the

vividness of the mental imagery or amount of visual details (e.g., objects, persons, location), the emotional valence and other perceptual inputs (e.g., one could feel the pleasant crunch and warmth when imagining biting into the croissant) or self-related aspects such as personal importance (e.g., having a croissant from Cyril Lignac is part of the plan when visiting Paris), (D'Argembeau & Van der Linden, 2004, 2006; Szpunar & McDermott, 2008).

3.3 The Role of the Self

As already alluded in the previous sections, the self, such as self-perspective, plays a fundamental role in episodic memory system and, thus, also in episodic future thinking. The self is a broad and complex concept that has been subject to intensive philosophical and psychological discussion (Kircher & David, 2003; Metzinger, 2003b, 2003a). Here, we will first consider how the self is theoretically integrated in memory following the Self-Memory-System. Subsequently processes related to the self are highlighted from a neuroscientific perspective and how these can be measured in episodic memory and future thinking.

3.3.1 Memory and the self

The Self-Memory-System ([Figure 10](#)), proposed by Conway and colleagues (Conway, 2005; Conway et al., 2004; Conway & Pleydell-Pearce, 2000), is a conceptual framework that interconnects concepts of the self and executive processes (i.e., cognitive control; more on this topic in the following Chapter) with autobiographical memory.

“Within this framework memory is viewed as the data base of the self” (Conway, 2005, [Figure 10A](#)). The autobiographical memory knowledge base is hierarchically structured by two types of memory representations: autobiographical knowledge and episodic memories. This structure ranges from highly abstract over event specific conceptual knowledge to episodic memories. The self is conceptualized as an intricate collection of active goals and related self-images, collectively termed the working self (Conway, 2005). Executive processes function as a central executive system (similar to the central executive component of working memory discussed in Chapter 4.2.2) providing control for the working self over the information accessed in the autobiographical memory knowledge base during different processing stages, such as encoding and retrieval. The self, i.e., the conceptual self (e.g., possible selves, self-guides, attitudes, values, beliefs) and working self, selects information according to two principles: coherence and correspondence ([Figure 10B](#)). Coherence guides accessibility of memories to make the

memory consistent with the beliefs about, and knowledge of, the self (e.g., goals, self-image, values, attitude). It allows to keep a coherent, stable self that is able to operate efficiently, achieve goals, and is characterized by a strong positive sense of wellbeing and high self-esteem. On the contrary, correspondence refers to the need for memory representations to precisely map the real world (encoding all kinds of details). It thus allows us to keep in touch with reality in order to verify realness and plausibility of information. Demands of coherence (coherent and effective self) and correspondence (reality depiction) are weighed against each other to optimize retention for any given experience beneficial for fitness and survival. Maintaining such adaptive coherence forms the guideline for the working self, tasked with goal management, partly by influencing the construction of memories, and shaping their accessibility and inaccessibility (inhibition of access). In long-term memories, however, the principle of coherence pre-dominates to provide a profound grounding of the self in goal-relevant memories and self-defining experience, which subserve self-regulation (see Chapter 4.1) The relationship between the working self and long-term memory is reciprocal. While the working self modulates access to long-term knowledge, autobiographical knowledge can constrain what the self is, has been, and can be.

Episodic autobiographical memories can be either accessed directly (i.e., almost instantaneous retrieval through perceptual details like “the madeleine de Proust” phenomenon) or via generative retrieval. The latter is an iterative procedure following the search-evaluate-elaborate principle, where a cue activates part of the autobiographical knowledge base entailing an evaluative control process that stops or newly iterates a memory search cycle. In every newly iterated cycle, the knowledge base is searched with a cue elaborated on the basis of the preceding search. In this line of thought, semantic memories may enter iteration and be used as cues to focus the mental search toward an episodic memory. Generative processes, moderated by the central executive related to goals of the self, are not only limited to memory retrieval but also manage the memory formation involved in the encoding of new personal events or imagining the future (see for an example, Coste et al., 2015).

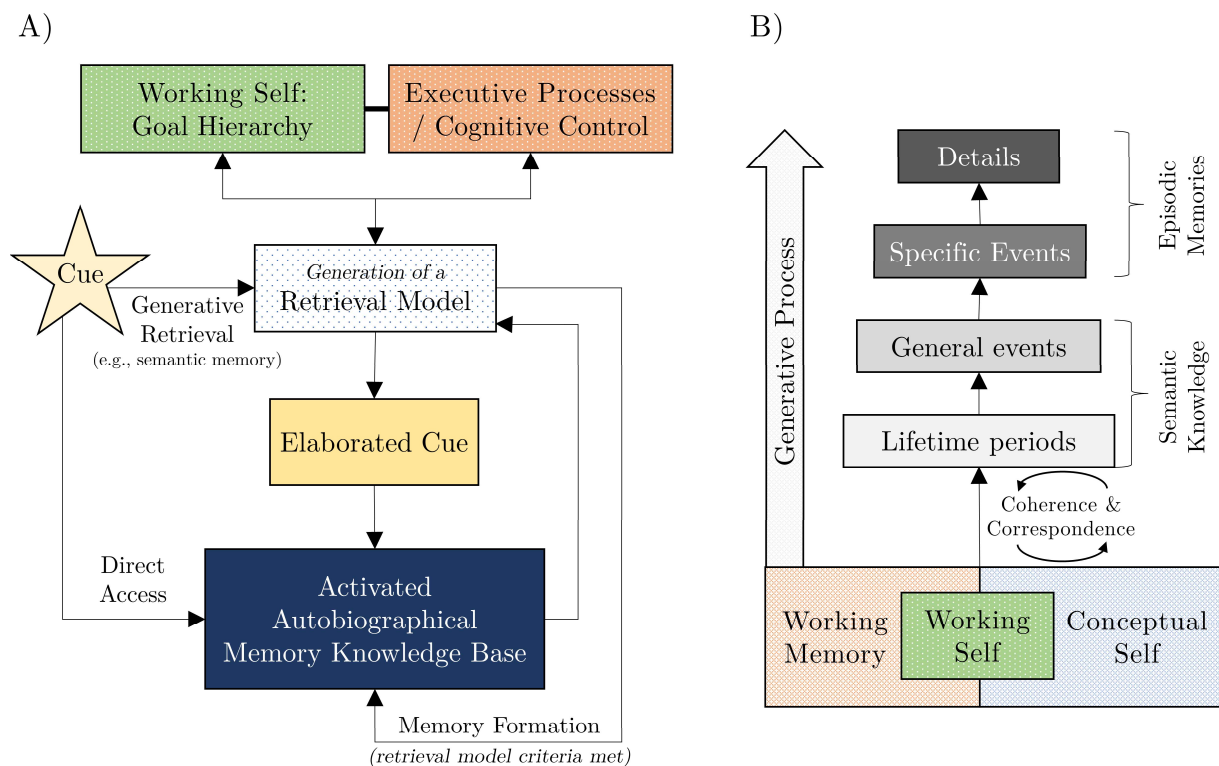


Figure 10 – The Self-Memory System

Note. **A)** Interaction between the working self, executive processes, and autobiographical knowledge base in the formation and retrieval of memories. Figure adapted from Conway (2005). **B)** Encoding and retrieval of semantic and episodic memories through a generative process through a central executive control system related to the goals of the self that is moderated by principles of coherence (coherent and effective self) and correspondence (reality depiction). Figure adapted from Conway & Piolino (2009) and Piolino et al. (2008).

3.3.2 Self-referential processing and cortical midline structures

Comprehensive models for the neurocognitive integration of self-referential (or here interchangeably with self-related) processes have been previously provided by Northoff and colleagues (Northoff et al., 2006; Northoff & Bermpohl, 2004; Qin et al., 2020). According to their definition, “self-referential processing accounts for distinguishing stimuli related to one’s own self from those that are not relevant to one’s own concern” (Northoff et al., 2006). Findings originate primarily where neuroimaging data was compared between behaviors that were self-referential (e.g., judging one’s character), non-self-referential (e.g., judging whether a trait-adjective is desirable in society) or other-referential (e.g., judging a person they know but never met). Overall, the authors provide very consistent evidence that self-referential processing is rooted in the activity and connection between structures of the cortical midline.

In their early work (Northoff & Bermpohl, 2004), they identified four distinct regions of the cortical midline associated with four different functions: representation (orbital and adjacent medial PFC), monitoring (pre-/sub-/supragenual ACC), evaluation (dorsomedial PFC), and integration (posterior cingulate cortex). Representation is associated with cognitive functions such as self-judgment or thinking about one's own personality. The orbital and adjacent medial PFC is also associated with the general presentation of emotional stimuli and is responsible for the integration of emotions with representations. Monitoring refers to the tracking of one's own behavior or performance. Evaluation comprises the judgement of the ownership of a process or characteristic (e.g., this is my voice). Finally, the last function is the integration of self-referential information with the concept of the self (e.g., judging whether a trait-adjective describes the own person, retrieval of autobiographical memories whose context is rich in personal information).

In a subsequent meta-analysis, Northoff et al., (2006), identified three clusters corresponding to the ventral, dorsal, and posterior cortical midline structures, which activate across all functional domains (e.g., verbal, emotional, memory).

- **Dorsal**: This part includes the pre-/sub-/supragenual ACC, dorsomedial PFC and is linked to reappraisal and evaluation in the context of non-self-related stimuli.
- **Ventral**: The cluster in the front part of the cortex includes the orbital and adjacent medial PFC, ventromedial PFC, posterior ACC, and is concerned with the coding the “self-relatedness of stimuli” and “degree of self-referentiality of thoughts” (Northoff et al., 2006). This cluster crucially links exteroceptive and interoceptive information for outside inside the internal *milieu* of the body.
- **Posterior**: This network, situated further to the back of the brain, is comprised of the posterior cingulate cortex, retrosplenial cortex, medial parietal cortex. Together, they provide temporal context to thought by connecting self-referential stimuli with past self-referential stimuli (e.g., during episodic memory).

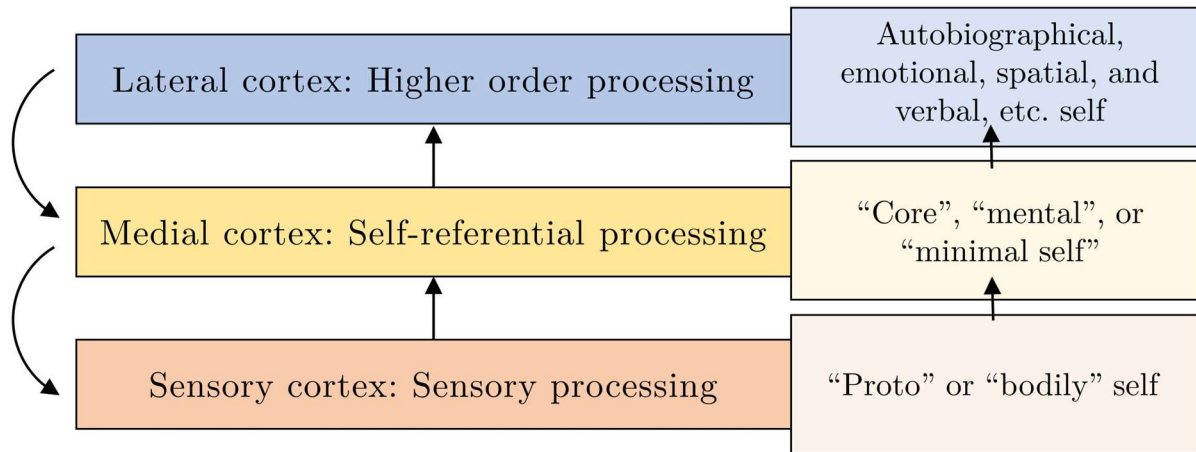


Figure 11 – Three-Layer Model of Self-Processing

Note. Three-layer model according to Northoff et al. (2006) by which information relevant to the self is passed from the sensory cortex over the medial cortex to lateral cortex that represent different level processing levels of the self.

The cortical midline structures connect to cortical and subcortical structures, which led to the suggestion of an intermediary role of self-referential processing between sensory and higher-order cognitive processing. The authors posited that a three-layer model (sensory, experiential, high-order) explains the allocation of self-relatedness to internal and external states ([Figure 11](#)).

In their more recent framework and meta-analysis they elaborated on the three-layer model connecting sensory and cognitive processing in a hierarchical structure (Qin et al., 2020). They stipulated that cortical midline structures represent a “gradient organization in self-processing, through which body-environment information is integrated for the self via propagation from Interoceptive processing to Mental-self-processing” (Qin et al., 2020). In other words, sensory signals informing about the inner body state (interoception) are linked to sensory signals about the environment (exteroception) and integrated by the higher order mental-self-processing system. At the base of this organization is the interoceptive processing at the level of the insula. Interoception integrates sensory information from internal (body), such as cardiovascular variables, and external (outer world) environment for self-processing. According to this model, self-consciousness arises from interoception (i.e., sensory information about internal body state). Exteroceptive processing system then links the internal and external environment. Structurally, it envelopes the interoceptive

processing system, adding additionally the temporal-parietal junction, antero-medial PFC, and premotor cortex. These help to associate the projection of one's own bodily signals (e.g., biofeedback) to the self by linking multisensory signals (you watch your hand touching an object and know it is your hand). Finally, mental-self-processing at the top of the hierarchy includes all lower-level structures and the ventromedial PFC, dorsomedial PFC, and posterior cingulate cortex. It attributes self-relatedness to external mental or virtual stimuli other than bodily signals, such as episodic memories, one's character or name. It thus incorporates interoceptive, exteroceptive information and integrates it with the external non-body environment to give self-related meaning.

This structure forms the basis for various different kinds of self, such as the “pre-reflective self” (S. Gallagher & Zahavi, 2020; D. Legrand, 2007), or “minimal self” (Blanke & Metzinger, 2009; H. L. Gallagher & Frith, 2003; S. Gallagher, 2000) which describe self-consciousness before reflection on the experience (e.g., knowing where your hand is in space without thinking about it). More importantly, the described models explain the interaction of the self in different behaviors such as memory or future thoughts. In total, it provides a neural basis on how memory and thoughts become integrated with the self, reflecting the degree of self-relatedness.

Besides the hierarchical three-layer model, further neuroanatomical models exist that may underlie the influence of the self on memory and future thinking. For instance, the Self-Attention Network (Humphreys & Sui, 2016) has been tightly related to self-referential processes involved in memory (Kelley et al., 2002; Macrae et al., 2004; Martinelli et al., 2013; Northoff et al., 2006). The model proposes that the ventromedial PFC activates upon self-relevant stimuli and drives attention by activating the posterior superior temporal sulcus towards self-stimuli, causing a self-bias in perception and attention. For example, it would explain why hearing your own name in a noisy environment captures your attention, whereas another unfamiliar name would not. Furthermore, a top-down attention control network involving the dorsolateral PFC and intraparietal sulcus can either reinforce or suppress attention orientation towards the self. Accordingly, the interaction between activity of the ventromedial PFC and its interaction with the dorsolateral PFC would determine the amount of attention resources allocated towards self-relevant stimuli or thought and how well it is memorized.

It thus becomes obvious that a large structural network exists that influences memory and future thinking alike by linking and integrating information with different types of

self. Autobiographical memories that are by definition self-relevant show strong involvement of the medial PFC and particular the ventromedial PFC (Cabeza & Jacques, 2007; Gilboa, 2004; Maddock, 1999; Maddock et al., 2003). Such activation has for example been shown in the above studies when investigating self-referential memory through self-encoding of personality traits (see following section). Since medial PFC activation has been found during encoding and retrieval, it has been suggested that self-referential processing might operate at both memory stages. This is an interesting aspect, since it allows the assessment of self-referential processing based on different paradigms (e.g., self-referential encoding, self-referential episodic future thinking).

3.3.3 Self-reference manipulation in thought

The most well-known paradigm for studying the role of the self in episodic memory is the self-reference manipulation (Klein, 2012; Rogers et al., 1977; Symons & Johnson, 1997). By linking new to-be-remembered information to the self, either via its narrative component (e.g., pre-stored self-knowledge and autobiographical memories) or its minimal component (e.g., the “I” who is experiencing “here and now” or the body self), (H. L. Gallagher & Frith, 2003; S. Gallagher, 2000) subsequent memory retrieval success is enhanced; a phenomenon known as the Self-Reference Effect. This effect persists in healthy aging and cognitive impairment such as Alzheimer's disease (Lalanne et al., 2013; Leblond et al., 2016) but not in schizophrenia which is known to disturb the self-representation (Compère et al., 2016).

Previous findings suggest that the self-reference effect is mainly linked to processes taking place during encoding when memories are generated (Kalenzaga et al., 2015; Morel et al., 2014). However, it is also possible that during consolidation and retrieval, memory traces are manipulated by re-accessing or re-association in the context of the self, which might increase the self-relatedness of an initially non-self-referential memory. This is particularly important, as information can change its degree of self-relatedness and thus personal relevance after initial encoding, e.g., when recalling or implementing a memory in future thought it becomes more or less self-relevant.

Memory of episodic events is also improved when events simulated in the future integrate autobiographical knowledge (Jeunehomme & D'Argembeau, 2021). The study conducted two experiments which showed that event recollection was better for future simulations of the self compared to simulations of an acquaintance, and when self-

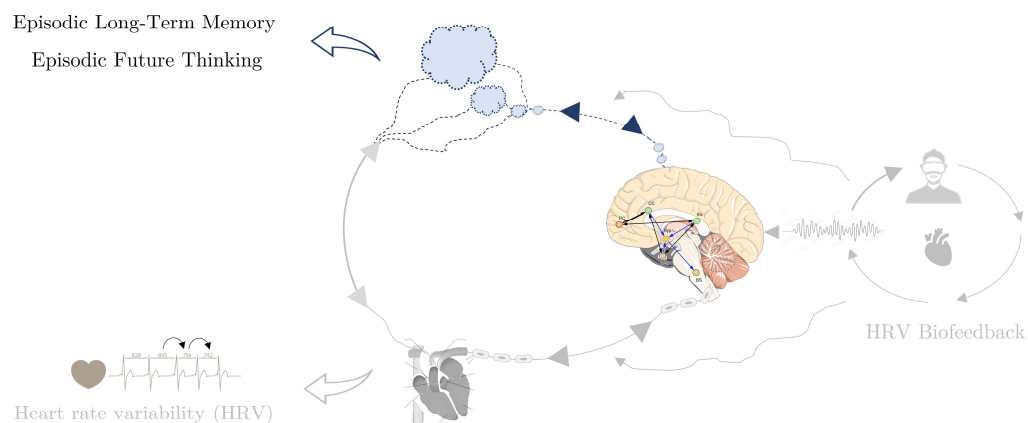
related simulations involved a personal goal compared to when it involved no goal. During recall, self-reported phenomenological characteristics (e.g., level of detail, emotional valence, etc.) were assessed, of which the following were especially affected by self- and goal-relatedness: vividness, visual perspective (first-person vs third-person), emotional valence and intensity, probability of occurrence, and personal importance. It thus can be assumed that future thinking also engages self-referential processes when it engages self-relevant information, which is visible in changes in phenomenological characteristics of the remembered event.

Regarding the three-layer model, self-referential processing would be part of mental self-referential processing and is reflected in the activity of the cortical midline. Integration of sensory contextual information with self provides more context and thus richer episodic memory trace. Especially the ventromedial PFC has been reliably linked to the Self-Reference Effect (for a meta-analysis on brain structures underlying the declarative self, specifically episodic autobiographical memory; Martinelli et al., 2013). Patient studies showed that ventromedial PFC brain damage eliminates that Self-Reference Effect for both judgment of the present and future thinking (i.e., judging the future self), (Stendardi et al., 2021).

3.4 Chapter Summary

- The declarative long-term memory contains semantic memory (facts, knowledge about the world) or episodic memory (personally experienced events).
- Autobiographical memories are detail-rich memories of the personal past (abstract knowledge and specific events).
- Episodic (autobiographical) memories are characterized by autonoetic consciousness or recollective experience of the event and its spatio-temporal, emotional context and thus specific and detailed re-experience or “reliving”.
- Memory processes are encoding (initial memorization of new information), consolidation (strengthening memory trace), and retrieval (access).
- Future thinking is the capacity to envision the future which strongly relies on long-term memory and also contains semantic and episodic components.
- Episodic memory and episodic future thinking are both forms of mental time travel (i.e., re-experience, pre-experiencing). Both processes recruit the medial-temporal lobe, notably the hippocampus.
- The self is a fundamental feature of mental time travel. This has been highlighted in the Self-Memory System (SMS) model as well as a large neural base linking the self-processes to cortical midline structures.
- Cognitively, the SMS links the long-term memory system with self-processes (e.g., goal, self-concept representation) and cognitive control.
- Neuronally, sensory interoceptive and exteroceptive information are processed and integrated into mental self-projection, such as episodic autobiographical memories, most notably at the ventromedial prefrontal cortex.
- The neural basis also indicates important projections to emotional processing.
- Episodic thoughts are shaped by self-referential, emotional, and executive processes that guide self-regulation.

4 Chapter 4 – Cognitive Control over Thought



Episodic memory and episodic future thinking are very dynamic processes that underly a variety of mechanisms. In this chapter, we will highlight the role of self-regulation and associated cognitive control in these thought processes. Finally, major brain networks underlying self-referential processing, cognitive control as well as autonomic control will be reviewed providing a basis for the integrative review in the following chapter.

4.1 Self-Regulation

Self-regulation refers to the ability to manage and control one's thoughts, emotions, and behaviors. It is a multifaceted psychological construct that encompasses processes through which individuals actively manage, monitor, and modulate their thoughts, emotions, and behaviors in order to attain desired goals, adhere to internal or external standards, and adapt to changing circumstances. It involves, besides a sense of self (Chapter 3.3), executive functions such as attention, inhibition, and planning, as well as the ongoing evaluation and adjustment of one's actions based on feedback and internal or external cues. Self-regulation is crucial for maintaining attention, overcoming impulses, and navigating complex social and cognitive tasks. It often involves the coordination of cognitive, emotional, and motivational resources to achieve optimal functioning and well-being across various domains of life. Therefore, it also plays a crucial role in regulating memory and future thought processes by influencing the new acquisition and retrieval of episodic memory including episodic autobiographical memory. Theoretical frameworks for self-regulation draw on concepts from cognitive psychology, neuroscience, social psychology, and other disciplines to

understand the underlying processes and mechanisms that contribute to effective self-regulatory behavior. Differences in self-regulation capacities occur in individual which have been highlighted by ego depletion and the strength model of cognitive self-regulation (Barutchu et al., 2013; Hagger et al., 2010). In this line, self-regulatory or self-control capacities can be depleted, for example by effort and fatigue, and be replenished, for example through rest or glucose intake. Thus, self-regulation is considered to draw upon a common resource that underlies individual differences, often exemplified in analogy to a muscle or battery that can tire/ be empty and recover. Importantly, self-regulation and its far-reaching consequences. Motivation plays in this context an important role since subjects that are highly motivated to perform well (nor not to give in urges) shows to reduce depletions effects and increase task performance (Wehrt et al., 2022). Besides incentives and motivation, self-regulation heavily draws on cognitive control capacities. In the following, we will highlight the role of cognitive (or executive) control which is a cornerstone to self-regulation and thus the regulation of thought.

4.2 Cognitive Control

Cognitive control is the process by which behavior is adapted according to goals, plans, and contextual knowledge. Also called executive control, this process supports flexible, adaptive responses and complex goal-directed thought through the selection and monitoring of behaviors and regulating and coordinating attention-, memory-, and action-related functions (Kok, 2022). Various terms have been employed to characterize the underlying ability that influences performance on complex cognitive tasks, including executive control (Logan, 2003), attentional control (Balota et al., 1999), controlled attention (Engle et al., 1999), and inhibitory control (Hasher et al., 2007). Executive functions, as a description of cognitive control, have emerged from an approach that incorporates the large number of cognitive functions involved into a conceptual framework. Many models of executive functions have been proposed (Diamond, 2013; Goldstein et al., 2014; Miyake et al., 2000), none of which completely dominates over all others, but all emphasized the role of a supervisory executive center. Norman & Shallice (1986) proposed a framework of attentional control of executive functioning. The Supervisory Attentional System is a higher-level mechanism that monitors conscious, deliberate planning of actions, and novel situations. The Supervisory Attentional System is involved in the executive component of working memory, which is assumed to be an attentional control system responsible for strategy

selection and for control and coordination of the various processes involved in short-term storage and more general processing tasks (A. Baddeley, 1986). More recently, some research has highlighted the key role of three core executive functions: inhibition [including inhibitory control over responses and interference control (selective attention and cognitive inhibition)], updating in working memory, and cognitive flexibility (Diamond, 2013; Lehto et al., 2003; Miyake et al., 2000). Some others emphasized the concept of attentional control, the capability to choose and sustain attention to what we want to concentrate on, and what to ignore (Müller-Oehring & Schulte, 2014). While many executive functions have been identified, a large cross-sectional study provides support that executive functions and working memory underly a unitary construct (McCabe et al., 2010). This unitary character has been ascribed to the central executive component of working memory (A. Baddeley, 1986), the central executive of the supervisory attentional system (Norman & Shallice, 1986; Shallice & Burgess, 1996). This does not exclude that different executive functions tasks measures different task-specific cognitive abilities, but rather implies that all of them rely on a common factor, the ability to control attention during goal directed activity, which has been termed “executive attention” (McCabe et al., 2010). Cognitive tasks relying on executive functions, such as inhibition and double task tasks, are associated with PFC activity (Miller & Cohen, 2001; O’Reilly, 2006) and prefrontal-subcortical functional connectivity (Gangopadhyay et al., 2021; Salzman & Fusi, 2010; Yizhar & Klavir, 2018). Indeed, the term frontal lobe functioning has been used in place of cognitive control when describing the cognitive functions associated with the voluntary control of behavior (Carlson, 2005; R. T. Knight & Stuss, 2002; Salthouse et al., 2003). Frontal-lobe functioning is also associated with other higher-level functions such as social behaviors, including emotion regulation and impulse control (Gray et al., 2009) as we have seen in the previous chapter, to episodic memory and future thinking.

4.2.1 Control processes

From the above section, it is clear that cognitive control and the central executive encompass several conceptually distinct processes. For a better overview, some important ones are listed below:

- **Executive functions** , a key component of cognitive control, encompass higher-order cognitive processes responsible for goal-directed behavior. These include working memory, inhibitory control, and cognitive flexibility (Diamond, 2013).

- **Working memory** allows the temporary storage and manipulation of information necessary for complex cognitive tasks. This also includes goal maintenance, which involves keeping relevant information active in working memory to guide behavior toward the achievement of a specific goal (A. Baddeley, 1986).
- **Inhibitory control** involves the ability to suppress or inhibit irrelevant or inappropriate responses. This is crucial for maintaining attention and avoiding impulsive behavior (Hasher et al., 2007).
- **Cognitive flexibility** refers to the ability to adapt and switch between different tasks or mental sets in response to changing environmental demands. It is crucial for problem-solving and response to novel situations (Monsell, 2003).
- **Attentional control** is a critical aspect of cognitive control, involving the ability to focus attention on relevant information while ignoring distractions (Posner & Petersen, 1990).
- **Planning** and **problem-solving** involves the ability to formulate and execute plans, solve problems, and achieve goals. It encompasses strategic thinking and organizing actions toward a specific outcome (Shallice et al., 1997).
- **Fluid intelligence** refers to the ability to think and reason abstractly, solve novel problems, and adapt to new situations independent of acquired knowledge. It involves the capacity to identify patterns, make inferences, and generate creative solutions in unfamiliar contexts. While fluid intelligence is considered to be relatively independent of prior learning and experience crystallized intelligence involves the application of learned knowledge and skills (Cattell, 1963).

4.2.2 Working memory

Baddeley developed the notion of working memory which considers the active form of short-term memory that conceptually puts a stronger notion on the manipulation of information before long-term entry. It is involved in encoding and retrieval of long-term memory and is thus crucial to episodic memory. It is to note, though, that a parallel conception has been proposed according to which sensorial input and parallel entry is possible in short-term and long-term memory. For example, single-case studies in patient K.F. showed that traumatic brain injury diminished short-term memory capacities but left the long-term memory system intact (Shallice & Warrington, 1970; Warrington & Shallice, 1969). Consequently, it is possible that some information is processed directly in the long-term memory system without prior treatment. Working memory has been divided into three subcomponents that are the phonological loop

(verbal working memory), visuospatial sketchpad (visual-spatial working memory), and central executive (A. D. Baddeley, 2000; A. D. Baddeley & Hitch, 1974). Verbal and visual-spatial processing takes place independently and is guided by the central executive, which selects and executes the processing operations to be carried out by attentional control. Additionally, the so-called *episodic buffer* links manipulated information from all subcomponents with information from long-term memory (A. Baddeley, 2000, 2003). The established associations between perceived and past information improve efficiency in storing and retrieving information. Consequently, working memory can be seen as the main entry port of information into long-term memory, whose processing operations determine encoding success. Empirical studies showed that disturbances of working memory led to lower recall success of studied information (Ranganath et al., 2005), and negatively impact the encoding of contextual information (Plancher et al., 2018) and episodic memory (Unsworth & Spillers, 2010). Working memory processes, as well as the episodic memory system and episodic buffer, strongly rely on the PFC and hippocampal activity (Buckner & Koutstaal, 1998; Davachi & Wagner, 2002; Ranganath et al., 2005; Ranganath & D’Esposito, 2001). Specifically, the dorsolateral PFC is associated with encoding success (Blumenfeld & Ranganath, 2006). In addition, the hippocampus is involved in the creation of rich associative binding between processed information, creating the context necessary for episodic memory (Bergmann et al., 2012; Davachi & Wagner, 2002; Yonelinas, 2013). Memory encoding and, thus, its later recall success, is dependent on working memory capacities associated with the prefrontal and feature binding dependent on hippocampal activity. Working memory also affects memory during retrieval. Unsworth and colleagues posit that the efficacy of retrieval hinges on the capacity to confine the memory search to pertinent information exclusively (Unsworth, 2007; Unsworth & Engle, 2007). Their research indicates that individuals with low working memory capacity exhibit heightened vulnerability to distractions or irrelevant stimuli, preventing retrieval of pertinent information. Unsworth et al. (2012) assert that individuals with high working memory capacities not only excel in generating a greater number of retrieval cues, thereby providing a more expansive context for memory search, but also demonstrate adept strategic control over the search process within these contexts. Consequently, this results in swifter, well-organized, and resourceful retrieval. Working memory and episodic memory performance are very closely related across adulthood (McCabe et al., 2010; Piolino et al., 2009). Consequently, working memory is also important for future thinking. By the same principles in episodic

memory, working memory is required for manipulating extracted episodic details (de Vito et al., 2012), and scene construction (Hassabis & Maguire, 2007), which are prominent features of episodic simulation (Szpunar et al., 2014). Since working memory has limited capacities, it is necessary to filter and select relevant. This is realized by attention and inhibitory control functions.

4.2.3 Attention

Attention is what we typically understand as focusing our awareness on a certain stimulus while ignoring others. It is thus strongly tied to inhibitory control functions that aid in suppressing prepotent stimuli or stop ongoing actions. Different theoretical models have been proposed to characterize attention.

An early theory, the *filtering model* (James, 1890), assumes that all sensory information is received, but that filters are applied to the perceived information based on the characteristics of the stimuli, so that some information is received by subsequent cognitive processes (working memory, semantic processing) and some is not. In this line, these filters are needed to cope with the overwhelming amount of information by selecting and inhibiting relevant information.

According to the *capacity model* (Kahneman, 1973) attention is a limited reservoir of resources. These resources can be distributed on different tasks or environmental stimuli, allowing for multi-tasking, or be grouped on a particular task or stimuli increasing the attention to this point (focalized attention) and decreasing attention to allocated to other stimuli. Resource allocation is controlled by two types of processes: top-down (attention driven to stimuli by executive control), bottom-up (attention is captured automatically, e.g., through saliency). Both require executive control to maintain attention focus on the object and reduce interference from other information (Hopfinger et al., 2000).

A more comprehensive model is provided by the theory of *attentional networks* consisting of three interconnected networks that differ in behavioral characteristics and underlying neural basis (Posner & Petersen, 1990). These networks are posited to be responsible for various attentional functions, each contributing to the overall cognitive processing of information. The model typically identifies three primary attentional networks: Alerting, Orienting, and Executive control. The alerting network is responsible for enhancing and maintaining a vigilant state of readiness. It involves the regulation of overall arousal and preparedness for sensory input, enabling individuals

to respond more efficiently to incoming stimuli. The orienting network directs attention to specific information among multiple sensory stimuli. It facilitates the selection and prioritization of sensory input by orienting sensory receptors toward relevant stimuli, thereby enhancing the processing of selected information. As in the capacity model, orientation can be exogenous (bottom-up), i.e., reflexive, and automatic attention in response to stimuli (e.g., a spontaneous thought captures your attention), or endogenous (top-down), i.e., voluntary and goal-driven attention (e.g., actively reflect) which tonically inhibits exogenous orientation. The executive control network is involved in the monitoring and resolution of conflicts among competing stimuli and the coordination of multiple cognitive processes. It plays a crucial role in goal-directed behavior, response inhibition, and the management of cognitive resources. It strongly relies on parts of the PFC and cingulate cortex, especially the anterior part (see for a review, A. Raz & Buhle, 2006). ACC engagement has been observed during conflict monitoring and emotional evaluation of conflict, but it remains unclear whether it resolves or monitors conflict. It has been found that the ACC triggers prefrontal activation, especially in the dorsolateral region, and activates before and after the dorsolateral PFC response, which suggest it plays a role in predictive coding (comparing obtained and predicted outcome).

Attention also plays a critical role, besides long-term memory, for other executive functions such as working memory (see previous section). If memory storage in short-term memory is serial, information needs to be selected before entering. The filter model suggests that attention function as working memory entrance control (Raymond et al., 1992; Reeves & Sperling, 1986). Also, the active manipulation of information (e.g., recombination of elements) or its protection from interference (e.g., exogenous processes), is calling for attention through orientation and executive processes. Thus, attention ensures that the working memory is not overloaded, and maintains and manipulates its inherent information. Consequently, as attention is directly involved in working memory it also affects information transferred to or re-accessed from long-term memory. Moreover, attention activates the *recollection mode* (Lepage et al., 2000) when access to the memory trace representation system will be relatively automatic, thus allow for a faster and detailed memory retrieval for episodic event construction of the past (episodic memory) of future (episodic future thinking). Attention has also been found to strongly impact both incidental and voluntary encoding (Naveh-Benjamin et al., 2014; Naveh-Benjamin & Brubaker, 2019) such that greater attention will lead to more profound encoding and thus memory retrieval.

4.3 The Influence on Episodic Memory and Future Thinking

Episodic memory is an active constructive process that involves elaborative encoding, strategic search, evaluation, and verification of search results. In contrast to information retrieval due to familiarity, based more on associations of similar information, it is a far more costly process, and therefore sensitive to the influence of cognitive control and specifically attention. Indeed, episodic memory has been shown to strongly rely on executive functions, specifically attentional activity, including inhibition and working memory (Marchetti, 2014). Moreover, recollections draw from an autobiographical knowledge base which contains knowledge about the self (e.g., personal factual knowledge, episodic memories). In this context, Conway & Pleydell-Pearce (2000) proposed that autobiographical memory is generated within a self-memory system, composed of the autobiographical knowledge base and a working self. The latter consists of self-concepts, goal hierarchies, and other forms of self-knowledge and may function, similar to working memory, as a central control process to exercise inhibitory control over the knowledge base (Conway et al., 2004). Hence, the executive system is linked to the purpose of the self which selects which information is encoded or retrieved. The interaction between the working self and the autobiographical knowledge base is bidirectional. While the working self has the capacity to regulate the accessibility of autobiographical knowledge, the autobiographical knowledge base also limits the goals and self-images of the working self. The control by the working self is not limited to episodic memory encoding and retrieval, but expands in general to auto-noetic consciousness and recollective experience (i.e., mental time travel into future and past), (Coste et al., 2015). Consequently, the self-memory system (Conway, 2005; Conway et al., 2004; Conway & Pleydell-Pearce, 2000) demonstrates an interconnection between memory, self, and executive functions which will be reflected in measures of episodic autobiographical memory and episodic future thinking.

Indeed, executive functions were found to explain individual differences in episodic memory performance across the adult lifespan due to age-related decline (McCabe et al., 2010). As we have seen in the previous section, episodic memory and episodic future thinking are tightly linked since prospective scene construction is based on retrospective knowledge. Therefore, it seems logical that executive functions underlie future thinking similarly. D'Argembeau et al. (2010) showed using a principal component analysis in young, healthy adults a correlation of executive processes involved in organization and monitoring of retrieval with several episodic memory measures (i.e., fluency, amount of

episodic details, sensory descriptions) for events both in the past and the future. Another study showed that in traumatic brain injury patients impairments in episodic and semantic self-representation during episodic future thinking as past remembering were predicted by altered executive functions, and that in healthy controls episodic self-representation was mediated by executive functions (Coste et al., 2015). In addition, executive processes were associated with event specificity, but only for future events. The authors assumed from these results that “executive processes may support the strategic aspects of autobiographical knowledge retrieval (e.g., establishing retrieval goals, initiating and guiding search, monitoring and selecting retrieved information; Conway & Pleydell-Pearce, 2000; Rubin, 2006), which certainly play a key role in both remembering past events and imagining future events”. Furthermore, they surmised that “generating representations of unique episodes that are precisely located in space and time places higher demands on executive processes for the future than for the past. Additional executive processes may therefore be required for selecting a particular spatiotemporal context (among multiple possible contexts) that is plausible and coherent with other features of the simulated event (e.g., the persons involved)” (Coste et al., 2015). Those cognitive functions involved, including organization, selection, and monitoring of information, strongly rely on or overlap with the concepts of working memory, attention, and inhibition. Hence, in the following, we will put a special emphasis on the role of those executive functions on episodic memory and episodic future thinking.

4.4 False Memory and Episodic Event Construction

As we have seen in the previous sections, executive processes, specifically attentional control and inhibition, are crucial to how we think by selecting, suppressing, and modifying thought-related information. Two types of thought processes are particularly sensitive to cognitive control: false memory and episodic event construction.

Assessing the production of false memory and the experienced richness of past and future thought can both be seen as measures of cognitive thought control due to the reliance of executive functions (involvement of working self in episodic autobiographical memory; Conway & Pleydell-Pearce, 2000). False memory, for example, requires selection of the true memory and suppression of competing memories mainly at the encoding and retrieval phases, which calls for attention, working memory, and inhibition. Indeed, false memory production has been associated in many instances with working memory (Abadie & Camos, 2019; Holden et al., 2020; Mirandola et al., 2017;

Peters et al., 2007; Ruffman et al., 2001) and inhibition (Alberts, 2010; Colombel et al., 2016; Howe, 2005; Lövdén, 2003; Ruffman et al., 2001) in children, young, and old adults. As predicted, better inhibition and working memory resulted in lower false memories and more specific personal events both into the past and future. Inversely, diminished capacity for cognitive control in aging were associated with higher production of false memories (Abichou et al., 2020; Colombel et al., 2016; Lövdén, 2003; Sommers & Huff, 2003). Furthermore, this decline could primarily be attributed to the age-related deterioration in the functioning of the PFC (Craik & Grady, 2002). On the other hand, future event simulation requires the recombination of information retrieved from memory with novel information. For this process, stored memory needs to be accessed, monitored, and transformed into a coherent scene. Therefore, better control over the access and manipulation of autobiographical memory will lead to a more vivid imagery and higher amount of experienced detailed during simulation.

4.5 Functional Brain Networks

Our perception, behavior, emotions, and thoughts are not underpinned by the physiological activity in single, isolated brain regions but rather by the interplay between many brain parts. Brain imaging techniques have uncovered the existence of several important large-scale brain networks. In the following, we will discuss three main networks that make up the triple-network model of brain function (Menon, 2018) involved in the cognitive and emotional information processing system previously discussed: the Default Mode Network, the Central Executive Network, and the Salience Network ([Figure 12](#)). Moreover, related cognitive functions are shortly recapped. These networks and thus cognitive processes share notable connections to processes of the ANS which will be examined in the following chapter. It is important to note that other important networks also exist that show some function overlap. For example, the limbic system shows great overlap with the CAN and is responsible for regulation of emotion, motivation, and memory. Or, the dorsal attention network, which connects to Central Executive Network, holds task-directed external attention, enabling a person to focus and to ignore environmental stimuli.

4.5.1 Default Mode Network

The Default Mode Network (DMN) is active when a person is not focused on the external world or engaged in specific tasks. It is often referred to as the “resting state” network because it is most active during restful and introspective states, e.g., during

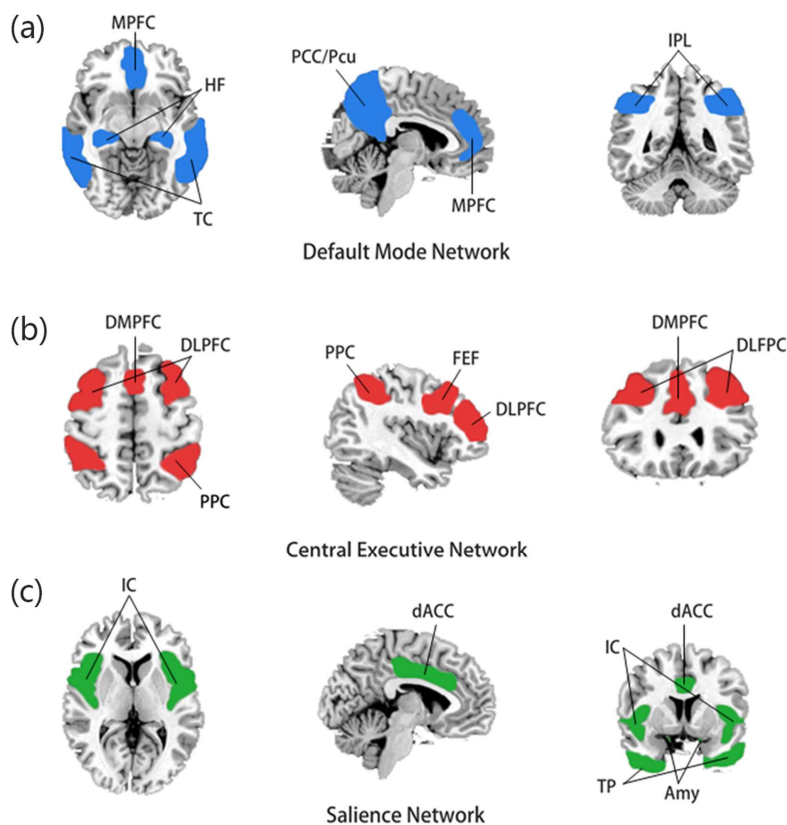


Figure 12 – Components of the Triple Network Model

Note. (A) The default mode network is mainly composed of the medial prefrontal cortex (mPFC) and posterior cingulate cortex/precuneus (PCC/PCu), and the temporal cortex (TC), hippocampus formation (HF) and inferior parietal lobule (IPL) are also closely related to this network. (B) The Central Executive Network is mainly composed of the dorsolateral prefrontal cortex (dlPFC) and posterior parietal cortex (PPC), dorsomedial prefrontal cortex (dmPFC) and frontal eye field (FEF). (C) The salience network is composed of the insular cortex (IC), dorsal anterior cingulate cortex (dACC), temporal pole (TP) and amygdala (Amy). Reproduced from Dai et al. (2019, CC-BY 4.0).

daydreaming and mind-wandering. It is thus believed to be responsible for generating spontaneous thoughts often directed into past or future (Raichle, 2015). The DMN is associated with various cognitive processes related to self-referential thinking, introspection, and prospection. Anatomically, the DMN is closely related to the medial frontoparietal network and is constituted several brain regions distributed across the frontal, parietal, and temporal lobes, with connections between them, including the dorsal medial and medial temporal subsystems. Its main components are pregenual and subgenual ACC, medial PFC (including ventromedial PFC and dorsomedial PFC), tempo-parietal junction, posterior cingulate cortex, precuneus, hippocampus, and inferior parietal lobe including the angular gyrus.

4.5.1.1 Self-Referential Processing and Memory

One of the major functions of the DMN is self-referential thinking (Greicius et al., 2003). The DMN is heavily involved in thinking about oneself (Uddin et al., 2007), including introspection, self-awareness, and the processing of personal experiences and traits. In fact, regions of mental-self processing identified in the cortical midline discussed earlier including the anterior, ventral, dorsal parts of the medial PFC, as well

as the temporal-parietal junction, and posterior cingulate cortex are core centers of the DMN. Given the involvement of the medial temporal lobe, including the hippocampus, the DMN is also implicated in memory formation, integration, and retrieval, especially in the context of self-referential and autobiographical memory processes. Moreover, The DMN is thought to be involved in consolidating and integrating information from various cognitive processes, helping to create a coherent sense of self and personal narrative.

4.5.1.2 Emotional Processing

The ventromedial PFC plays a pivotal role in self-referential processing but is also linked to positive affect. It may contribute to the evaluation and processing of emotional content related to oneself such as memories and future thoughts. However, while the DMN is often associated with self-referential and positive thinking, it can also be involved in processing negative emotions and self-relevant fears.

4.5.1.3 Future Thinking

Future thinking often occurs during periods of mind-wandering, when the mind “slips away” during strong DMN activity, as individuals contemplate their future goals, aspirations, and potential challenges (Mooneyham & Schooler, 2013). However, the DMN is also involved in mental time travel when one is deliberately or not projecting oneself into the past and future. In addition, the DMN supports the construction and maintenance of narratives by linking various pieces of information and experiences into a coherent and meaningful storyline. It is also involved in the process of envisioning and planning for (episodic) future events, allowing individuals to mentally explore different future possibilities, anticipate potential outcomes, plan and set goals accordingly. Medea et al. (2018) showed when those personal goals become concrete, greater thoughts is dedicated to the self and future during mind wandering. Specifically, resting-state functional connectivity of the hippocampus with the ventromedial PFC is concerned with specified goal description, demonstrating the role of the ventromedial PFC in mapping personal importance in future thought.

Moreover, the DMN shows important interactions with the Central Executive Network involved in executive functions supporting episodic future thinking and prospective memory (Buckner & Carroll, 2007; Spreng et al., 2018). Cognitive control is required to detect cues, switch between tasks, uphold goals in working memory and inhibit ongoing processes.

Lastly, the DMN is also engaged when thinking of others and their mental states, known as theory of mind. This aspect of social cognition is critical for understanding the perspectives and intentions of other individuals.

In summary, the DMN is a network of brain regions that is active during restful and introspective states. It is associated with processes related to self-awareness, autobiographical memory, future thinking, and spontaneous thought generation. Its activity provides insights into the brain's intrinsic functions and its capacity for self-reflection.

4.5.2 Central Executive Network

The Central Executive Network, generally equivalent to the fronto-parietal network in literature, is a key functional brain network that plays a crucial role in cognitive control processes (Fassbender et al., 2006; Sherman et al., 2014; Zanto & Gazzaley, 2013). It engages in tasks that require attention, working memory, decision-making, and goal-directed thinking. Anatomically, it comprises several brain regions located primarily in the frontal and parietal lobes. The exact boundaries of this network are not as well-defined, but its main components include the dorsolateral PFC, posterior parietal cortex, and also shows activation in the dorsomedial PFC in interaction with the DMN. The Central Executive Network is responsible for diverse cognitive control processes of which the main functions are summarized here:

4.5.2.1 Attentional Control and Cognitive Flexibility

The Central Executive Network plays a critical role in directing and maintaining attention on specific tasks or stimuli. It helps in filtering out distractions and focusing on relevant information. The network participates in maintaining attention to tasks that require focused concentration, inhibiting distracting stimuli, and switching attention between different tasks or stimuli. Moreover, it allows individuals to adapt to changing circumstances by switching between different modes of thinking (e.g., tasks, rules, etc.). The dorsolateral PFC and ACC are particularly important for monitoring and regulating attentional processes as well as task switching.

4.5.2.2 Working Memory and Inhibition

The Central Executive Network helps in inhibiting automatic or habitual responses in favor of more deliberate and controlled actions. Moreover, it is involved in working memory's function of maintaining and updating this information temporarily for tasks

like problem-solving and decision-making. Both, inhibition and working memory, especially engage the dorsolateral PFC.

4.5.2.3 Decision Making and Problem-Solving

The network is involved in making choices by evaluating different options, considering their potential outcomes, and selecting the most appropriate action by integrating information from various sources to guide decision-making processes. Furthermore, it is also responsible for setting goals, coordinating actions to achieve them, and monitoring progress toward those goals, thus contributing to planning and executing goal-directed behaviors.

4.5.2.4 Multitasking and Cognitive Load

When individuals engage in multitasking, the Central Executive Network plays a role in rapidly shifting attention and cognitive resources between different tasks. Moreover, its activity increases when cognitive demands are high, such as during complex problem-solving tasks or situations that require a significant amount of mental effort.

Overall, the Central Executive Network is critical for higher-order cognitive functions such as self-regulation that require attentional focus, working memory, flexible thinking, and goal-directed behavior. Key regions are the dorsolateral PFC, which is strongly associated with inhibitory control and working memory due to its crucial role in maintaining and manipulating information, and the dorsal ACC engaged in detecting conflicts, monitoring errors, and exerting behavioral control. The Central Executive Network works in coordination with other brain networks, like the DMN and the Salience Network, to achieve seamless cognitive processing across various contexts and tasks.

4.5.3 Salience Network

The Salience Network integrates sensory, emotional, and cognitive information and acts as an interface between the DMN and the Central Executive Network to integrate and balance internal mental processes with external stimulus-driven cognitive and affective processes (Goulden et al., 2014; Menon & Uddin, 2010; Uddin, 2016). It participates in various cognitive and emotional processes, including attention, social cognition, decision-making, and emotional regulation. The network comprises several brain regions, primarily located in the frontal and insular cortex. Its key cortical hubs are dorsal ACC, bilateral insula cortex, supplementary motor cortex, and amygdala. The

Saliency Network 's primary function is to help the brain direct its attention and resources towards important or salient stimuli, both external and internal. Listed below are some key aspects of its function:

4.5.3.1 Switching between Networks

The Saliency Network acts as a switch between other major brain networks, such as the DMN (associated with introspection and daydreaming) and the Central Executive Network (associated with goal-directed thinking and attention), (Goulden et al., 2014). It helps transition between tasks and allocate cognitive resources (e.g., attention, working memory) effectively.

4.5.3.2 Detecting Salient Stimuli

Network switching is often required upon detection of relevant stimuli. In this line, the network's major task is to identify stimuli that are relevant to an individual's current goals, emotions, or states via bottom-up processes. These stimuli could be important sensory inputs, social cues, or even internal bodily sensations. Moreover, it is involved in resolving conflicts in information and making decisions. It helps adjust attention and cognitive resources based on the significance of various stimuli.

4.5.3.3 Emotional Processing and Self-Awareness

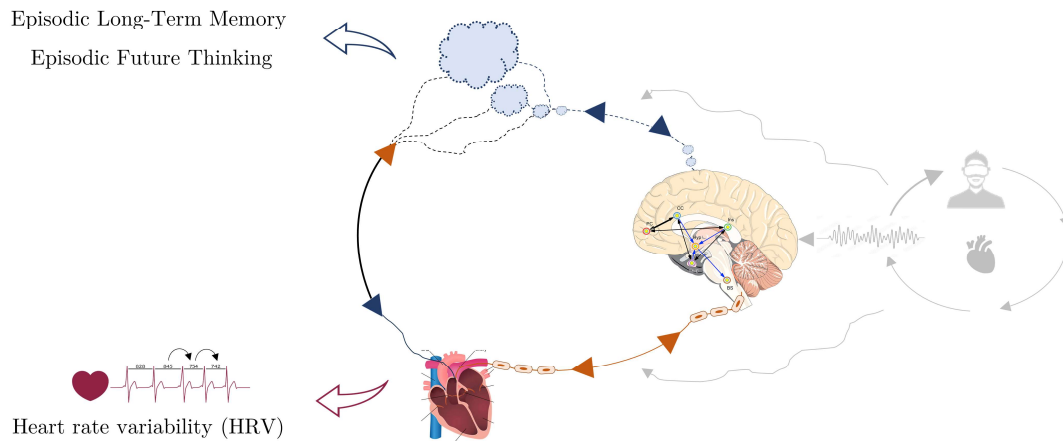
The insular cortex, a key component of the Saliency Network, is implicated in self-awareness, body awareness, and the ability to distinguish between oneself and others. Moreover, the Saliency Network is closely linked to the processing of emotional information due to its involvement of limbic structures. It is involved in recognizing emotions in oneself and others, as well as in regulating emotional responses.

In summary, the Saliency Network is a complex network of brain regions that helps the brain identify and prioritize relevant stimuli, switch between different brain networks, regulate emotions, and engage in social and self-awareness processes. Its integration of external and internal information is essential for adaptive behavior and cognitive control.

4.6 Chapter Summary

- Cognitive control involves processes that support goal-directed behavior according to the context. It is a fundamental feature of self-regulation in adapting behavior and controlling thought.
- Cognitive control encompasses many functions such as inhibitory control, attentional control, and working memory.
- The central executive component of working memory is responsible for controlled processes such as directing attention, maintaining task goals, conflict resolution, and memory retrieval.
- Also, the Self-Memory System model contains an executive component that crucially guides memory access and formation.
- Cognitive control is tightly linked to prefrontal activation, especially in the dorsolateral prefrontal cortex and anterior cingulate cortex (ACC).
- False memory is particularly concerned with cognitive control, and measuring true-to-false memory discrimination can provide a proxy of memory control.
- Episodic memory and episodic future thinking require cognitive control for organization, selection, and monitoring of information.
- It supports strategic aspects of autobiographical knowledge retrieval, particularly in future thinking, and is involved in all memory processes, from encoding to mental construction.
- Measuring aspects of mental scene construction can provide means to assess cognitive control over thought.
- The Default Mode Network (DMN) is particularly concerned with self-processing and thought processes at rest while the Central Executive Network (CEN) is active during active task engagement requiring cognitive control.
- The Salience Network integrates the CEN and DMN by switching between network states and is responsible for salience and emotional processing. It includes the insular cortex, ACC, and amygdala and thus shows great overlap with the Central Autonomic Network.
- Autonomic and large-scale cognitive brain network are functionally and anatomically connected.

5 Chapter 5 – An Integrative View on Cognition and Cardiac Vagal Control



As we have seen in the previous chapters, the brain is in charge of controlling the heart and other organs as well as producing cognition and emotion. Therefore, the questions arise whether these processes underly common neural structures and whether neural circuits associated with autonomic control and behavior influence each other. If yes, this provides grounds to believe that their measurable components, such as HRV and thought processes, are linked. Psychophysiological theory and models are presented, proposing a connection between autonomic regulation, in particular cardiac vagal control and our behavior. Implications for cognitive control, self-processing, memory, and future thinking are discussed, and empirical evidence linking HRV and cognition is presented.

5.1 Embodied Cognition

Traditional theories in psychology have focused on the brain as the sole source of behavior by positing that perception is the input to a computational, representational system that mentally transforms the input into motor commands. Embodied cognition, on the other hand, is the concept that cognition is dependent upon the body and its environmental interactions also beyond the brain. By this idea of the *embodied mind* (Varela et al., 1991), embodied infers “first that cognition depends upon the kinds of experience that come from having a body with various sensorimotor capacities, and second, that these individual sensorimotor capacities are themselves embedded in a more encompassing biological, psychological and cultural context.” For example,

whether you will dwell on a negative thought or plan something delightful for the upcoming weekend would depend on the internal representations and actions of the body (e.g., the ANS signals you are stressed) and not only the brain. Cognitive features of embodied cognition include lower-level to higher-level cognitive functions such as attention, inhibition, memory, intellectual capacity, and language, and thus also previously discussed cognitive components. The aspects of the body include, besides motor control and perception, bodily interactions with environment (situatedness) and that mental representations are encoded in the physiological structure of the body (Shapiro, 2019). It is closely related to other theories like the extended mind thesis (the mind is not only bound to the brain; Clark & Chalmers, 1998), situated cognition (learning takes place while doing something, J. S. Brown et al., 1989), and enactivism (cognition arises through interaction with the environment; Hutto & Myin, 2012). In comparison, the embodiment thesis (Shapiro, 2019) also stresses the role of an individual's body (beyond the brain) and its cognitive processes, but does not mention aspects of biological and physiological components. In summary, embodied cognition can be seen as a more general founding of real-time interaction between the nervous system and cognition and, thus, the interaction between body and mind that we will investigate in this chapter.

The role of embodied cognition in attention (Casasanto, 2011), memory (Vallet et al., 2017; Versace et al., 2014), and aging (Vallet, 2015) has already been emphasized earlier. For example, Versace et al. (2014) posited the theory that activation and integration mechanisms play a key role in memory processes. Central to the theory is that “memory traces reflect all the components of past experiences and, in particular, their sensory properties, actions performed on the objects in the environment and the emotional states of individuals. Memory traces are therefore distributed across multiple neuronal systems which code the multiple components of the experiences.” In this line of thought, cardiac vagal control would also be involved in the memory and underlying processes. Moreover, if cognitive processes are reliant on the body and susceptible to change when the body changes (due to aging for example, Vallet, 2015), then this should also be evident regarding the relationship between the ANS and thoughts. In the following psychophysiological models will highlight the role of cardiac vagal control in cognition and emotion.

5.2 Psychophysiological Theory

Psychophysiological models deal with the interaction between body states and behavior involving cognitive and affective processing. Much research focusing on autonomic regulation has been made in the context of sympathetic arousal and emotion. In this context, Critchley and colleagues provided ample theoretical and empirical contributions to the study of the brain-body connection and the integration of emotional, motivational, and cognitive processes (Critchley, 2005, 2009; Critchley et al., 2011, 2013; Critchley & Harrison, 2013; Quadt et al., 2022) including notions of cognitive control, self-related processing, memory, and prospection. This embodied approach binds psychophysiological processes to arousal and interoceptive processing. However, these works have mainly discussed the integration in relation to sympathetic markers. First, we present the broader context of brain-body connection and interrelation with cognition. Thereafter, models will be discussed that link cognitive and emotional processes with cardiac vagal control.

5.2.1 Allostasis, predictive coding, and self-regulation

We have seen in Chapter 1, the ANS takes action to regulate organ functions to maintain the body's functional integrity through principles of homeostasis (stable internal environment) and allostasis (adaptation towards homeostasis). This overarching regulation is predominantly orchestrated by the brainstem and hypothalamus within the brain through efferent and afferent pathways. These areas serve as central hubs for coordinating a range of responses to external demands to uphold a stable internal environment. However, autonomic control cannot be limited to the homeostatic reflexes at the brainstem but involves higher brain-centers. In this context, the CAN (Benarroch, 1997) was proposed as a pivotal anatomical model that forms the basis for the subsequent psychophysiological models underlying the body-mind intercorrelations and associated with the mental processing of information. In his seminal works, Critchley (2005, 2009) delineates the efferent and afferent mechanisms and the functional brain structures, based on the CAN, underlying the dynamic interaction between mind and body, which “may translate thoughts into autonomic arousal and bodily states into feelings”. Important to the psychophysiological integration of mind and body is the notion of “allostatic policies” that incorporates not only physiological but also psychological self-regulation.

Homeostasis strives to maintain internal equilibrium, for instance, to stabilize blood pressure, which is brought of balance by certain stressors. Allostasis enacts on these stressors by constantly shifting internal physiological states. However, beyond merely controlling peripheral functions in response to changing demands, autonomic control also plays a crucial role in enabling a range of behaviors at the organism level. Autonomic responses arise from afferent signals, giving rise to specific motivational states linked with emotional experiences (e.g., being hungry or thirsty). These states, in turn, give rise to physiological and behavioral self-regulation that seeks to shift the state for a beneficial future outcome (e.g., drinking water not to be thirsty). Such allostatic responses include particular patterns and/or sequences of psychological and behavioral changes, termed “allostatic policies”. Hence, these policies involve affective and cognitive representations integrated into peripheral and central states to form future-oriented action policies (i.e., goal-directed behavior).

Efficient self-regulation or goal-directed behavior requires learning that arises from prediction errors. Internal and external information are encoded through intero- and exteroception and via meta-cognitive processes monitored and contrasted to predicted outcomes. This predictive processing, also known as predictive coding (Stephan et al., 2016), thus constantly and mentally (re-)models the environment by comparing perceptual inputs, with predicted input signals. In this process of coupling and integrating psychophysiological information streams, detection of prediction errors will lead to allostatic adaption and control (Allen et al., 2022). Thus, from a predictive coding view, allostatic action can be seen as an “internal neural model of self-efficacy” (Quadt et al., 2022). Conclusively, allostatic self-efficacy reflects the organism's capacity to regulate bodily states for efficient physiological and psychological self-regulation. It is consequently involved in the generation of various mental states, that in concert with autonomic regulation aid the organism in handling adaptively internal and external challenges. However, being stuck in patterns of allostatic policies (e.g., a fear-conditioned stimulus that initially served body preparation for fight and flight is evoked spontaneously without any adaptive reason) can lead to the development of psychopathologies such as post-traumatic stress disorder, anxiety, or depression. Hence, allostasis is crucial to preserve the body's integrity and promote health. Deficits in allostasis show in reduced cardiac vagal control (Thayer & Sternberg, 2006), which, as discussed earlier, underlies self-regulation and healthy physiological functioning. In the following, psychophysiological models will be discussed that will highlight the pivotal role of cardiac vagal control in healthy mind-body integration.

5.2.2 Polyvagal Theory

The Polyvagal Theory, first published by Porges (1995), elucidates the intricate neurophysiological underpinnings of emotions, attachment, communication, and self-regulation within the context of the ANS. This theory postulates a comprehensive conceptual framework that views the ANS as a complex and adaptive system characterized by specialized subsystems operating in coordination (Porges, 2011). Central to this theory is the role of the vagal nerves, which contain distinct, interconnected subsystems that orchestrate different adaptive reactions in the face of diverse challenges. The theory introduces a dichotomy between unmyelinated fibers originating from the dorsal motor complex (dorsal vagal system) and newer myelinated nerves originating from the nucleus ambiguus in the ventral vagal system. These subsystems engender distinct behavioral strategies to environmental stimuli, with the unmyelinated fibers predominantly associated with immobilization, passive avoidance, and shutdown responses, collectively referred to as the “freeze response”. In contrast, the myelinated vagus is conceptualized as a vagal brake, fostering adaptive social interactions through enhancement of the feeling of safety and inhibition of sympathetic efferent activity. Porges posits that emotional experience as well as the adaptive regulation of behavior and emotions are defined by the ANS functioning with different physiological states representing different behaviors. From an evolutionary perspective, he emphasizes the impact of the ANS’s development on emotional and social functioning. Porges asserts that the evolution of the ANS has underpinned the emergence of emotional experiences and their regulation, forming the bedrock of social behaviors unique to humans. Notably, the theory introduces the concept of the “social engagement system”, underpinned by the myelinated vagus. This system enables humans to engage in pro-social behaviors, transcending mere fight-or-flight reactions and encompassing a wider repertoire of adaptive responses, such as the “tend-and-befriend” approach. Essential to the functioning of the myelinated vagus is the suppression of the SNS activity, which allows us to calm ourselves. Consequently, the healthy operation of the myelinated vagus or ventral vagal system emerges as a vital determinant of one’s self-regulatory capacity.

The Polyvagal Theory also emphasizes the physiological foundation of emotional expression, communication, and self-regulation. Porges expounds on the intricate neural connections between higher brain structures and autonomic regulatory centers, underscoring the role of afferent signaling within the ANS. This theory postulates that physiological states exert adaptive influences, supporting diverse categories of behavior. In juxtaposition with the SNS and the endocrine system, the Polyvagal Theory thus discerns the ANS’s adaptive mechanisms. While the SNS triggers mobilization, fight-or-flight responses, and active avoidance to safeguard against threats, the vagal system operates with a more sustained and gradual effect, governing processes such as heart rate deceleration and bronchial tone elevation. Hybrid behavioral states have been proposed (Figure 13) arising from the interaction between the ventral (myelinated) and

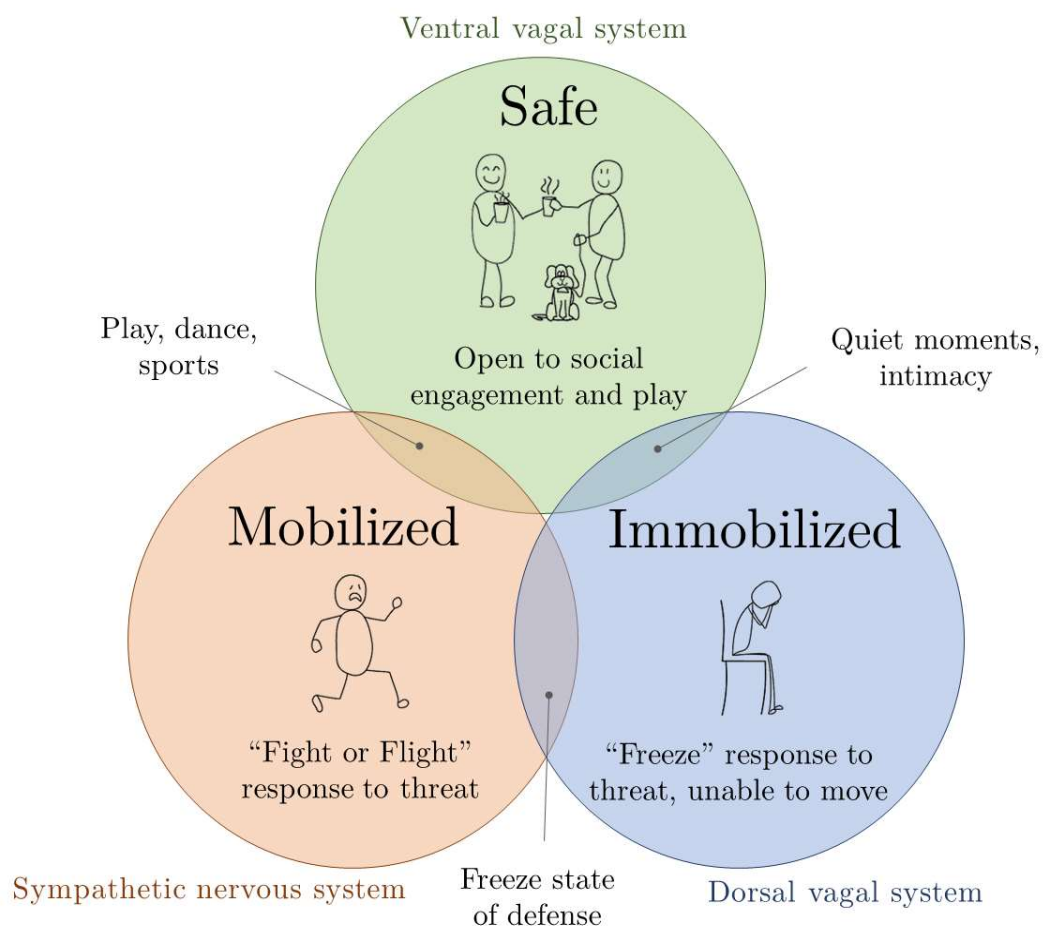


Figure 13 – Behavioral States According to the Polyvagal Theory

Note. The activity of unmyelinated fibers originating from the dorsal motor complex (dorsal vagal system) and newer myelinated nerves originating from the nucleus ambiguus in the ventral vagal system in concert with the sympathetic nervous system define social behavior. (Co-)activation and suppression of the different systems will lead to various behavioral states. Figure adapted from https://en.m.wikipedia.org/wiki/File:Polyvagal_theory_Ventral_Vagal.png (CC-BY-SA 4.0).

dorsal (unmyelinated) vagal systems as well as the SNS. While the SNS in conjunction with the ventral system will drive play, dance, and sports, the combination of the SNS with the dorsal system will trigger a freeze state of defense. Coactivation of the ventral and dorsal vagal system, on the other hand, will lead to the experience of intimacy and quiet moments.

In sum, the Polyvagal Theory, delineated comprehensively by Porges, provides a nuanced and holistic perspective on the ANS's role in emotional experiences, communication, and self-regulation. This theory underscores the interplay between two distinct subsystems within the vagal nerves, positing an evolutionary context that shapes human emotional expression and behavior. Central to this theory is the notion that the ANS operates as a dynamic and adaptive system, linked to both physiological and psychological responses, with its effects pervading multiple facets of human experience and cognition. A pivotal role has been ascribed to the activity of the vagal efferent and afferent nerve fibers for self-regulation to initiate pro-social behavior.

5.2.3 Neurovisceral Integration Model

The neurovisceral integration model, pioneered by Thayer & Lane (2000, 2009) is a comprehensive and influential theoretical framework that illuminates the intricate interplay between the central nervous system and ANS within the realms of physiological, emotion, and cognitive regulation. The model draws insights from Claude Bernard's concept of "milieu intérieur", which was later coined by Walter Cannon as "homeostasis", and the related phenomenon of allostasis (which denotes the body's adaptive efforts to maintain stability through physiological adjustments in response to stressors). In this context, the proposed framework offers profound insights into the functional and structural features of the associated regulatory systems and how their dynamicity contributes to both adaptive and maladaptive responses, shedding light on their pivotal role in shaping human experiences and health outcomes. Furthermore, the framework puts to the fore the role of the PFC and vmHRV in indexing and interlinking psychophysiological and cognitive processes.

The initial work of Thayer and Lane (2000) introduces the neurovisceral integration model, establishing the groundwork for understanding the relationship between emotion regulation and neurovisceral processes. The model emphasizes reciprocal communication between the central nervous system and the ANS, underpinning both the adaptive capacity to respond to environmental demands and the potential for

dysregulation leading to psychopathological conditions. The paper commences by providing a functional description of attention regulation and affective regulation for behavioral and physiological flexibility placed in a regulation system framework. Based on “behavioral systems” (Timberlake, 1994), emotions arise in the organism for guidance towards goal-directed behavior. This process requires coordination of oscillating and intertwined circuits of neural and physiological subsystems. In line with the system perspective, the feedforward and feedback loop system is the cornerstone for behavioral systems to coordinate behavioral responses during organism-environment interactions. In the state-space, i.e., the behavioral repertoire of the organism, emotions represent attractors or preferred configurations that drive the behavioral system towards stability. Disorders of affect, such as anxiety, arise from a distorted emotional state space in which, instead of moving toward attractors or emotions appropriate to the situation, one is trapped in a pattern of behavior that is not adapted to the demands of the environment (as in the previous example of repeated thinking about fear-conditioned stimuli). Thayer & Lane (2000) further accentuate the importance of integrating affective and attention regulation. They argue that selective attention, which sustains and shifts the focus, determines what information is processed and is coupled with emotional regulation because attentional processes are often emotionally motivated. Hence, considering psychophysiological processes associated with attention is paramount in the context of self-regulation and adaptability.

Furthermore, Thayer & Lane (2000) expound upon the structural framework that instantiates the functional system of emotion regulation. They delineated the importance of the CAN involved in autonomic regulation (Benarroch, 1997) and its interwoven relationship and structural congruence with neural circuits orchestrating attentional regulation (Devinsky et al., 1995) and affective regulation (Damasio, 1998). In addition, the authors highlight the existence of parallel frontal-subcortical neural connections between the frontal cortex and the thalamus. Within this context, Thayer and Lane present compelling empirical evidence for the correlation between HRV – which we have seen is a discernible marker of autonomic control – and the regulation of emotional, attentional, and physiological systems, and with blood flow dynamics. Noteworthy within their model is the prominence attributed to negative feedback loops in the context of psychophysiological regulatory systems. These feedback loops induce the inhibition of neurovisceral circuits, exerting a suppressive effect on ongoing behaviors. This facet stands as a fundamental tenet of self-regulation. Conversely, positive feedback loops engender preserved system activity, inadvertently constricting

behavioral flexibility and thereby culminating in the perturbation of psychophysiological equilibrium. Central to their discourse is the pivotal function of inhibitory control, which enables a departure from entrenched behavioral patterns and promotes heightened organismal flexibility and adaptability. Lastly, the authors posit that cardiac vagal control indexes inhibitory circuits and thus represents a “psychophysiological resource” for the organism to efficiently adapt to environmental demands.

In their subsequent elaboration on the neurovisceral integration model (Thayer & Lane, 2009), the authors emphasize the interplay between physiological, emotional, cognitive regulation, along with its association to vmHRV and cortical forebrain structures. The vagal nerve, a linchpin of the ANS, assumes paramount significance in the neurovisceral integration model. As we have seen in Chapter 1, the vagal nerve serves as a conduit for the exchange of signals between the brain and bodily systems, thereby enabling the regulation of autonomic functions. Furthermore, the authors propose a pathway by which the PFC ([Figure 14](#)), most notably the medial and orbitofrontal parts, via interconnected cortical and subcortical structures affect the cardiac chronotropic state. In this context, the prefrontal, cingulate, and insular cortices form an interconnected network reciprocally connected to the amygdala. The latter is under tonic inhibitory control via prefrontal vagal pathways. From the amygdala, the inhibitory pathway extends to the nucleus of the solitary tract from where neural connections affect rostral ventrolateral medullary sympathoexcitatory neurons via the caudal ventrolateral medulla and vagal motor neurons in the nucleus ambiguus and the dorsal vagal motor nucleus. In addition, the amygdala can directly activate the sympathoexcitatory neurons in the rostral ventrolateral medulla. Consequently, deactivation of the PFC would lead to disinhibition of the amygdala and thus of medullary cardioacceleratory circuits, resulting in an increase in heart rate and decrease in vmHRV. Consequently, the PFC exerts top-down control to modulate subcortical circuits governing cardiac control. This regulatory engagement transpires through the mediation of an inhibitory conduit entwined with vagal functionality and discernible by measuring HRV. The paper exposes numerous literature findings from investigations involving pharmacological blockade and advanced neuroimaging techniques that substantiate their assumption. They further stress the importance of the subcortical inhibition through the PFC. Hypoactivity of the PFC is linked to energy mobilization due to the disinhibition of sympathoexcitatory neurons. Therefore, prolonged hypoactivity, and thus a lack of neural inhibition through the PFC, leads to increased allostatic load due

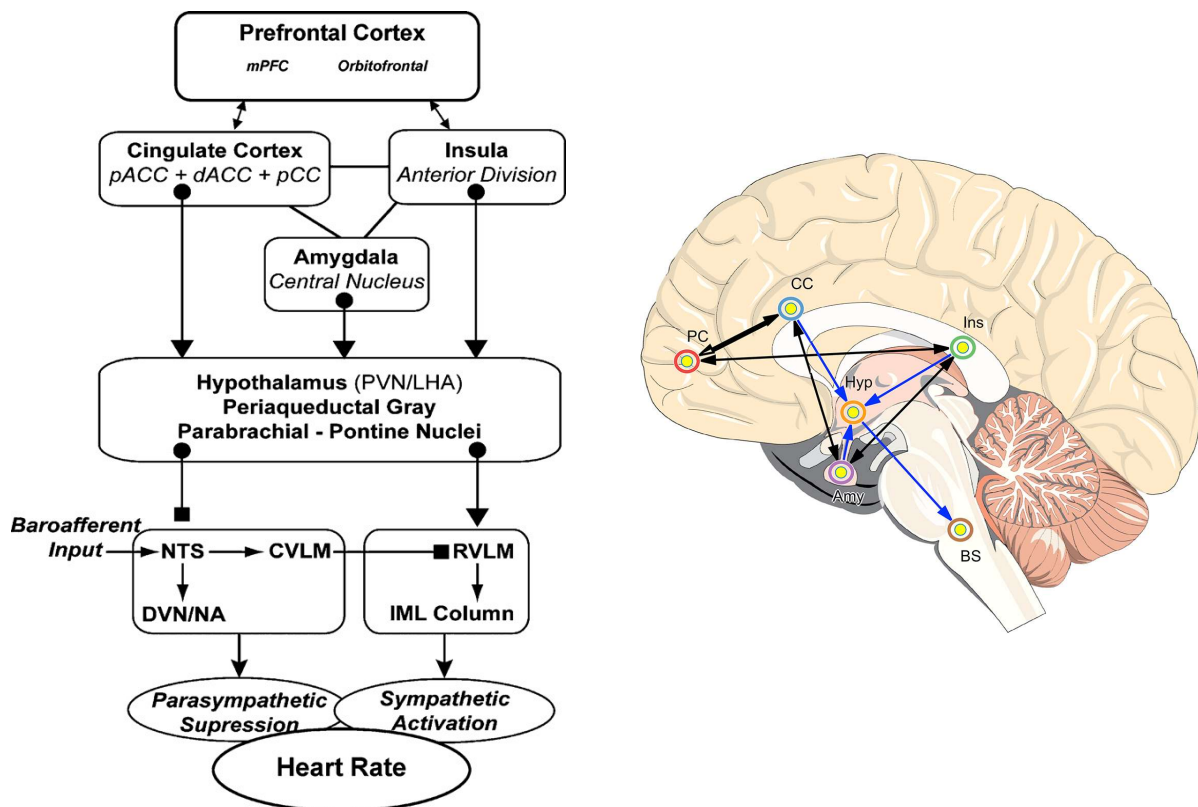


Figure 14 – Heart-Brain Connection in the Neurovisceral Integration Model

Note. (A) Neural pathways of the neurovisceral integration by which the brain interacts with the heart rate proposed by Thayer & Lane (2009). (B) Main brain regions relevant to the neurovisceral integration. Adapted from (Nikolin et al., 2017, CC-BY 4.0). PC = prefrontal cortex; CC = cingulate cortex; Ins = Insula; Hyp = hypothalamus; Amy = amygdala; BS = brainstem; ACC = anterior CC; mPFC = medial prefrontal cortex; pACC = posterior ACC; dACC = dorsal ACC; PCC = posterior CC; NTS = nucleus of the solitary tract; CVLM = caudal ventrolateral medulla; RVLM = rostral ventrolateral medulla; DVN = dorsal vagal motor neurons; NA = nucleus ambiguus; IML = intermediolateral cell column.

to chronic adaption costs (McEwen, 1998). The authors posit that sustained allostatic load may lead to wear and tear on the body, contributing to the development of chronic health conditions. Moreover, they show that greater resting-state vmHRV, reflective of prefrontal activation, is linked to a decreased negativity bias, which has strong ties to depression. The model, in this context, highlights the importance of optimal neurovisceral integration in mitigating allostatic load and promoting overall health.

Lastly, the model highlights that the PFC, besides its role in autonomic control, is also associated with executive functions (Chapter 4) providing grounds for a connection between cognitive and autonomic regulation. In this context, Thayer & Lane (2009) list some initial studies that demonstrate correlations between resting-state HRV and processes involved in cognitive regulation including inhibition, working memory, and

attention. In a publication of the same year, Thayer et al. (2009) delve into the neurovisceral integration perspective's implications for cognitive performance. Within their work, they review the literature corroborating the role of HRV for cognitive functioning, which shows specificity to executive functions. The authors propose that high HRV facilitates effective cognitive functioning, as increased variability signifies a flexible autonomic system that can rapidly adjust to cognitive demands. In contrast, low HRV may hinder cognitive performance due to limited autonomic responsiveness.

In summary, the neurovisceral integration model, as delineated in the seminal works of Thayer, Lane, and colleagues, presents a comprehensive framework for understanding the complex interaction between the central nervous system, ANS, and various self-regulatory processes. This coordination is orchestrated through an intricate network of neural pathways and feedback loops, providing a common neural basis for cognitive, affective, behavioral, and physiological functions. The model assumes that a set of cortical-subcortical neural circuits, associated with cardiac and cognitive regulation that is modulated via an inhibitory pathway linked to the PFC that can be interrelated with vagal traffic. Hence, the authors proposed that vmHRV reflecting cardiac vagal control is positively correlated with PFC activity, which in turn is linked to diverse cognitive functions. Consequently, the model elucidates the critical role of vmHRV as a key indicator of this neurovisceral interaction, emphasizing its significance in cognitive functioning, emotional regulation, and health outcomes. By shedding light on the dynamic interactions between neural, physiological, and cognitive systems, the neurovisceral integration model offers a robust foundation for advancing our understanding of the psychophysiological interaction between autonomic and cognitive regulation.

5.2.4 Psychophysiological Coherence Model

5.2.4.1 Definition of psychophysiological coherence

The model proposed by McCraty and colleagues (McCraty et al., 2009; McCraty & Childre, 2010; Tiller et al., 1996) is based on the phenomenon of *psychophysiological coherence* introduced by Tiller et al. (1996), which depicts the level of temporal arrangement, concordance, and steadiness in the diverse rhythmic behaviors within living systems (e.g., respiration, heart rate, blood pressure, cortical activity). This state of harmonious order within and between bio-oscillators signifies a coherent functioning system, where optimal functioning directly translates to the smooth and unhindered progression of life's processes. On the other hand, an irregular and discordant activity

pattern characterizes an incoherent system, indicating stress and ineffective energy utilization in the organism's functioning. The psychophysiological coherence model directly translates these characteristics to the dynamics of the autonomic and central nervous systems. Specifically, the harmonious pattern of the heart's chronotropic state, termed *cardiac coherence*, has been of popular interest. In this line, it has been proposed that the pattern and stability of beat-to-beat heart rate, described by HRV, encodes information of the central-peripheral activity. This information is communicated across multiple subsystems which help synchronize the organism as a whole affecting cognitive performance and emotional experience. The psychophysiological coherence model forms the basis of the coherence training which we have briefly reviewed in Chapter 2.2.2. The model posits that establishing increased stability or coherence influences the autonomic and central nervous system activities, reflected in HRV, consequently promoting efficiency and optimal functioning of a multitude of regulatory processes including emotional regulation. In turn, cognitive functions are affected by increased emotional stability and states of calm linked to "flow", which facilitate cognitive processing and thus improve performance. It is important to note that the model posits the relationship between physiological and psychological coherence (i.e., optimal emotional and cognitive functioning) is bidirectional. In that sense, not only evoking stability through coherence training improves psychological scores, but inversely, the researcher's findings reveal that positive emotions like appreciation and compassion, as opposed to negative emotions such as anxiety, anger, and fear, manifest in a heart rhythm pattern that exhibits greater coherence (McCraty et al., 2009; McCraty & Zayas, 2014). Notably, the vagal nerve, through its efferent and afferent pathways, has been found to play an instrumental role in generating (cardiac) coherence and its associated effects on the brain.

5.2.4.2 Inner baseline

The model supposes that humans inherently hold "internal baseline reference" which determines how perception, emotions, and behavior are organized. The concept is based on the idea of Pribram and Melges (Pribram, 1970; Pribram & Melges, 1969) that emotions and associated behavioral responses become "set points in the neural architecture which act as a type of implicit memory, or baseline reference" (McCraty & Zayas, 2014). Such set points are established through the integration of sensory inputs that establish neural patterns in integrated feedback loops of the central-peripheral neural system. The structure of neural architecture thus functions as an

implicit memory or default pattern to evaluate new sensory input and coordinate the organism accordingly. These behavioral and physiological setpoints and their integration in organism-environment interactions follow the principle of homeostasis and allostasis (shift to homeostasis). Once established, the organism strives to maintain its default pattern whenever its functioning is brought into disequilibrium. Thus, the concept is comparable to the neurovisceral integration model's preferred configurations and behavioral state-space systems (Thayer & Lane, 2000). Set points are attractors or preferred configurations in a behavioral state space that can get an individual stuck in maladaptive behavior leading to the development of psychopathologies.

5.2.4.3 Baseline shift

The psychophysiological coherence model has its roots in improving health and well-being. Its stated goal is to change the internal reference base that is believed to underlie trauma and psychosocial well-being (McCraty & Zayas, 2014). To move away from maladaptive behavior, it is necessary to re-pattern the neural architecture and associated set points. To do so, coherence training is applied involving the activation of positive emotions and slow breathing to persistently harmonize bodily processes and related information processing. The theory posits if coherence is repeatedly increased, this harmonization process will cause psychophysiological coherence to become the new, neuronally wired baseline reference. By training self-regulation of emotions, up-regulation of coherence becomes entrained and eventually automatic, so that spontaneous surges in coherence occur become more frequent. Thus, training based on the coherence model is believed to reestablish self-regulatory capacities and a new form of allostasis with a propulsion towards efficient psychophysiological functioning. This would increase behavioral flexibility and resilience as one gets unstuck from attractors. Moreover, due to the linkage between coherence and positive emotions, this would affect affective processing, potentially reducing negativity bias and increasing positivity bias. In summary, baseline change is central to sustained behavioral and cognitive change and positive health outcomes.

5.2.4.4 Comparison to other psychophysiological models

The psychophysiological coherence model shows remarkable consistency with the polyvagal theory (Porges, 2007) and the neurovisceral integration model (Thayer et al., 2009). Like the previous theories, it focuses on the interaction between the central and ANS described by the CAN model in which cortical and subcortical structures are involved in the output of cardiorespiratory centers in the brain stem as well as

emotional processing. Thus, like the neurovisceral integration model, the coherence approach also places a particular emphasis on emotional and cognitive regulation based on physiological coupling in the neurovisceral integration. Moreover, in all models, the role of heart activity and the influences through the parasympathetic (vagal) activity, reflected in HRV, are paramount. In this line, all models suggest that vmHRV is indicative of self-regulation capacities and that low HRV indexes diminished system functionality with important implications for behavior, emotional and cognitive processing, and health. Moreover, the neurovisceral integration model and psychophysiological coherence model encapsulate that physiological resonance in the cardiovascular system is reflected in increased vmHRV, positively affecting cognition.

All models are consistent in the assumption that physiological regulation is underpinned by an increased phasic dynamic in efferent and afferent activity of the vagal nerve in connecting the heart and the brain via the brain stem. Intertwined circuits in subcortical and cortical are involved in bottom-up processing and cardiac top-down control. Still, they are also concerned with regulating neural structures concerned with emotions and cognition. Therefore, all models are in congruence that vmHRV indicates efficiency in central-peripheral neural feedback mechanisms, and that intra- and inter-individual differences in states of vmHRV are reflective of efficiency differences in the organization of physiologic resources and behavioral flexibility ultimately linked to self-regulation capacities and cognitive performance.

In contrast, the psychophysiological coherence model emphasizes more on the aspect of information encoded in the dynamic patterns of physiological activity within and between oscillating systems. It focuses on the association between coherent physiological patterns and positive emotions as well as vagal effects via afferent pathways to positively shift the “internal baseline reference”. In total, they provide a more holistic view on the neurovisceral integration by putting a stronger emphasis on the positive health outcomes through increased coherence. The model goes even further and extends the implication of coherence for personal health to physical and social phenomena taking place between living beings, around the world and in the solar system. With that, they argue that “increasing our coherence [...] is also reflected in the global field environment which helps strengthen a mutually beneficial feedback loop between human beings and the earth itself” (Alabdulgader et al., 2018; McCraty et al., 2012; McCraty & Childre, 2010).

5.2.5 Vagal Tank Theory

5.2.5.1 Definition

The Vagal Tank Theory (Laborde et al., 2018) is a more recent conceptual framework rooted in the psychophysiological concepts from the polyvagal theory and neurovisceral integration model to elucidate the multifaceted dynamics of cardiac vagal control functioning in shaping physiological and psychological responses. The model adopts a resource perspective based on principles of the integrative self-control theory (Kotabe & Hofmann, 2015) and the strength model of self-control (Baumeister et al., 2007). Vagal tone plays a primary role in the regulation of energy exchange by synchronizing respiratory and cardiovascular processing during metabolic and behavioral changes. Linked to the phenomenon of ego depletion (Baumeister et al., 2007), according to which self-regulation relies on limited resources that can be depleted and replenished, just like a batterie, causing variations in performance in tasks involving self-control. Analogously, the vagal control of the heart is treated as a form of resource. However, it is important to note that cardiac vagal control itself is directly not considered as a resource, but rather, the efficiency in mobilizing resources and using them for self-regulation is indicated by its pattern of change. In this line, the cornerstone of the Vagal Tank Theory is the consideration of PNS regulation across distinct systemic levels – Resting, Reactivity, and Recovery (the “Three Rs”). In this context, the “vagal tank” concept is introduced, serving as a metaphorical reservoir for cardiac vagal control to describe adaptive physiological functioning underlying effective self-regulation across the three Rs.

5.2.5.2 The Three Rs

Resting, the first element of the theory, pertains to the baseline level of cardiac vagal tone during quiescent states. It underscores the inter-individual variability in resting vagal tone, influenced by genetic predispositions, early-life experiences, and environmental factors. The vagal tank's capacity, as reflected in resting vagal activity, is proposed to influence an individual's emotional and physiological baseline.

Reactivity delves into the dynamic autonomic adjustments that transpire in response to external or internal stimuli. Such stimuli can encompass physical, emotional, or cognitive triggers (i.e., retrospective or prospective thinking). The vagal tank during this phase reflects the momentary cardiac vagal modulation (i.e., withdrawal, augmentation, or equilibrium) compared to the baseline prompted by these stimuli.

Intriguingly, the theory advances the notion of vagal tank depletion, suggesting that prolonged or intense reactivity may lead to diminished vagal resources, rendering the individual more susceptible to subsequent stressors or challenges.

Recovery, the third phase, underscores the restorative aspects of cardiac vagal control. Following periods of reactivity, the vagal tank signifies the recuperative trajectory of parasympathetic re-engagement. Adequate recovery periods are hypothesized to replenish vagal resources and enhance overall autonomic flexibility, thus contributing to long-term physiological resilience. Effective recovery is proposed to be indicative of emotional resilience and overall well-being.

Previous models drew empirical evidence to support their assumption mainly on analyses of tonic measures of HRV during rest (i.e., while the participant is calmly sitting) or more rarely during HRV in response to a stimulus (e.g., while completing a cognitive task). Thus, the advantage of the Vagal Tank Theory lies in the systemic consideration, including not only resting HRV (tonic) but also change pattern in cardiac vagal control (phasic), measured as vmHRV. Systematic investigation of all multiple phases, instead of singular investigations, may lead to the emergence of cardiac vagal control patterns that might otherwise remain unrevealed. Vagal Tank Theory

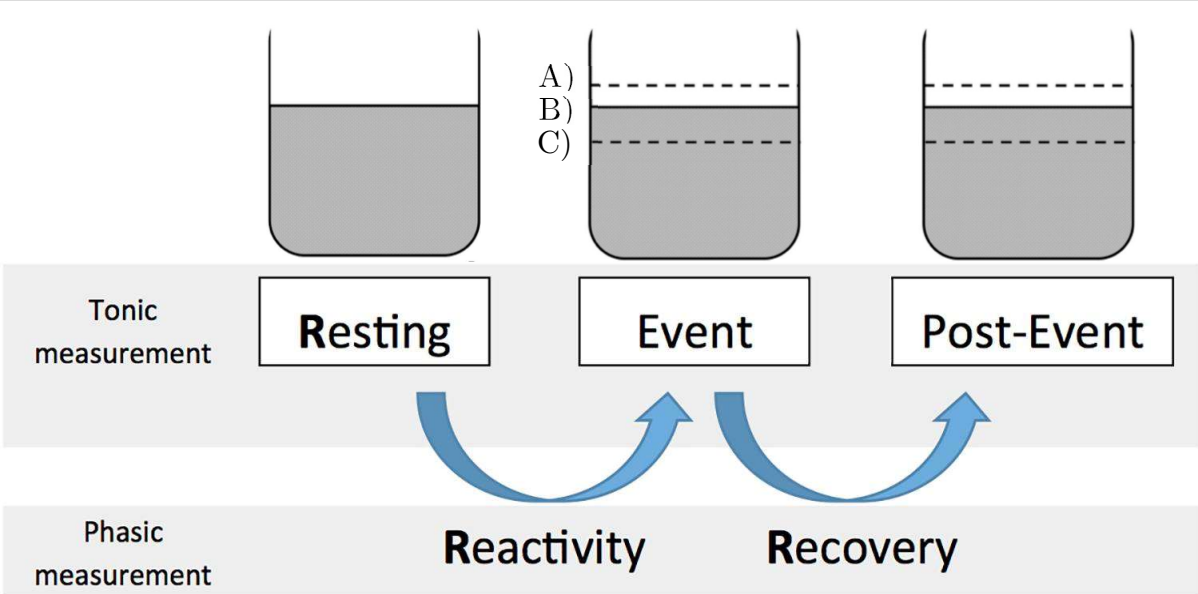


Figure 15 – The 3 Rs of Cardiac Vagal Control: Resting, Reactivity, and Recovery

Note. Illustration of the vagal tank and the three Rs (resting, reactivity, and recovery) with a factor replenishing (A), unaffected (B), or depleting (C) cardiac vagal control. Phasic measures of cardiac vagal control represent changes between tonic states. During situations of high executive and low physical demand, less depletion (C) will be indicative of better self-regulatory efficacy. Reproduced from Laborde et al. (2018, CC-BY 4.0).

assumes for each of the three Rs how patterns predict the effectiveness of self-regulatory mechanisms ([Figure 15](#)).

5.2.5.3 Predictions based on the three Rs

Resting prediction. The Vagal Tank Theory assumes in congruence with the neurovisceral integration model and polyvagal theory that higher resting cardiac vagal control levels indicate better executive performance, specifically working memory and inhibition, emotion regulation, and health. Thus, the authors go with the motto “the higher, the better”; however, they also denote important delineations to this principle. For instance, elevated or extreme resting levels may not be adaptive but may even indicate health problems, such as pulmonary airway constrictions or eating disorders. Furthermore, motivation seems to play an important, yet unclarified, role in moderating cardiac vagal control. The initial level of cardiac vagal control is also important in phasic measures. Because a higher resting level reflects more adaptive self-regulation, it also contributes to greater efficiency during periods of reactivity and recovery.

Duschek et al., 2009 argue that whether vagal dis-(engagement) is adaptive depends on the other contexts, such as if there is time pressure. The authors suppose that under time pressure, stronger vagal withdrawal would predict better performance in an attention task.

Reactivity prediction. The prediction about the effectiveness of the self-regulation mechanisms reflected by the reactivity level is suggested to be dependent on two contextual factors: the degree of physical activity and top-down executive control involved in the response to the stimuli or task. It is predicted that in situations requiring high activity when metabolic demands are high, for instance in response to immediate threat, greater vagal withdrawal is adaptive. Inversely, when the situation demands only a low level of activity but great executive top-down control, for example, during voluntary memorization, smaller vagal withdrawal (or a greater increase) indicates better self-regulation and cognitive performance.

Recovery prediction. The model posits that the recovery prediction depends on whether a vagal withdrawal or an increase was recorded in the previous reactivity phase. Was a withdrawal denoted, a return of the cardiac vagal control level back to baseline, or even an increase above it, is considered adaptive. Specifically, the delay and speed with which the cardiac vagal control replenishes indicates the degree of self-regulation. In

this line, the faster the return, the better the self-regulation. Where an increase in reactivity has previously been observed, longer periods in which vagal control of the heart remains above baseline levels reflect better self-regulatory abilities. In addition, the authors assume that a longer duration of phasic increases between reactivity and recovery supports long-term self-regulation as it helps to sustainably increase resting cardiac vagal control.

In conclusion, the Vagal Tank Theory offers a comprehensive framework that accentuates the temporal pattern of cardiac vagal control functioning. By delineating the Resting, Reactivity, and Recovery phases, the theory sheds light on the interplay between vagal modulation and physiological responses to environmental demands underlying self-regulation and thus cognitive performance. Predictions about the level of self-regulation effectiveness by patterns of the three Rs are made, although the authors caution that important differences may appear depending on health status and age. Overall, this conceptual model holds significant promise for advancing beyond the previous understanding of the polyvagal theory and neurovisceral integration model of autonomic, emotion and cognitive regulation.

5.3 The Neuroanatomical Basis of Autonomic and Cognitive Processes

In the previous section, different models were discussed that highlight the brain-heart connection through the CAN and the integration of autonomic and brain functioning with cognitive performance, especially cognitive and emotional control. The outflow of the ANS adjusts bodily responses to align with contextually adaptive behaviors, ensuring that the body meets the metabolic demands posed by motor, emotional, and cognitive challenges (Critchley, 2005; Laborde et al., 2018; Thayer & Lane, 2000). Central to the discussion was cardiac vagal control, assumed to reflect how effectively resources are deployed for psychophysiological self-regulation. States and dynamic patterns of cardiac vagal control, discernible by measuring vagal efferent inputs to sinoatrial node as vmHRV, are thus theorized to be related to cognitive performance. In the following, we will focus on executive control, self-referential processing, memory, and future thinking. In this context, neural circuits underpinning autonomic control and cognition are discussed. Furthermore, evidence from cognitive neuroscience and psychophysiology is presented to shed light on the role of cardiac (vagal) control for cognitive performance.

5.3.1 Brain networks

Chapter 4.5 discussed the triple network model that underlies a large part of our cognition. The DMN, associated with resting-state, is engaged in endogenously mediated and self-referential mental activity, while the Central Executive Network is exogenously-driven and active during cognitively demanding mental activity. The Salience Network, which integrates sensory and limbic inputs, is responsible for detection of salient cues and switching between networks (i.e., DMN: internally-oriented vs. CEN: externally-oriented attention), (Goulden et al., 2014). Importantly, these networks, that play a crucial role in executive, self-referential, emotional processes as well as episodic autobiographical memory and future thinking, notably overlap with the CAN ([Table 2](#)).

In Chapter 1 the role of the CAN in autonomic regulation and as interface between central and ANS was discussed. It is characterized by a hierarchical structure in which the insular as well as medial and various prefrontal cortical regions play a crucial role in overseeing 'high-order' autonomic control, while the amygdala participates in functions related to emotional states. The hypothalamus is associated with maintaining homeostasis, encompassing neuroendocrine activities and responsiveness to stress. Additionally, the periaqueductal gray is emphasized as a coordinator of autonomic responses to pain, as well as specific stress-related aggressive and reproductive behaviors. Brainstem centers are acknowledged for their close connections to autonomic effector functions at target organs, particularly in cardiovascular and respiratory control (e.g., cardiac control, baroreflex, etc.). This characterization of a comprehensive autonomic system within the brain underscores the reciprocal interconnectedness of central hubs that support internal physiological regulation through parallel organization (Benarroch, 1993).

Pivotal work on the autonomic functioning in the active brain has been provided in a meta-analysis (Beissner et al., 2013) based on 43 functional neuroimaging studies, that identified brain regions of the CAN associated with activity PNS and SNS and during specific tasks (cognitive, affective, somatosensory; [Figure 16](#)). The study highlighted that salience and executive processing networks are predominated by structures associated with sympathetic activity and whereas the DMN was overall is more strongly associated with parasympathetic regulation. Quadt et al. (2022) recently updated this review of brain centers linking cognition, such as memory, thoughts, and feelings, with autonomic function, with a special regard to arousal. The authors revisited the CAN

and regional attribution of cognitive, emotional, and sensorimotor processes in humans, as well as the role of functional brain networks in autonomic and emotional processing. Also, they concluded that the Salience Network, which engages in action-ready states, is linked to sympathetic efferent drive, whereas the DMN couples to antisympathetic/parasympathetic control. Indeed, the Salience Network and DMN are considered to be anti-correlated, meaning that when one is active, the other tends to be less active, because of internal-to-external attentional switch initiated by the Salience Network.

Table 2 – Overlap Between Functional Brain Networks

Overview of main hubs in the Default Mode Network (DMN), Salience Network (SN), Central Executive Network (CEN) and brain regions involved in the Central Autonomic Network (CAN) according to Beissner et al. (2013) and Quadt et al. (2022).

Brain regions	DMN	SN	CEN	CAN
Ventromedial prefrontal cortex (vmPFC) (including subgenual and pregenual anterior cingulate cortices)	X			X
Dorso medial prefrontal cortex (dmPFC)	X		X	
Dorsolateral prefrontal cortex (dlPFC)			X	
Dorsal anterior cingulate cortex (dACC)		X	X	X
Precuneus / Posterior cingulate cortex (PCC)	X		X	X
Amygdala (Amy)		X		X
Insular cortex (IC)		X		X
Supplementary motor cortex		X		X
Hippocampus	X			X
Lateral parietal lobe	X			
Hypothalamus				X
Brainstem				X

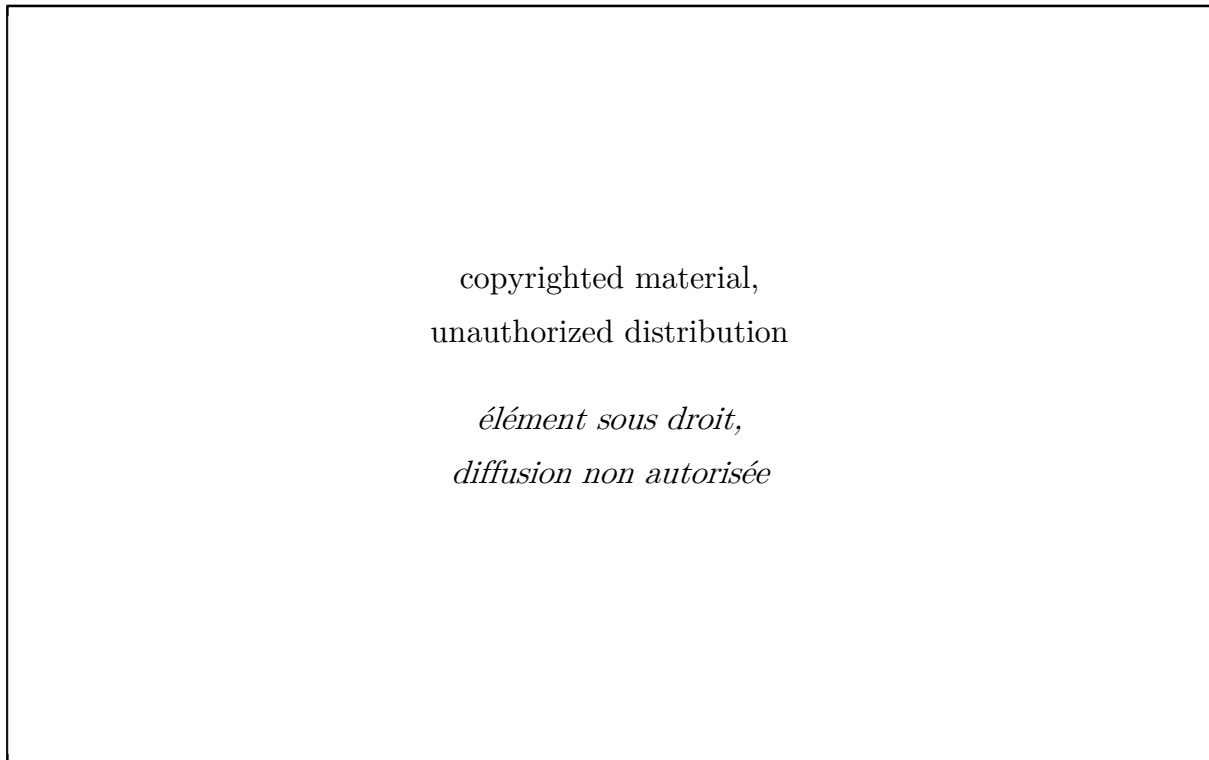


Figure 16 – Brain Regions Involved in Autonomic Control and Cognition

Note. Conjunction analyses for three common task categories and the two ANS division to identify sympathetic and parasympathetic contributions to CAN modulatory regions observed for different tasks. pSMA, Presupplementary motor area; pMCC, posterior MCC; SI, primary somatosensory cortex; Thal, thalamus; mdThal, mediodorsal thalamus; VTA, ventral tegmental area; Hyp, hypothalamus; PAG, periaqueductal gray; L, left; R, right. Reproduced from Beissner et al. (2013).

Arousal is tightly linked to sympathetic regulation and Salience Network activation, and consequently disengagement of the DMN, to initiate action readiness. It not only facilitates motor processes (fight-or-flight) but also executive cognitive processes associated with action selection, preparation and cognitive effort, for example during conflict resolution (Kobayashi et al., 2007). Particularly prominent neural structures in this process are the insular cortex and dorsal anterior cortex, which play a critical role in executive control (see Chapter 4.2). Elevated arousal levels have the potential to enhance cognitive functions, such as memory retrieval. In their famous work Yerkes & Dodson (1908) propose that an optimal level of arousal for performance on a task exists. Performance relates to arousal in an inverted U shape, it improves with increased arousal, but after reaching the climax, further increases in arousal lead to a decline in performance. Though, the Yerkes-Dodson is probably far too simplistic to account for the complex interaction between arousal and cognition (Hanoch & Vitouch, 2004), its

usefulness in predicting learning outcomes (Broadhurst, 1957) and memory (Jeong & Biocca, 2012) has been confirmed. One possible explanation for this phenomenon is the connection between the peripheral state of arousal and the metabolic requirements of neuromodulatory transmitters. Brief episodes of physiological activation may amplify the action of neural metabolites, thereby promoting more strenuous cognitive processes (Quadt et al., 2022).

An important overlap autonomic of memory- and thought-relevant functions can also be observed at the ventromedial PFC and posterior cingulate cortex, which extends to the medial-temporal lobe, including the hippocampus. Consequently, autonomic regulation may affect memory formation and recollection especially in the context of the self. Furthermore, this interaction might be modulated by emotional affect due to the strong connection of ventromedial PFC with the amygdala and its involvement in social and emotional functions, such as fear extinction and positive states during rest.

5.3.2 Modular brain structures

From the previous chapters, we have seen various brain structures and networks that underlie the ANS regulation and cognitive functions. Importantly, it is notable that some of these circuits show structural overlap, which would give rise to the idea that a central processing scheme underpins both autonomic and cognitive processes. In the following, we will summarize, based on previous chapters and reviews, the most critical brain regions, with particular highlights on cardiac vagal control as well as cognitive/emotional processes, self-referential processing, memory, and future thinking.

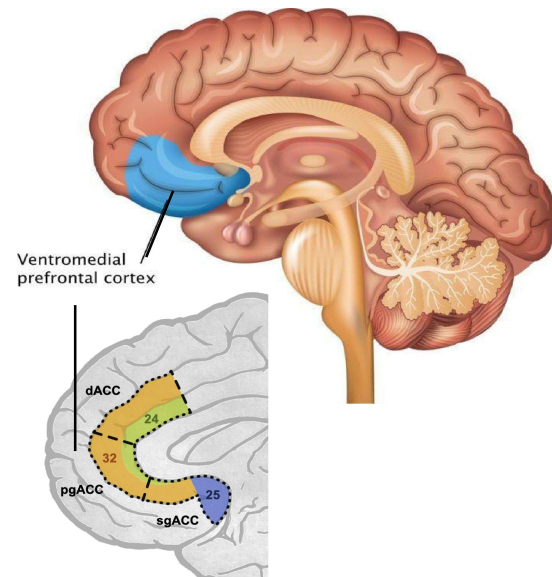
5.3.2.1 Ventromedial prefrontal cortex

5.3.2.1.1 Structure

The ventromedial PFC is positioned in the frontal lobe at the bottom of the cerebral hemispheres ([Figure 17](#)). It is often discussed in a wider context including the subgenual ACC, located just below the corpus callosum and above the inferior ventromedial PFC, as well as the pregenual ACC, located anterior to the corpus callosum and superior to the subgenual ACC. This cluster shows structural overlap is functionally related to the orbitofrontal cortex. It has been proposed that, while the ventromedial PFC seems to be more related to internal processing the orbitofrontal cortex is more associated with external processing (Bouret & Richmond, 2010).

Figure 17 – Ventromedial Prefrontal Cortex

Note. The ventromedial prefrontal cortex is part of the forebrain and in its wider definition also includes the structurally adjacent subgenual anterior cingulate cortex (sgACC) and pregenual anterior cingulate cortex (pgACC), which are part of the dorsal anterior cingulate cortex (dACC). Top image: Retrieved from <https://h10.homes/corteza-prefrontal-ventromedial>. Bottom image: Reproduced from Alexander et al. (2021, CC-BY 4.0).

**5.3.2.1.2 Autonomic processing**

The ventromedial PFC is in direct relationship with autonomic control at rest and when involved in cognitive tasks and motor processes (Bär et al., 2015; Beissner et al., 2013). Its function has been predominately linked to anti-sympathetic/parasympathetic drive (Hänsel & von Känel, 2008; Nagai et al., 2004; Wager et al., 2009). It plays a critical role in the CAN by controlling cardiovascular functions such that cardiac vagal activity increases with ventromedial PFC, potentially by increasing parasympathetic input to the baroreflex system (Hänsel & Kamel, 2008). Ventromedial PFC activity is linked with attenuating sympathetic state to control arousal states (Nagai et al., 2004) and is involved in allostatic control, due to its top-down influence on the adrenal medulla (Dum et al., 2016, 2019).. It has been proposed that sympathetic suppression is action specific (e.g., in low ambivalence avoidance), (Dundon et al., 2021). It is to note, though, that the ventral portion of the ventromedial PFC that contains an important sympathetic regulation cluster has been suggested to belong to a limbic network rather than the DMN itself (Yeo et al., 2011).

5.3.2.1.3 Cognition and Emotion

The ventromedial PFC is a highly interconnected structure that binds together large-scale brain networks involved in self-perception, emotion processing, decision-making, memory, and social cognition. Hence, functionally, this cluster, and most notably the ventromedial PFC, has been proposed as an integrative hub for self-referential, emotional, memory, sensory, and social information processing (Roy et al., 2012). As

part of the previously discussed cortical midline, the ventromedial PFC subserves interoception, exteroception, and the mental self and thus lies at the core, integrating internal and external information with the self.

An essential role of the ventromedial PFC is the representation and anticipation of value and affect relevant for value-based decision making and goal-directed behavior. Neuroimaging studies associate ventromedial PFC activity with the feeling of thirst, subjective decision value, or “self-relatedness” (Gusnard et al., 2001; Hare et al., 2009; Northoff et al., 2006; Qin et al., 2020). Also in primates, a strong recruitment showed to map value information related to actions and thirst (Bouret & Richmond, 2010). Studies on heartbeat-evoked potentials, as the brain response to each heartbeat, revealed that such responses in the ventromedial PFC predicted the degree of thinking about oneself (i.e., the self as the subject), (Babo-Rebelo et al., 2016) and self-reflection and subjective value encoding underlying preference-based decision making (Azzalini et al., 2021).

Given that the ventromedial PFC is fundamental for goal, value, and outcome representations as well as other components of the self, it is expected to mediate memory and future thinking processes. The medial PFC, being a more overarching structure involved in self-referential thinking and considerations of others, exhibits close interactions with key brain areas such as the hippocampus, anterior temporal lobe, and posterior cingulate cortex (Campbell et al., 2018; McCormick et al., 2018; St. Jacques et al., 2011). The integration of event simulations with higher-order autobiographical knowledge is suggested by [D’Argembeau \(2020\)](#) and [Martinelli et al. \(2013\)](#), emphasizing the possible role of the medial PFC in integrating layers of autobiographical representations for mental time travel. Furthermore, numerous studies have demonstrated greater activation of the ventromedial PFC during higher-level self-referential cognition (D’Argembeau et al., 2007; Denny et al., 2012; Martinelli et al., 2013; Northoff et al., 2006; Yaoi et al., 2015).

Furthermore, the medial PFC is acknowledged for its established involvement in the retrieval of self-knowledge (Lieberman et al., 2019; Denny et al., 2012). It supports access to conceptual knowledge, facilitates simulations drawing on rich knowledge, and enables the simulation of people and social scenarios, particularly those involving location-specific interactions with individuals (D’Argembeau, 2020). This contribution extends to the construction of scenes, enhancing both episodic detail and coherence, especially within broad scenarios, for both retrospective and prospective simulations.

In addition, the ventromedial PFC is implicated in signaling the anticipated value of an event, thereby mediating farsighted decisions. Lesion studies underscored its critical role in episodic foresight (Bertossi et al., 2016, 2017; Bertossi & Ciaramelli, 2016; Kurczek et al., 2015).

Another notable aspect is the association of the ventromedial PFC with emotions. The associated orbitofrontal cortex is structure, well known to be responsible for the reinforcement of affective states via reward processing and linking reward with stimuli, while the subgenual ACC in specific is essential for positive emotional appraisal and emotion regulation (Scharnowski et al., 2020). Given the integrative functions involving the self and emotion-related representations, alterations in ventromedial PFC activity and connectivity, particularly with other brain structures, are anticipated to impact “hot” cognitions associated with emotions and value. Indeed, ventromedial PFC plays a multifaceted role in emotional regulation, exhibiting connections to both positive emotional states and the suppression of negative emotions.

Studies have demonstrated that the regulation of positive emotions is linked to heightened top-down signals originating from the prefrontal cortices. These signals concurrently modulate bottom-up emotional responses within the amygdala (Koush et al., 2019; Young et al., 2018; Zotev et al., 2014). Specifically, the upregulation of self-referential positive emotions (involving a first-person perspective) has been consistently associated with the direct influence of the ventromedial and dorsomedial PFC onto the bilateral amygdala (Koush et al., 2019).

In the realm of inhibitory control, Munakata et al. (2011) propose a framework illustrating that activating the ventromedial PFC suppresses the fear-related dorsal raphe nucleus. It forms a crucial circuit with the amygdala, exerting inhibitory control over fear conditioning and emotion regulation (Dundon et al., 2021). This control extends to the representation and anticipation of stimuli with negative affect. In addition, the ventromedial PFC demonstrates the ability to modulate arousal states through inhibitory control, influencing the perceived aversiveness or threat level of stimuli. Consequently, through inhibitory control, it allows for the extinction of fearfully conditioned stimuli and positive behavioral adaptation after encountering adversity or trauma (Hänsel & von Känel, 2008). The inhibitory features associated with ventromedial PFC activation, which contribute to the effective suppression of arousal and negative emotional responses, likely influence memory outcomes. Notably, cardiovascular arousal serves as a contextualizing factor for the memory of fearful

stimuli. Deviations from this context, as evidenced by varying activities of the ventromedial PFC, may disrupt memories (Wing et al., 2021).

Decreasing arousal, fear behavior, and memory representation as well as enhancing coping responses is particularly relevant in conditions such as anxiety and post-traumatic stress disorder. Studies employing anodal transcranial stimulation of the ventromedial PFC in healthy adults have shown a reduction in arousal towards visual stimuli, highlighting the role of the ventromedial PFC in extinguishing arousal (Nejati et al., 2021). Moreover, the dysregulation of the ventromedial PFC circuit is implicated in various psychopathologies such as anxiety, PTSD, and depression. For instance, in individuals with cocaine addiction, characterized by deficits in inhibitory control, the ventromedial PFC is hyporeactive during inhibitory control processes (Kaufman et al., 2003). However, administering methylphenidate results in increased ventromedial PFC activation, accompanied by improvements in inhibitory control function (Li et al., 2010). This underlines the significant role of the ventromedial PFC in influencing inhibitory control underlying cognitive and physiological self-regulation processes (Hänsel and von Känel, 2008; Thayer et al., 2009; Maier and Hare, 2017) with potential implications for understanding and treating various neuropsychiatric conditions.

This interplay highlights the multifaceted role of the ventromedial PFC in autonomic, cognitive, and emotional processes, ranging from self-referential processes, and emotion regulation to memory and future thinking. Thus, it seems possible to influence the ventromedial PFC by changes in the cardiovascular system, which in turn may influence cognition.

5.3.2.2 Dorsal anterior cingulate cortex

The dorsal ACC, located in the medial part of the frontal cortex, is with its ventral-anterior parts (subgenual, pregenual) directly adjacent to the ventromedial PFC.

In contrast to the ventromedial PFC, the ACC is related to sympathetic drive that drives context-driven changes of bodily arousal states (Critchley et al., 2003). It regulates basic autonomic functions, including blood pressure and heart rate according to environmental demands. For example, when performing a physical or cognitive task (involving cognitive effort), the ACC will mediate a rise in blood pressure (Critchley et al., 2000).

As discussed earlier, the ACC is core node of the salient network and is crucial to executive control. It engages in salience processing, detecting conflicts, monitoring errors, and exerting cognitive control over attention and behavior, and thus a key region for regulating goal-directed behavior. ACC activity is associated with psychophysiological arousal as it maps mental and physical stress and therefore behavioral and cognitive effort (Paus et al., 1998). Consequently, cognitively very challenging tasks will evoke the recruitment of the ACC to initiate arousal processes, that potentially support cognitive processes.

5.3.2.3 Insula

The insula, or insular cortex, is a folded cortical region deep within the lateral sulcus, which separates the frontal and temporal lobes. The insula is a key component of the CAN (Chapter 1.2), cortical midline (Chapter 3.3.2), and Salience Network (Chapter 4.5.3) involved in the processing of interoceptive and emotional information (Nieuwenhuys, 2012). The insula is a region often discussed in the overlap between the networks due to its integrative function of sensory inputs ability to shift between internally focused (default mode) and externally focused (salient) modes of processing.

The insula is integral to the processing of visceral sensations, including those related to the internal state of the body such as responses from the cardiovascular system, hunger, thirst, and physiological conditions like pain and temperature. Connected with the ANS, the insula helps regulate autonomic functions such as heart rate, blood pressure, and respiratory rate. It integrates sensory information from the body to guide appropriate physiological responses.

Moreover, the insula is involved in the processing and integration of emotional experiences internal body state and representations (Singer et al., 2009). It integrates nociceptive information and contributes to the emotional and affective aspects of pain experience. Furthermore, it plays a role in subjective feelings and the awareness of emotions, contributing to empathy, compassion, and the understanding of emotional states in oneself and others. The integration of emotional and physiological also informs decision-making processes, particularly those related to risk and uncertainty. By contributing to assessing potential choices based on psychophysiological aspects, the insular also plays a role in the allocation of attention and the regulation of cognitive resources and it thus implicated in cognitive control.

5.3.2.4 Amygdala and locus coeruleus

The amygdala is a fundamental component of the limbic system, emotion processing and emotion regulation. Most notably the left amygdala has been linked to both sympathetic and parasympathetic regulation for affective as well as cognitive processes (Beissner et al., 2013). Just as the insular the amygdala is sensitive to visceral afferent (interoceptive) arousal signals during threat and integrating these in the construction of an emotional fear response. As reviewed above, the amygdala has important projections to the medial PFC which exercise inhibitory control on the amygdala to regulate fear conditioning and behavior. Besides, it is involved in mental effort, attention regulation, and most notably in the formation and modulation of emotional memories, particularly those associated with fear and reward. The amygdala interacts with the hippocampus as well as the locus coeruleus which contribute to the consolidation of emotionally charged memories and enhanced emotional processing.

The locus coeruleus is a nucleus in the brainstem and is the primary source of norepinephrine (noradrenaline) release. It has widespread projections to various brain regions, including the amygdala, hippocampus, and medial PFC. The locus coeruleus modulates the amygdala's activity through the release of norepinephrine, influencing emotional responses and memory consolidation. Autonomic function further contributes to this modulation, impacting epinephrine release, which, in turn, regulates LC activity and norepinephrine release in the aforementioned brain regions.

The interplay extends beyond the local neural network, as the vagus nerve plays a significant role in this cascade. Ascending branches of the vagus nerve and projections of the nucleus of the solitary tract extend to limbic structures, activating norepinephrine release during the crucial phase of memory consolidation. For example, during stress or arousal, the locus coeruleus is activated, leading to an increased release of norepinephrine. This release enhances the amygdala's sensitivity to emotional stimuli, facilitating a more robust emotional response and consolidating emotionally charged memories. Typically, stressful, or emotionally significant events are often better remembered, contributed by the influence of the locus coeruleus on the amygdala. In turn, the amygdala can affect the locus coeruleus by modulating its activity. This reciprocal connection allows for a bidirectional regulation of emotional and stress responses.

The convergence of emotion-related pathways with autonomic functions underscores the integrative nature of the neural circuits involved in regulating emotional and memory-related phenomena.

5.3.2.5 Posterior cingulate cortex

The posterior cingulate cortex is thought to contribute to the CAN through its connectivity with other autonomic centers and is implicated particularly in the context of cardiovascular regulation. For instance, [Critchley et al. \(2003\)](#) found that the posterior cingulate cortex, along with other regions such as the ACC, is associated with the central representation of autonomic arousal. Moreover, it is another key hub of the DMN strongly connected to other brain regions involved in self-referential thinking and introspection and relatively deactivated during attentionally demanding task ([Raichle et al., 2001](#)). Thus, its major role has been ascribed to internally-directed cognition. It is important to note that the functions of the posterior cingulate cortex are interconnected and often involve interactions with other brain regions within the DMN (e.g., precuneus, ventromedial PFC) and the hippocampus. In this line, the posterior cingulate cortex is supposed to engage in processing information about oneself, including autobiographical memories, personal experiences, and traits, self-referential emotional experience. The posterior cingulate cortex is sometimes associated with higher-order consciousness and awareness. Its activity has been linked to the sense of self and the integration of various cognitive and sensory inputs to create a sense of a coherence of the self and outer world. It is notably involved in autobiographical memories retrieval, future thinking, visual-spatial imagery ([Irish et al., 2012](#); [Raichle et al., 2001](#); [Rolls, 2019](#); [Wagner et al., 2005](#)), and self-referential thoughts and worry (e.g., [Christoff et al., 2009](#); [Paulesu et al., 2010](#)). The posterior cingulate cortex, nonetheless, is a heterogeneous structure which has been attributed with diverse roles in manipulating arousal states and attention focus by influencing other brain circuits ([Leech & Sharp, 2014](#)).

This integration of autonomic functions within the broader context of the DMN highlights the complexity of the posterior cingulate cortex 's contributions to both cognitive and autonomic processes.

5.3.3 Association between HRV and anatomical structures

Several studies have delved into the intricate association between HRV and various brain structures, shedding light on the neural mechanisms underpinning autonomic

cardiac control, emotional regulation, and psychological resilience. Thayer et al. (2012) conducted a comprehensive meta-analysis that linked regional cerebral blood flow in the ventromedial PFC encompassing parts of the ACC, and the amygdala to HRV. Sakaki et al. (2016) explored correlations between RMSSD and medial PFC – amygdala connectivity, specifically focusing on emotional regulation in both young and older adults. Their findings illuminated age-related differences in the relationship between HRV and the connectivity of these emotional processing regions. An age influence on the relationship with HRV was also found in a recent study that explored the relationship between tonic HRV during an emotion regulation task and functional connectivity of the amygdala in younger and older adults (Tupitsa et al., 2023). Notably, greater tonic HRV was found to correlate with weaker amygdala-medial PFC connectivity in younger adults but not in older adults. Furthermore, task-based covariations were observed between tonic HRV and functional connectivity of the amygdala with the ventrolateral PFC and with the posterior cingulate cortex. A positive association of emotional task-related HRV has been also demonstrated with the subgenual ACC activity, a region, as we have seen, that is also crucial for emotion regulation (Lane et al., 2013). Another study employed fMRI data to investigate functional resting-state connectivity, revealing that connectivity strength between the perigenual ACC within the medial PFC and HRV was more strongly associated with autonomic cardiac control than connectivity within the DMN and the Salience Network in midlife adults (Jennings et al., 2016). Structural aspects of the prefrontal brain, including the orbitofrontal cortex and ACC, have also been implicated in HRV. Two studies demonstrated a positive correlation between greater structural thickness in these regions and higher RMSSD, highlighting the structural substrates linked to autonomic function (Winkelmann et al., 2017; Yoo et al., 2018). Carnevali et al. (2018) extended these investigations into psychological resilience, demonstrating the involvement of the structural morphology of the ACC in both HRV and psychological resilience.

In addition, many other neuroimaging studies have found a correlation between changes in neuronal activity in the brain and fluctuations in HRV. Key brain nodes have been elucidated, notably the medial frontal, anterior cingulate, and insular cortices (Chang et al., 2009, 2013; Critchley et al., 2003; Kumral et al., 2019; Sakaki et al., 2016; Schumann et al., 2021; Thayer et al., 2009, 2012) as well as important subcortical hubs, including among others the amygdala, hypothalamus, and brain stem (Chang et al., 2009; Kumral et al., 2019; Manuel et al., 2020; Mulcahy et al., 2019; Sakaki et al.,

2016). For example, temporal changes in HRV have been correlated with dynamic changes in prefrontal connectivity, involving regions such as the middle cingulate cortex, left insula, supplementary motor area, dorsomedial PFC, and ventromedial PFC (Schumann et al., 2021). In specific, psychological stress has been shown to suppress the baroreflex and HRV; effects that were tightly linked to the activity within cingulate, insula, amygdala, and periaqueductal grey matter (Gianaros et al., 2012).

A recent systematic review focused on resting HRV in healthy subjects regarding its relationship with brain structure, activity, and connectivity (Matusik et al., 2023). Structurally, the study revealed that orbitofrontal cortex thickness exhibits a correlation with HRV, and this correlation diminishes with age. This observation is also consistent with the findings by cortical thickness increases with after HRV biofeedback which increases HRV (Yoo et al., 2022). Notably, the study underscored that the strongest correlations between HRV and structural brain properties were observed in the cingulate cortex. Regarding brain activity, the strongest correlations with HRV were identified in various brain regions, including the insula, cingulate cortex, frontal cortex, PFC, hippocampus, thalamus, striatum, and amygdala. Furthermore, the review delved into the connectivity between HRV and specific brain regions. It was found that HRV positively correlates with connectivity in key regions such as the amygdala, cingulate cortex, and PFC. This indicates that the functional connectivity of these regions is associated with the variations in HRV, further highlighting the intricate interplay between autonomic regulation and neural networks.

In summary, the findings shed light on the multi-faceted relationship between HRV and the human brain. It suggests that not only does HRV correlate with structural properties of certain brain regions, but it is also intricately linked to the activity and connectivity of a network of brain regions involved in autonomic control and cognitive functioning, specifically emotion regulation. Associations have also been evidenced for structures involved in self-processing, underscoring the connection of HRV with self-referential processing, memory and thought.

5.4 Associations between HRV and Cognition

In the last two decades, a vastly growing research body has started to investigate the relationship between individual levels of HRV and numerous behavioral measures (see for a review, Forte et al., 2019; Magnon et al., 2022). Psychophysiological associates have been derived from various populations, mostly young, healthy adults. Pathology

can strongly influence this relationship due to disturbances in cardiovascular regulation. Since the target sample of our studies is young, healthy adults, the following sections will mainly focus studies on young, non-clinical samples, if not stated otherwise. Cognitive functions are considered in regard to the psychophysiological models and brain circuits underlying autonomic control and mental processes that should connect to HRV. This, as summarized from the sections above, most notably envelopes cognitive processes that involve executive functions (or cognitive control), self-referential processing, or aspects of emotion regulation including past and future thought.

5.4.1 Cognitive control

As discussed earlier, cognitive control envelopes various executive functions that aid in selecting, maintaining, updating, and inhibiting information and guides many different processes such as flexible and adaptive thinking.

In their early review, Thayer et al. (2009) demonstrated that executive functions associated with the PFC, including attention, working memory, and inhibition were linked to HRV on an individual and population level. Higher levels of HRV were specifically associated with better inhibition of No-Go responses and better reaction times and accuracy in working memory task which also involves inhibitory control to prepotent responses. For instance, detraining male military sailors decreased scores of HF-HRV and RMSSD, while there were no re-test improvements in working memory (i.e., reaction time, accuracy) compared to sailors that kept training (Hansen et al., 2004). Similarly, a positive link between HRV with working memory and sustained attention was reflected in military sailors when comparing HRV and cognitive performance between two groups exhibiting high or low RMSSD (median-split), (Hansen et al., 2003). Gianaros et al., 2004 furthermore underlined that those results might relate to increased cerebral blood flow in the PFC correlated with HF-HRV during working memory task in mid-to-late-life adults (Gianaros et al., 2004).

Further ample evidence has been found supporting a link between vmHRV and the capability to discriminate and inhibit salient or pre-activated stimuli. Regulating cognitive interference, as measured by the Stroop effect (Stroop, 1935), was positively associated with resting state HRV in multiple studies (Forte et al., 2023; Laborde, Allen, Borges, Hosang, et al., 2022; Zeki Al Hazzouri et al., 2018). In a large sample of 2118 mid-life adults, SDNN even predicted Stroop performance assessed 5 years later

(Zeki Al Hazzouri et al., 2018). Moreover, there is some evidence that correlations seem to be specific to suppression success rather than processing speed of pre-potent stimuli, as higher RMSSD predicted lower Stroop error rates and but not reaction time (Laborde, Allen, Borges, Hosang, et al., 2022). Also, in another cognitive conflict task, the Eriksen Flanker task, which measures sustained and inhibitory control mainly based on accuracy, higher resting HRV was associated with better performance (Sørensen et al., 2019; D. P. Williams et al., 2016). Similarly, higher resting HRV linked to greater response accuracy in Go/NoGo Tasks in problematic internet users (Moretta et al., 2019). It has been theorized that possible confounders such as sex, impulsivity or the body mass index might mediate the relationship between HRV and inhibition. Ottaviani et al., (2019) showed that resting HRV was related to the performance to inhibit strongly activated responses based on two tests (Rule Shift Cards, and Hayling Sentence completion Test) after controlling for such confounders. The implication of HRV for inhibition and attention also extends to appropriate choice selection. In this line, Forte et al. (2022) presented in their review the beneficial role of higher resting HRV in decision-making, especially under risk and uncertainty. Overall, vmHRV associates robustly with cognitive control, but it is to note that those correlations, as revealed by two meta-analyses, remain very small ($r = 0.09$, Holzman & Bridgett, 2017; Zahn et al., 2016; $r = 0.15$).

5.4.2 Long-term memory

Some empirical evidence pointed out a positive association between HRV and verbal short-term and long-term memory in the middle-aged (Shah et al., 2011) and elderly population (Frewen et al., 2013; Shah et al., 2011; Zeki Al Hazzouri et al., 2014). However, inference to the younger, healthy adults would be flawed since HRV and memory strongly decline with age. Moreover, negative results in elderly adults were also observed for both short-term memory (Britton et al., 2008) and long-term memory (Mahinrad et al., 2016). Preliminary findings derived from young, healthy adults showed a positive link between vmHRV and performance scores for memory processes that particularly involve cognitive control. Higher resting HRV was found to predict enhanced capability to suppress memories Gillie et al., (2014a) and false memories (Feeling et al., 2021) that may arise from pre-activation. Memory suppression was assessed using the Think/No-Think paradigm, which is close to the Go/No-go Task involving attentional and inhibitory control. The false memory paradigm was based on the Deese-Roediger-McDermott task, which required participants during memory

recognition to discriminate true memories from new but pre-activated stimuli that can be easily confused as true memories. Both studies used neutral word stimuli and thus did not manipulate the emotional mode. In addition, Magnon et al. (2022) could extend the results by showing that HRV positively correlated with memory discrimination between humanoid characters with low visual distinctiveness. Like in the previous study, they demonstrated that the relationship was moderated by the degree of distinctiveness between stimuli (visual, semantic). Although, their setup assessed memory discrimination in a more ecological way (realistic fictional characters performing actions), it produced a very similar effect size ($r \approx 0.33$) compared to the previous studies (Feeling et al., 2021; Gillie et al., 2014). In summary, it can be observed that vmHRV associates with memory performance, likely due to the involvement of cardiac vagal activity in cognitive control to self-regulate behavior towards an adaptive response.

5.4.3 Emotional processing

Previous theoretical models underpin the link of autonomic control with emotional processing due to the involvement of limbic structures and connection with the PFC. Hence, the emotional content and the level of arousal are critical to the relationship between HRV and cognitive processes. Indeed, an interaction was found between inhibitory control and the emotional response related to the stimuli (Krypotos et al., 2011). In this context, in young, healthy participants, who completed an emotional stop-signal task, higher resting HRV supported response inhibition of high arousing negative pictures but not of low-arousing neutral. The moderating effect of valence and arousal was underlined by the finding that HRV plays a role in downregulating attention to negative stimuli in anxious but not healthy volunteers (Forte et al., 2021). Moreover, HRV was associated with better inhibition of conditioned fear in young, healthy adults (Wendt et al., 2015).

While negative emotions (e.g., anxiety, frustration, stress) have been associated with low HRV, positive emotions relate to higher HRV levels (McCraty et al., 2009). Especially, feelings of compassion, love, and appreciation seem to be reflected in increased HRV, as demonstrated in a meta-analysis (Di Bello et al., 2020). Notably, the effect size was medium and larger for measures of RMSSD or HF-HRV than RSA. If greater HRV is linked to lower negative and more positive emotional processing, this might also have important consequences on more complex behavior. Indeed, previous studies emphasized the role of HRV in prosocial behavior (Kok, 2022; Muhtadie et al.,

2015; Stellar et al., 2015) perception of safety, and physiological defensive responses (Brosschot et al., 2017; Petrocchi & Cheli, 2019). The results are consistent with the polyvagal theory, corroborating the hypothesis that the vagal nerve is involved in pro-social behavior and safety (Porges, 2007, 2022) and thus linked to the expression and regulation of emotions. Such behavior and perception are also accompanied by the ongoing stream of thoughts we encounter every day. Consequently, it seems very likely, if HRV affects or is an output measure of emotional and executive processes influencing behavior, it will also associate with the way one thinks.

5.4.4 Thought processes and the self

An important aspect of thought been studied, other than laboratory-assessed memory performance (see 4.6.2.), is perseverative cognition (Brosschot et al., 2006). The latter refers to continuous thinking about negative past and future events and is strongly tied to mental imagery, ruminative thoughts, and the development of depression. Theoretical frameworks based on empirical evidence (Ottaviani et al., 2017; Thayer & Friedman, 2002) propose that regulatory inhibition guides efficient mental functioning but when diminished gives rise to perseverative cognition; a state that can be evaluated by characterized by HRV. Autonomic markers have been identified (Ottaviani et al., 2016), showing that perseverative cognition associates with lower HRV but also increased levels of blood pressure, heart rate, and cortisol levels. It can be seen as a thought pattern previously adaptive mind wandering becomes rigid and inflexible, which will be also reflected in autonomic rigidity (low HRV), (Ottaviani et al., 2013, 2015). Thus, given its ties to mind wandering and the DMN (Hamilton et al., 2015; Zhou et al., 2020) it may also involve a substantial part of self-directed thought, and thus self-referential processing, in an emotional context. Frequent mind wandering is per se not health decreasing, probably because mal-adaptive self-rumination is cancelled out by adaptive self-reflection (Takano & Tanno, 2009). However, during perseverative cognition, rumination takes the upper hand. It has negative consequences on task performance which, unlike mind-wandering, are also reflected in autonomic dysregulation and, thus, HRV (Ottaviani et al., 2015). Hence, studying the relationship between HRV and adaptive self-thinking might provide important clinical leads but has not yet come into research focus.

The DMN is known for self-referential cognition, but its hubs are suppressed when switching attentional focus from internal to external. One study showed this neural activation is attenuated in anxious but also healthy subjects with higher trait

perseverative, and HRV predicts those neural changes during attention switch. Furthermore, low HRV was found not only to predicted traits of higher ruminative thinking and depressive symptoms but also to mediate the relationship between rumination and depressive symptoms around three years later. It thus seems that high HRV underlies thought processes that can prevent generation of mental disorders. Underlying causes might have been greater executive control and emotion regulation, which are linked to vmHRV and aid in controlling memories (Gillie et al., 2014) and thoughts (Gillie et al., 2015). The latter study found that higher resting HRV moderated greater deliberate and automatic suppression of intrusive thoughts related to a personally relevant and negative (i.e., car accident of a loved one). When asked to suppress thoughts, participants with higher HRV could reduce thought frequency, independent of the suppression effort. On the contrary, low HRV participants could deliberately decrease intrusive thoughts only when suppression effort was low. These results suggest that higher HRV is associated with better cognitive control functions that act automatic and effortless in regulating (self-related) thoughts, especially when they are emotionally negatively valenced. Furthermore, research suggests that perseverative cognition also impairs the positive valence system when processing self-relevant information by increasing prediction errors between expected and obtained goals (Schettino et al., 2021). Thus, individual levels or changes in HRV may also predict positive self-referential processing. Furthermore, the role of HRV in emotional self-processing has been underlined by the observation that high levels of HRV are positively associated with the capability to recognize emotions (Quintana et al., 2012). It thus seems plausible that HRV's role in self-regulation, besides thought suppression, may also extend to support adaptive self-related thought, for example, by down- or up-regulating emotional or self-referential components (e.g., perceived valence, self-importance, or self-focus) when facing internal or external cues.

To the best of my knowledge, no study has so far investigated the direct relationship between the self-referential processing system in thought and memory with HRV. A possible relationship between self-referential processing and HRV was hinted in a study with young, healthy women (Herbert, 2021). In this study, the Interpersonal Reactivity Index (M. H. Davis, 1980) was assessed that presents word pairs consisting of either a positive, negative or neutral noun preceded by a pronoun which was either self-descriptive (“my”), other-descriptive (“his”), or self- or other-descriptive (“the”), (e.g., “my joy”, “the house”, “his fear”). Each pair was followed by a rapid valence judgement (positive, neutral, negative), and valence congruency and response reaction time were

coded. An exploratory analysis suggested a positive correlation between RMSSD and the total score, indicative of emotion processing related to self-other referential processing. Another study on depressive individuals enrolled either in 8 weeks of Mindfulness-Based Stress Reduction intervention or waiting list showed that changes in intervention related changes in self-criticism, a form of negative self-bias, correlated negatively correlated with changes in HR. A magnetoencephalography study revealed that neural responses of the heartbeat encode self-related thoughts during mind wandering in the DMN (Babo-Rebelo et al., 2016). The “I” competent (involvement as an agent) related to the ventral precuneus, and the “Me” component (degree of thinking about oneself) was associated with the ventromedial PFC, however, none of the peripheral physiological measures including HRV was associated with self-relatedness. However, it is to be noted that HRV was assessed as the standard deviation of trial-based interbit intervals from only 20 participants and thus might have been a sensitive metric to capture self-referential processing.

It remains an open question whether HRV also underlies self-referential processing and its interaction with emotional and cognitive control functions that shape how we think.

5.4.5 Tonic and phasic HRV during cognitive activity

It is to note that almost all above discussed findings are based on correlations between behavioral outcomes and HRV measured at rest. While prior research has predominantly focused on assessing resting HRV, fewer studies have delved into HRV during tasks. In line with the Vagal Tank Theory, phasic reactivity (i.e., baseline change), and recovery (i.e., return to baseline) values or tonic measures during the cognitive activity might provide a deeper insight into the interaction between autonomic control and the mind. An expanding body of literature has started to explore phasic changes in HRV, encompassing reactivity to and recovery from task-related stressors and events in relation to baseline HRV levels (Butler et al., 2006; Denson et al., 2011; G. Park et al., 2014; Segerstrom & Nes, 2007), (see for a review, Laborde et al., 2018).

It is well recorded that HRV decreases (and heart rate increases) during cognitive, especially stressful, activity (Järvelin-Pasanen et al., 2018; Kim et al., 2018; Taelman et al., 2009). This also includes cardio-vascular parameters like reduced baroreflex sensitivity and RSA, which demonstrate an overall decrease in PNS and increase in SNS activity (Duschek et al., 2009). These autonomic markers will then return in

direction baseline during subsequent recovery, and the respective changes between phases (reactivity, recovery) might be reflective of self-regulation efficacy (Laborde et al., 2018).

While values are usually considered separately, combining measures into one model might yield better predictions (Magnon, Dutheil, et al., 2022). By testing different combinations of resting and phasic measures in a Bayesian multiple regression analysis to predict decision-making, the authors showed that the best (and extreme) prediction was made when reactivity and recovery were included.

Findings on HRV reactivity during thought suppression, indicate that such chronic suppression places a strain on regulatory resources, leading to diminished heart rate variability (HRV) responsivity (Garland et al., 2012). This effect was particularly prominent when individuals with a high trait for suppression engaged in intensive suppression of thoughts related to drinking under stressful conditions. These results align with the proposition put forth by Gillie et al., (2015), suggesting that trait (resting) HRV serves as an indicator of the ease or effortlessness of suppression. Building on this notion, [Legrand et al. \(2020\)](#) contribute further insights by demonstrating that the impact of thought suppression, as observed in the Think-/No-Think task, is reflected in cardiac slowing during thought suppression. Importantly, this suggests that the effects of thought suppression might be quantifiable during cognitive activities, providing a measurable physiological marker for this cognitive process.

Empirical evidence consistently supports the idea that increases in phasic HRV signify self-regulatory effort and successful emotion regulation (Butler et al., 2006; Denson et al., 2011; Ingjaldsson et al., 2003; G. Park et al., 2012, 2014; Segerstrom & Nes, 2007). Importantly, the resting levels of HRV have been identified to positively interact with such phasic HRV increases (Park et al., 2014). For example, women with higher resting HRV exhibited more substantial phasic HRV increases during successful voluntary emotion regulation through reappraisal and emotional suppression compared to those with lower resting HRV (Butler et al., 2006). Similarly, robust positive correlations have been observed between resting HRV and HRV measured during stress (Wang et al., 2009) and a demanding working memory task (Heffner et al., 2022). Collectively, empirical evidence suggests that individuals with higher resting HRV are more likely to exhibit phasic HRV increases when confronted with stimuli or events

demanding self-regulatory effort. This pattern reflects a more adaptive response to task demands and successful emotion regulation.

Studies on memory outcomes, on the contrary, indicate no robust link between memory retrieval success and on-task HRV (Hilgarter et al., 2021) or vmHRV reactivity at encoding (Paige et al., 2020). A reason might be, why tonic resting but not tonic on-task or phasic measures predicted memory could be that these studies measured recognition memory relying less on cognitive control compared to the memory suppression and discrimination tasks discussed earlier (Feeling et al., 2021; Gillie et al., 2014; Magnon, Mille, et al., 2022).

5.4.6 Influencing factors and limitations

When considering the factors that influence the relationship between HRV and cognitive function, several factors and limitations emerge. Health condition, age, and potential inconsistencies in the literature are critical factors shaping this relationship.

Age emerges as a key determinant, with studies revealing a significant association between lower HRV and impaired cognitive function (Magnon, Vallet, et al., 2022). For instance, in individuals aged 50 and over, lower HRV during resting and paced breathing periods was linked to worse global cognitive function (Frewen et al., 2013). Moreover, among older adults at high risk of cardiovascular diseases, lower resting HRV correlated with poorer inhibitory control and processing speed tasks, with lower HRV predicting a steeper decline in processing speed over time (Mahinrad et al., 2016).

Moreover, multiple studies, have not found a robust relationship between HRV and cognitive function (Britton et al., 2008; Duschek et al., 2009; Jennings et al., 2015; Mann et al., 2015). For example, two studies examining middle-aged adults found no reliable correlation between resting HRV and cognitive function (Britton et al., 2008, Mann et al., 2015). Notably, Mann et al., 2015 showed that an initial association between HRV and EF diminished when controlling for age. The age-related decline in both HRV and cognitive function introduces a challenge, as controlling for age may mask associations between these variables.

In addition, the general prediction that HRV is universally adaptive has limitations. Research indicates that this relationship may be specific to executive functions involving inhibition and working memory components (Jennings et al., 2015). Moreover, considerations from neurophysiology, medicine, and cognitive and social

psychology reveal potential drawbacks to excessive cardiac vagal control. Factors such as extreme levels, abnormal heart rate patterns in the elderly, and elevated cardiac vagal control in individuals with eating disorders may have deleterious consequences. Motivation also emerges as a potential moderator, with social psychology and motivational accounts emphasizing the need to clarify how motivation interacts with the vagal tank at different levels of analysis, including reactivity and recovery (Hagger et al., 2010; Kotabe & Hofmann, 2015; Laborde et al., 2018).

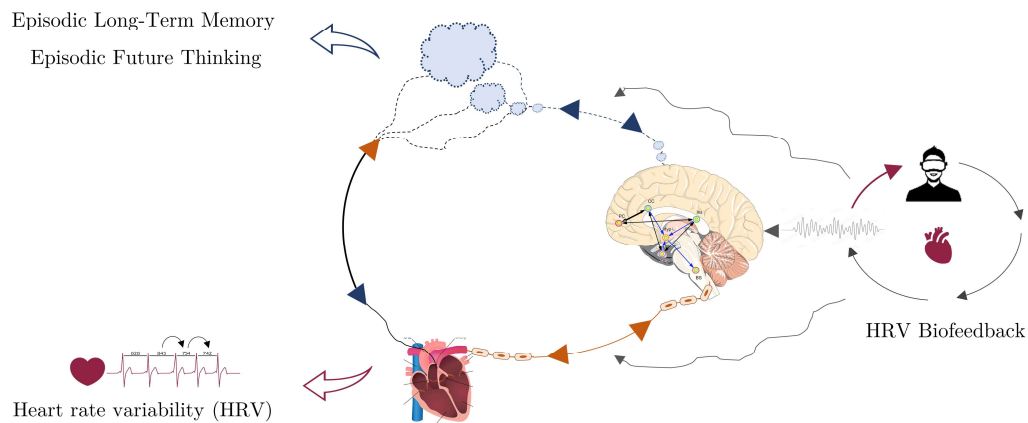
Furthermore, various factors influence the relationship between HRV and cognition. Studies, such as those by (G. Park et al., 2012, 2013), suggest that the correlation between HF-HRV and disengagement from fearful and veridical faces depends on presentation time and perceptual load. Additionally, higher HRV during baseline conditions is associated with a more robust increase in heart rate and decrease in HRV during tasks, as observed by in RSA and mid-frequency HRV (Duschek et al., 2009).

In conclusion, while there is evidence supporting the association between HRV and cognitive functions, various factors, including health condition, age, and motivational aspects, contribute to the complexity of this relationship. The nuanced interplay between these factors should be carefully considered in future research and clinical applications.

5.5 Chapter Summary

- Mind and body are connected by cognitive and psychophysiology theory.
- Allostatic policies by principles of homeostasis, allostasis (Chapter 1) and predictive coding involving affective and cognitive representations integrated into peripheral and central states regulate body functions and mental states.
- The Polyvagal Theory and Neurovisceral Integration Model based on the Central Autonomic Network ground the connection between cardiac vagal control and social, cognitive, emotional processes associated with brain functioning.
- The Neurovisceral Integration proposes an intricate network of neural pathways and inhibitory feedback loops, providing a common neural basis for psychological and physiological self-regulation.
- Vagally mediated HRV, which indexes brain-body interactions, emerges as an indicator of self-regulatory capacity and prefrontal executive functioning.
- A review of brain structures highlights the dual role in autonomic regulation and cognition (ventromedial PFC, posterior cingulate cortex – self-processes, anterior cingulate cortex – attention control, amygdala/ locus coeruleus – emotion processing).
- Ample evidence supports that higher resting HRV is over all related to better emotion regulation, cognitive control (specifically attention, working memory, and interference control), and overall health.
- The Vagal Tank Theory proposes phasic HRV as a sensitive measure of executive functioning and self-regulatory efficacy. Empirical evidence overall underlines the validity of the model.
- A few studies demonstrate that HRV is associated with memory and thought control relying on executive control.
- Associations between episodic autobiographical memory, episodic future thinking and mental self-processing have so far been discarded.

6 Chapter 6 – Neurocognitive Effects of HRV Biofeedback



As we have reviewed in Chapter 2, HRV biofeedback affects different physiological regulatory systems primarily through slow breathing. As the breathing frequency approaches resonance (~ 0.1 Hz), heart rate oscillation amplitudes increase and synchronize with the respiration mainly due to the combined effects of the baroreflex mechanism and RSA. Also, positive activation through motivating feedback and relaxing sceneries can contribute to optimized dynamic structures and interplay of physiological rhythms. Enhanced HRV through HRV biofeedback or slow breathing is theorized to augment vagal afferent outflow affecting brain functioning, most notably forebrain structures. However, besides an increase in cardiac vagal activity, other related pathways exist that may mediate an effect on the brain and, thus, cognitive functions. This chapter discusses theoretical and empirical evidence for the effect of HRV biofeedback and slow breathing near resonance breathing on the brain and cognitive functions.

6.1 Effects of High-Amplitude Cardiac Oscillations on the Brain

In a recent review, Mather & Thayer (2018) hypothesize that high amplitude physiological oscillations affect brain connectivity involved in emotion regulation and self-control. The authors posit that high heart rate oscillations strengthen connectivity in medial prefrontal regulatory regions, including the ventromedial PFC and ACC with connections to the amygdala. Given the structural involvement, it is also to be expected that those brain oscillations influence self-referential processes. They propose brain

effects to be mediated by various pathways, including fluctuations in blood flow, carbon dioxide levels, and sensory input from breathing and heartbeats, as well as the modulation of arousal, which will be reviewed below.

6.1.1 Blood flow

Hemodynamic oscillations in blood flow play a significant role in brain activity and connectivity. As reviewed in Chapter 1, oscillations in breathing, heart rate, and blood pressure are the driving factors for blood flow. Researchers have observed that heart rate contributes to fluctuations in blood-oxygen levels during fMRI studies (Chang et al., 2009; de Munck et al., 2008; Shmueli et al., 2007). In addition, [Pfurtscheller et al. \(2017\)](#) identified a synchronization between heart rate and blood-oxygen-level-dependent oscillations in the mid and posterior cingulate cortex, occurring at the resonance frequency of 0.1 Hz. Another intriguing aspect of hemodynamics is the vascular delay times of blood delivery to different brain regions. These delays offer insights into the partial reconstruction of resting-state networks, where the timing of blood delivery mirrors the patterns seen in coordinated network activity. Especially large resting-state brain networks (including the DMN) show connective coupling at lower frequencies (~0.1 Hz) that match the slow rhythm of resonance breathing (Tong et al., 2015). Furthermore, it is worth noting that there is a relationship between high resting cerebral blood flow to a local brain region and its connectivity with other, specifically more distal, hubs (Liang et al., 2013). In this context, strong associations between functional connectivity and blood flow have been established for the medial PFC, anterior and posterior cingulate cortex, and the insula. Accordingly, those brain regions are expected to be specifically affected by oscillations in blood flow through HRV biofeedback.

6.1.2 Breathing

Breathing influences brain activity through modulation of neural activity in the brainstem and carbon dioxide levels. Thoracic mechanoreceptors sense changes in lung volume, airway constriction, and vascular congestion that inform the respiratory center in the CAN (Brinkman et al., 2023) which, as previously discussed, influence neural pathways up the brain. Moreover, breathing rate and depth determine arterial levels of carbon dioxide as it is expelled during exhalation. Carbon dioxide can freely pass the blood-brain barrier where it forms hydron ions that trigger vasodilation (Kitazono et al., 1995; Nelson & Quayle, 1995), and thus, increased cerebral blood flow. Different areas of the brain exhibit varying responses to these fluctuations in carbon dioxide, a

phenomenon likely linked to their proximity to major blood vessels. Notably, the insula and midline cingulate regions show robust correlations in this regard (Chang et al., 2009; Di et al., 2013).

Furthermore, Mather & Thayer (2018) underlined that slower physiological oscillations typical for slow-paced breathing organize and stimulate faster local oscillations in the brain, evident in higher EEG frequency bands. Breathing induces synchronized oscillations that span across a substantial portion of the neocortex, and the power of gamma waves fluctuates in tandem with the phases of the respiratory cycle (Heck et al., 2017). When we breathe through our nostrils, this synchronization extends to the olfactory cortex, as well as the amygdala and hippocampus (Zelano et al., 2016). Within these limbic regions, nostril breathing aligns with higher frequency oscillations in the delta, theta, and beta ranges, harmonizing with the rhythm of respiration (Zelano et al., 2016). Furthermore, practicing slow-paced breathing for only five to nine minutes showed compared to a resting control group to increase frontal theta power (Cheng et al., 2018), a biomarker of cognitive control and attention (Cavanagh & Frank, 2014). In the same study, the authors also showed that slow-paced breathing reduced the mean power of the alpha and beta bands, which are associated with anxiety regulation (Mennella et al., 2017; Pavlenko et al., 2009), even during a seven-day follow-up period (Cheng et al., 2018) and that the most extended session duration (9 min) showed most significant neurophysiological changes.

As a result, the breathing element of resonance breathing biofeedback practice is poised to make a significant contribution to neural oscillatory activity and cerebral blood flow, particularly within the PFC and limbic regions during nostril breathing (Jelinčić et al., 2022).

6.1.3 Heartbeat

Heartbeats trigger EEG responses known as heartbeat-evoked potentials, which are notably pronounced within brain regions closely linked to executive, emotional, and self-processing. These regions encompass the medial PFC, cingulate cortex, insula, and amygdala (Babo-Rebello et al., 2016; H.-D. Park et al., 2018). Consequently, it is highly probable that heartbeats exert a significant influence on brain rhythms within these specific areas. This notion finds support in the observation that blood-oxygen-level-dependent activity within the ventromedial PFC exhibits a stronger correlation with heart rate compared to other brain regions (Ziegler et al., 2009). In addition, recent

fMRI data demonstrated that lower heart rate is related to higher functional connectivity within the Autonomic Central Network (de la Cruz et al., 2019). Since tonic heart rate and vmHRV exhibit an inverse relationship, largely due to the cycle length effect (Shaffer & Ginsberg, 2017), this result underlines that cardiac activity, possibly through slower and larger variations, positively affects functional connectivity within and between networks involved in emotional, executive, and self-processing. Furthermore, the general pattern underpins the assumption that the medial prefrontal and anterior cingulate regions display activity patterns associated with HRV (Thayer et al., 2012).

6.1.4 Arousal pathways

The stimulation of the baroreflex through resonance-paced breathing is also expected to have an impact on the arousal pathways in the brainstem. As previously mentioned, beyond its influence on heart function, the baroreflex pathway engages in bidirectional interactions with brainstem and forebrain regions responsible for regulating arousal (Silvani et al., 2015). Breathing directly stimulates these brainstem arousal centers, and the signals related to breathing and blood pressure mutually influence sympathetic activity. Consequently, resonance breathing is likely to modulate arousal, with oscillatory influences being a probable mechanism. This notion is supported by observations during slow breathing, where sympathetic nerve activity exhibits a phasic reduction, ultimately reaching the same peak level as observed under control conditions but displaying intermittent periods of suppression (Mozer et al., 2014; Oneda et al., 2010; Raupach et al., 2008). Consequently, it seems that HRV biofeedback induced high-amplitude oscillations in heart rate lead to the phasic suppression of sympathetic activity while promoting parasympathetic action that might have important consequences on stress and emotional processing.

In summary, slow, high-amplitude physiological oscillations specifically evoked through slow breathing (e.g., heart rate, breathing), affect brain activity and connectivity through hemodynamic, chemical, and sensory pathways. These oscillations can be assessed by HRV and should be most evident in the RSA, as it reflects heart rate oscillations in synch with breathing. Oscillatory activity is theorized to particularly stimulate brain changes in networks involved in emotional regulation, cognitive control, and self-referential processing. Furthermore, it seems that HRV biofeedback-induced high-amplitude oscillations in heart rate lead to the phasic suppression of sympathetic activity while promoting parasympathetic action, which might have significant

consequences on cognitive and emotional processing. The role of vagal afferents and further evidence for the effect of HRV biofeedback on these neural circuits and associated cognitive functions is discussed below.

6.2 Vagal Afferent Activity May Shift the Psychophysiological Setpoint

Parasympathetic modulation may play a pivotal role in mediating the effects of HRV biofeedback and slow-paced breathing on the brain. The polyvagal theory, neurovisceral integration model and psychophysiological coherence model all emphasize the role of the vagal afferent fibers that carry information from the periphery to the brain. In line with the previous section, phasic changes in vagal activity evoked by large physiological oscillations may be a major pathway to stimulate the functional reorganization of the interface between cognitive centers and the CAN. In accordance with the previously discussed psychophysiological models, this would lead to a shift in setpoints, or inner baseline, embodied in the organism's neurophysiological architecture and homeostatic settings (Quadt et al., 2022). This in turn would entail a measurable change in the activity and reactivity of autonomic and behavioral responses to the environment, e.g., the way one might think back into the past or forth into the future.

The notion that HRV biofeedback based on resonance breathing can alter baroreflex setpoints has been supported by the observation that repeated practice increases cardiac vagal activity and baroreflex gain independent from cardiovascular and respiratory functions (Lehrer et al., 2003, 2006, 2020). For instance, Lehrer et al. (2003) showed increased baroreflex gain and HRV-LF power as well as decreased heart after 10 training sessions. This demonstrates that there is neuroplasticity in the baroreflex system allowing regular practice of HRV biofeedback to increase afferent activity that may affect the brain. Moreover, the previous section demonstrated that there is ample evidence for the assumption that HRV biofeedback based on slow-paced breathing increases brain connectivity and activity between brain hubs involved in large-scale brain networks, including the CAN, DMN, Central Executive Network and Salience Network. This notion is supported by a recent fMRI study investigating the impact of HRV biofeedback intervention, comprising five training sessions per week for eight weeks (Schumann et al., 2021). Their findings revealed that functional connectivity in the ventromedial left PFC exhibited significant increases, particularly with the insula, amygdala, middle cingulate cortex, and lateral prefrontal regions. Moreover, they could

demonstrate that connectivity changes covaried with changes in HRV. Furthermore, another set of fMRI data, showed increased activity during slow-paced breathing in contrast to spontaneous rate breathing (Critchley et al., 2015). This heightened activity was observed predominantly within the brainstem and limbic regions, including the periaqueductal grey matter, hypothalamus, and insula. HRV positively correlated with activity in the medulla and the memory-related hippocampus, while blood pressure variability, an index of sympathetic activation (Rosei et al., 2020), was negatively associated with regions related to cognitive control and interoceptive processing, including the dorsolateral PFC, right temporoparietal junction, insula and anterior cingulate. Critchley et al. (2015) supposed that slow-paced breathing simultaneously activates brainstem centers responsible for regulating homeostatic reflexes and forebrain regions that govern cognitive control, emotional state, and visceral sensation.

6.3 Cognition, Emotion, and Wellbeing

Modulating cardiac vagal activity through HRV biofeedback has, in many cases, been proven to be health enhancing across age groups for various physical and mental conditions (Dormal et al., 2021; Gevirtz, 2013; Lehrer et al., 2020; Moss & Shaffer, 2017). Probably the largest body of research on the effects of HRV biofeedback and slow-paced breathing on mental processes has been dedicated to emotional regulation and stress vulnerability. A meta-analysis showed that HRV biofeedback was specifically useful in decreasing anxiety, depression, and anger, as well as increasing sport and artistic performance, but also for post-traumatic stress disorder (Lehrer et al., 2020). Two further subsequent meta-analyses confirmed a large decreasing effect of HRV biofeedback across age on self-reported stress and anxiety (Goessl et al., 2017) and a medium effect in reducing depressive symptoms (Pizzoli et al., 2021) in basic and clinical populations. Also, studies based on cardiac coherence training carried out by the Heart Math Institute indicated decreased stress perception and enhancement of emotional balance as well as cognitive performance (Barrios-Choplin et al., 1997; Ginsberg et al., 2010; McCraty et al., 2009; McCraty & Zayas, 2014).

Given the shared relationship of prefrontal activity with vmHRV and executive functions (Hansen et al., 2004; Thayer et al., 2009), one would expect that HRV biofeedback prefrontal theta power would be accompanied by an increase in cognitive control. Indeed, HRV biofeedback benefits were also found by studies that assessed “cold” cognition, i.e., functions that do not engage in emotional processes, related to executive control (for a review, see Dessy et al., 2018). For instance, Prinsloo et al.

(2011, 2013) uncovered that only a single HRV biofeedback session compared to a control group stimulated EEG correlates related to enhanced internal attention as well as response inhibition in a small sample of senior managers ($n = 18$, mean age = 34 years). Moreover, improvements in children with attention deficit hyperactivity disorder for scores of verbal short- and long-term memory (i.e., immediate word recall and delayed recognition success) could be achieved (Lloyd et al., 2010). The authors noted that gains were unexpectedly large. One reason might be that HRV biofeedback increased the activity of the vagal nerve, which has been shown to improve memory formation when electrically stimulated (Hassert et al., 2004). In addition, HRV biofeedback has also been shown to enhance some cognitive elements of sports performance (Jiménez Morgan & Molina Mora, 2017). One major outstanding issue, however, is that previous results assessed acute cognitive improvements immediately or one day after the intervention. Thus, the maintenance of cognitive effects remains unclarified (Dessy et al., 2018). In this regard, preliminary findings were provided by two studies (one was sliced) that investigated the cognitive effects of HRV biofeedback on cognitive performance in female factory operators one week after intervention (Sutarto et al., 2010, 2012, 2013). These indicated improvements compared to a control group in emotional stability, sustained attention, and short-term memory. However, the results also point out that there was no group difference in cognitive inhibition as assessed by the Stroop Color Word Test. This raises an important point, as inhibition is probably the executive function most robustly related to HRV, questioning the physiological origin of the cognitive changes. Indeed, another HRV biofeedback intervention study concluded that lower impulsivity measured as short reaction times in stop-signal task was associated with HRV before the first training session, but did not improve after eight weeks of almost daily training (Schumann et al., 2019). Hence, it seems that HRV biofeedback improves some cognitive functions, especially when tied to emotional processing, but not inhibition per se.

Another critical point is that previous studies failed to link behavioral outcomes with autonomic signals, which would shed light on the mediating role of cardio-vascular modulation on cognition and emotion. In this regard, Sutarto et al. (2012) could demonstrate increases in relative HRV-LF during baseline, during an arithmetic stressor, and during a subsequent recovery phase revealing cardio-vascular system changes occurring simultaneous to cognitive changes. Also, congruent improvements could be observed in expressive and suppressive hostility in coronary artery disease patients (I.-M. Lin et al., 2015) as well as in stress-cognition in moderately stressed

subjects (Deschodt-Arsac et al., 2020) along with cardiac vagal activity following daily HRV biofeedback for five to six weeks. Nonetheless, none of these studies put in evidence a link between individual autonomic and behavioral changes. Furthermore, relatively small sample sizes and varying control group protocols limit an unequivocal interpretation of recent studies. In addition, the largest increases in HRV were typically seen in those with the lowest level at baseline. Hence, baseline autonomic activity seems to play a moderating role in HRV biofeedback related cognitive effects but often showed stark differences between the intervention and control group, potentially due to a lack of sufficient group randomization.

6.4 Linking Changes in Cognitive, Autonomic, and Brain Functions

A large-scale pre-registered HRV biofeedback intervention study ([ClinicalTrials.gov NCT03458910](https://clinicaltrials.gov/ct2/show/study/NCT03458910)), including physiological, behavioral, and neuroimaging data from (functional) MRI, assessed before and after the intervention, reveals great promises to overcome recent limitations. Data sets based on a healthy cohort of 193 adults (121 younger, 72 older) have been made publicly available (Yoo, Nashiro, Min, et al., 2023) and have already been drawn for numerous studies. The HRV biofeedback intervention included five weeks of daily training for 20 to 40 minutes to increase heart rate oscillatory activity, whereas an active control group targeted its decrease. Oscillatory activity was based on the cardiac coherence score (see Chapter 1.4.3.1) and positive feedback indicated its increase and decrease in the intervention and control group, respectively. Training in the HRV biofeedback group followed the resonance frequency training protocol, whereas the control group could choose between different not physically demanding strategies (e.g., imaging the ocean). Results derived from this cohort are discussed in this section. They provide meaningful insight into the relationship of HRV biofeedback induced changes in brain structure and functional connectivity and mental processes related to executive, emotional, and self-referential processing.

One striking observation of these cohort studies was that HRV biofeedback, compared to the control exercise, affected brain structure and functional connectivity that are crucial to emotion regulation and positive emotional processing (Nashiro, Min, et al., 2023; Yoo et al., 2018). Yoo et al. (2018) found increased left orbitofrontal cortex volume across age groups, a brain region, as previously discussed, that is functionally closely related to the ventromedial prefrontal and subgenual anterior cingulate cortices, associated with parasympathetic drive and involved in emotional regulation due to its strong connections to the limbic system. Specifically, the left part is believed to be

involved in the processing of positively evaluated information. This notion was underpinned by the observation that cortical volume changes were associated with more positive emotional outcomes (Yoo et al., 2018). Moreover, Nashiro, Min, et al. (2023) demonstrated in the younger adults sample that HRV biofeedback increased functional connectivity between the medial PFC and left amygdala that underpins automatic emotional processing. A very recent investigation extended the importance of HRV biofeedback for positive emotional processing in younger and older adults to the memory domain (C. Cho et al., 2023). The authors found that the medial PFC-left amygdala resting-state connectivity mediated the enhancing effect of HRV biofeedback on positive emotional memory biases. In this regard, emotional picture recognition memory was assessed based on the Remember-Know paradigm (Tulving, 1985a), including a one-week recall delay period. Compared to the controls, HRV biofeedback increased false alarm rates but not hit rates for positive compared to negative pictures. Overall, the findings indicated that positive recall was substantially ($p = 0.056$) higher after biofeedback. Furthermore, positive emotional memory bias was positively correlated with baseline RMSSD but not baseline mood. The mediation effect persisted even after controlling for baseline levels of RMSSD and mood. Together, this indicates a causal link between cardiovascular function related to parasympathetic activity and automatic positive emotional processing affecting memory and potentially further thought processes.

In another work, based only on the younger adult sample, the degree of the heart rate oscillations during training was found to predict with a moderate effect the functional connectivity between the orbitofrontal cortex and DMN core as well as the subjective ratings of awareness-related mindfulness. The core subsystem of the DMN consists of the anterior medial PFC and posterior cingulate cortex, (Andrews-Hanna, 2012; Andrews-Hanna et al., 2010, 2014). The core subsystem is particularly implicated in self-referential processing during ruminative and depressive thinking (Burkhouse et al., 2017; Cooney et al., 2010; Zhou et al., 2020), which are characterized by more negative, self-, and past-related thoughts (F. Hoffmann et al., 2016). Therefore, the results support the idea that repeated stimulation of cardiac vagal activity reduces connectivity between self-referential and emotional processing involved in negative self-processing and mind-wandering. However, Nashiro, Min, et al. (2023) also warrant that functional brain changes may affect implicit emotion regulation (no conscious desire to change emotions, e.g., automatic goal pursuit) but not explicit emotion regulation (conscious desire to change emotions, e.g., controlled reappraisal), (Braunstein et al.,

2017). Thus, future studies are needed to investigate implicit and explicit forms of thought emotion and thought processes, such as the mapping

In line with previously discussed HRV biofeedback studies, inhibitory control, working memory, and processing speed did not improve across age groups (Nashiro, Yoo, et al., 2023). Interestingly, only the flanker score (measure of inhibition and visual attention) was associated with heart rate oscillation amplitude. The flanker score accounts for accuracy (and reaction time) with participants during the Flanker Test correctly indicating the direction of the central arrow that was either congruent or incongruent with the direction of arrows on the left and right. Thus, The Flanker Test, like the Stroop Test, is a conflict task, but assesses response inhibition based on accuracy rather than reaction time. In the work of Sutarto et al. (2013), visual attention was also assessed, but in this case with the concentration performance score of the D2 Attention Test, which showed large increases after HRV biofeedback. Both flanker score and concentration performance strongly rely on accuracy during response inhibition when discrimination visually similar stimuli. Thus, these results suggest that parasympathetic activation through HRV biofeedback affects brain activity or connectivity specific to discrimination of perceptual inputs, potentially mediated by greater connectivity between brainstem regions and the ACC that processes salient information and monitors conflict (see Chapter 4.2)

Neuroimaging data revealed that HRV biofeedback decreased locus coeruleus contrast in younger adults and that these decreases were associated with degree of cardiac oscillatory stimulation (Bachman et al., 2023). As a reminder, the locus coeruleus is the main source of norepinephrine/noradrenaline, which released in limbic brain structures affects emotional processes and memory formation. Moreover, RNA sequencing showed that LC contrast was associated with gene expression indexing sympathetic nervous system signaling. This underlines that HRV biofeedback decreases sympathetic signaling and arousal related processes and that this effect is related to training stimulation. Furthermore, HRV biofeedback, compared to the control, reduced plasma levels of Alzheimer's disease-related proteins (Min et al., 2023). Reductions were associated with decreased gene transcription indicative of noradrenergic system, mainly involving the locus coeruleus. The results support the notion that HRV biofeedback induced vagal stimulation reduces noradrenergic activity and thus the release of the sympathetically-linked noradrenaline, which contributes to stress responses and Alzheimer's disease. Additional findings support that autonomic self-regulation

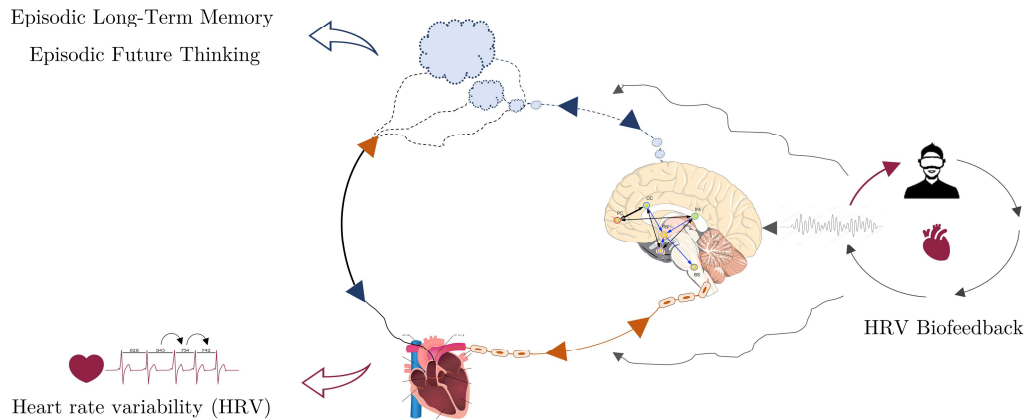
contributes to fronto-limbic connectivity can be found in clinical intervention based on regular electrodermal biofeedback (Nagai et al., 2018). Epilepsy patients showed, compared to a medication control group, greater functional connectivity between the right amygdala and both the orbitofrontal cortex and the frontal pole. The results thus indicate that volition reduction of sympathetic arousal, as it can also be achieved by HRV biofeedback, alters brains states of affective and cognitive arousal. Since emotional processing and its interaction with self-related thought processes are strongly influenced by arousal, one may assume in line with previous results that HRV contributes to contemplative thoughts that are more reflective, more positive, and less negative, especially in response to stressors. Moreover, the noradrenergic system plays a role in various cognitive functions (Holland et al., 2021), such as modulating response inhibition or memory and might also be a factor explaining the improvements observed in sustained attention (Sutarto et al., 2013), positive emotional memory, and correlations of training HRV with the flanker score (Nashiro, Yoo, et al., 2023).

In summary, very recent evidence demonstrates that HRV biofeedback affects brain structure and connectivity primarily within emotional networks. These effects also extend to brain circuits that are strongly involved in self-processing, memory, and future thinking. Although promising outcomes HRV biofeedback modulation have been observed, the long-term consequences of voluntarily controlling the ANS remain unclear.

6.5 Chapter Summary

- It is theorized that HRV biofeedback affects the brain through large physiological oscillations, such as during resonance frequency.
- Potential pathways are discussed including blood flow, CO² levels, sensory inputs from breathing and respiration, arousal as well as the vagal afferents.
- Repeated HRV biofeedback has lasting effects on cardiovascular functioning increasing HRV and baroreflex gain.
- Different theories such as the coherence propose that HRV biofeedback evokes the functional reorganization of the interface between cognitive centers and the Central Autonomic Network (shift of inner baseline).
- Consequently, this would change allostatic policies and thus self-regulation behavior and mental processing.
- HRV biofeedback shows being effective to alleviate disorders of affect such as depression, anxiety, and post-traumatic stress disorder.
- Little research has been directed toward the HRV biofeedback effect on cognition in healthy individuals.
- Preliminary studies indicate HRV biofeedback improves executive functions specific to attentional control and short-term memory after single and repeated training sessions. Effects may be maintained beyond the training.
- Studies from a recent large clinical trial demonstrate that HRV biofeedback alters connectivity between brain structures involved in emotion regulation and self-referential processing (amygdala, ventromedial prefrontal cortex), which mediate effects on emotional processing in memory.
- Cognitive changes show related to the success of the training (increase in HRV during training).

7 Chapter 7 – Promises of Virtual Reality



This chapter discusses the use of virtual reality (VR) for HRV biofeedback and cognitive assessments. In the framework of this thesis VR was deployed to enhance experimental robustness and efficacy of the training as further discussed in the following chapter.

VR is the computer-generated simulation of a three-dimensional image, or in this case environment, a person can interact with in real-time and in a seemingly real way. The immersion in such simulated VR environments is realized by special electronic equipment such as screens fitted into a helmet (i.e., head-mounted display), hand controllers and sensors that record and translate the user's movements and interactions in relation to the displayed VR environment.

7.1 Experimental Control

VR presents an important solution for psychological experiments and real-life applications to enhance the sense of presence and ecologic validity while maintaining a high level of experimental control (Fuchs, 2017). The presence is commonly defined as the feeling of being located and responding to a virtual environment as if it was real and is linked to the intensity of attentional commitment to stimuli (Sanchez-Vives & Slater, 2005). Thus, a high sense of presence is particularly useful to increase the attention towards experimental tasks (Sanchez-Vives & Slater, 2005) and to manipulate the emotional mode (Riva et al., 2007). In addition, VR offers a plethora of possibilities to realize different types of scenarios and experiments, as well as complete control over the environment. Due to the visual shielding and headphones implemented in the VR

helmet, perceptual distraction from the outer environment (e.g., the laboratory room) is reduced, contributing to greater immersion. Hence, VR, compared to computer screens, provides a better means to control perceptual inputs with important consequences for task focus and emotional affect. Moreover, VR allows the implementation of real-life-like settings to increase the ecologic validity of the experiment which supports the generalizability of laboratory results to the real world (Rose et al., 2000).

7.2 Attention, Motivation, and Feedback Learning

Another important component of VR is the experience of virtual embodiment, which lets a person momentarily exist within a virtual environment, for example, by placing users in a first-person perspective in an avatar that they can control and that resembles their own physique. Embodiment constitutes the sense of body ownership, agency, and self-location (Kilteni et al., 2012) and is thus linked to self-identification in the virtual world. Together, the sense of embodiment as well as the degree of immersion (e.g., multisensorial stimulation, real-time synchronization, interaction possibilities, etc.) can positively contribute to a high sense of presence and task engagement. These components are not only important for the validity of the results, but specifically motivation and agency, as discussed earlier (Chapter 2.3), are crucial for feedback learning. In this context, biofeedback can be represented in the VR environment, providing greater incentives for self-regulation. This, of course, depends heavily on the design of VR environments and tasks and can be augmented by introducing principles of game theory (i.e., gamification), e.g., the inclusion of reward systems and paths to skill mastery (Gaume et al., 2016). In this line, it has been shown that the perception and mastery of cardiac self-regulation through abstract biofeedback embedded in a virtual game mechanic is linked to greater engagement and agency (Houzangbe et al., 2019). However, not just any kind of biofeedback ensures enhanced mastery of cardiac self-regulation. In fact, the study showed that most participants had poor self-regulation competency when given abstract biofeedback. Therefore, providing understandable, clear, and coherent biofeedback is important. In this context, VR can introduce easily interpretable biofeedback, which, compared to the typically abstract 2D-graph representations on screens, may facilitate the ease of control and sense of agency in controlling the internal body processes. For instance, Monti et al. (2019) demonstrated that synchronizing the respiratory signal with the avatar's chest movement, which they termed "embreathment", improves the sense of embodiment.

Similarly, other studies have employed the “cardio-visual full body illusion” (Aspell et al., 2013), where a video of the own body including the flashing illumination of the silhouette in synchrony with the heartbeat is presented with a VR headset. Combining interoceptive and exteroceptive signals through such biofeedback not only increased self-identification but also influenced neural correlates involved in somatosensory (Heydrich et al., 2018) and visual processing (Ronchi et al., 2017), which may have important implications on self-processing, as discussed further below. Furthermore, higher degrees of presence and embodiment, as well as increasing similarity between real and VR behavioral responses to a task (Armougum et al., 2019), contribute to the transfer of skill to real-life applications (Grassini & Laumann, 2020; Sanchez-Vives & Slater, 2005), highlighting the benefits of VR for biofeedback interventions.

7.3 Relaxation and Cognitive Restoration

A very common application of VR for biofeedback is to promote relaxation by creating naturalistic and peaceful environments, such as forested areas or the seaside. Exposure to such natural environments has been associated with psychological benefits, such as stress reduction, elated mood, and restoration from cognitive load, and improved mental health (Bergmann et al., 2012; Hartig et al., 2014; Kaplan & Kaplan, 1989). An influential model, the Attention Restoration Theory (Basu et al., 2019; Berman et al., 2008; Kaplan & Kaplan, 1989) posits that experiencing natural environments with soft fascination restores focus linked to soft fascination because we are evolutionarily wired to relax in the face of threatening natural surroundings. Despite them model receiving some critique, a meta-analysis verified the benefits on cognitive flexibility, short-term, and working memory and the recovery of autonomic function after acute mental stress (D. K. Brown et al., 2013). Restored levels of positive affectivity as well as autonomic and attention control, are crucial for HRVB task success and may positively influence training outcomes. Indeed, multiple studies confirmed the benefit of VR for biofeedback purposes to improve neurocognition, supporting training, including enhanced attention and reduced stress (Blum et al., 2019; B. H. Cho et al., 2004; Rockstroh et al., 2019, 2020), deeper relaxation levels (Amores et al., 2018; Kosunen et al., 2016) or pain and anxiety treatment (Gromala et al., 2015; Repetto et al., 2009; Shiri et al., 2013). It is important to note that some of these studies demonstrated a benefit of VR coupling over the usage of biofeedback alone, however, most investigations lacked randomized control groups. Moreover, Blum et al. (2019) compared the psychological and autonomic effects of cardiac biofeedback in VR to a VR immersion alone. They found

that while biofeedback reduced ratings of perceived stress, and mind-wandering and increased relaxation self-efficacy, being in the present moment and attention, it did not affect cardiac control perse (i.e., higher RMSSD or cardiac coherence). In summary, VR has the potential to increase experimental task engagement and self-regulation success which may concomitantly increase relaxation and cognitive resources during and after biofeedback training. This may be useful for single-session experiments, but the greatest benefits will probably be revealed during longitudinal experiments or clinical applications with many sessions, where a high and sustained level of motivation is crucial for the outcomes.

7.4 Self-Referential Processing, Embodiment, Self-Awareness

Self-regulation presumes that attention is directed to self, which in terms of VR also extends to the embodied self, namely the virtual representation of the person's own body and physiological functions (Monti et al., 2019, 2020). As discussed earlier, combining intero- and exteroceptive processing by linking the biofeedback to the own body, such as during embreathment (Monti et al., 2020) or the cardio-visual full-body illusion (Aspell et al., 2013), increases embodiment and bodily self-consciousness (Blanke, 2012) and affects related neural processing. Thus, evidence points towards that biofeedback enforces self-awareness and self-reference processes (Vago & David, 2012), since it facilitates the monitoring of and neural integration of self-related processes, and that this effect is enforced by the VR through components of presence and embodiment. Since self-relevant processing is tightly linked to attentional bias, it is reasonable to assume its presence will elicit greater attention to self-regulation training (see Chapter 3.3.3). Consequently, unlike 2D screens, VR provides the opportunity to enhance biofeedback-related self-processing through increased embodiment and presence, which positively affect self-regulation engagement.

7.5 Drawbacks

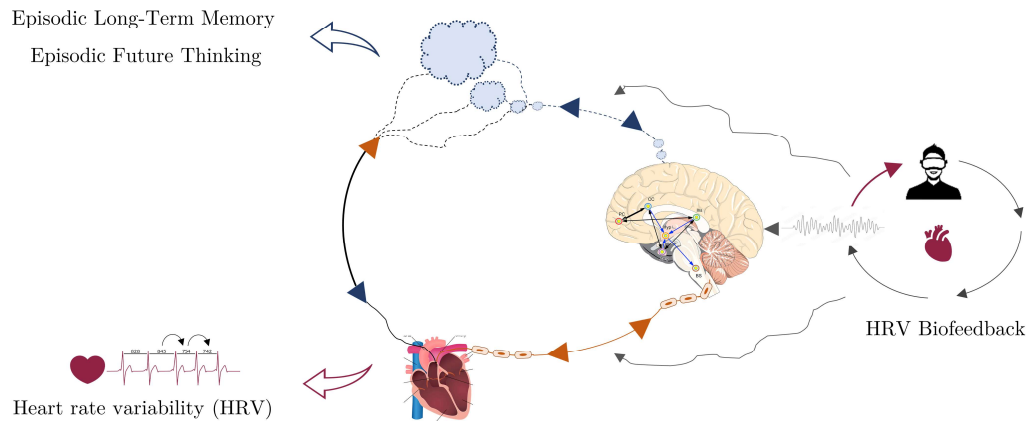
The use of VR equipment does not come with its constraints. The most reported issues are discomfort due the device weight and cybersickness which is similar to motion sickness (S. Davis et al., 2014). Typically, this includes nausea, visual discomfort (e.g., eyestrain), disorientation (e.g., dizziness), and vestibular disturbance. Moreover, VR can contribute to greater fatigue and drowsiness. Cybersickness may be experienced by some users depending on several individual, device, and task factors (S. Davis et al., 2014). For instance, cybersickness increases with longer exposure periods, certain

illnesses, such as the flu, and increased lag (delay between user action and system reaction). Avoiding incongruencies between the real body and environment are very important as they can be perceived as highly disturbing, decreasing comfort and the sense of embodiment (Penaud et al., 2023). Moreover, sitting is considered the safer posture since it demands less postural control.

7.6 Chapter Summary

- Virtual reality (VR) introduces new ways in which an agent can experience and interact with its environment. Users can be embodied in their own avatar, thus experiencing the world as it would be real.
- Complete control over environment including ongoing perceptual inputs (visual, auditory, and partly tactile) provides a very high degree of experimental control.
- VR immersion increases the sense of presence (as being there) which is linked to attentional commitment and the possibility to affect the emotional mode.
- Ecologically valid setups can be introduced that allow for better generalizability and transfer of experimental results and skills to real life.
- VR can trigger attention, motivation, and feedback learning which are crucial elements for HRV biofeedback (Chapter 2).
- Immersion in a naturalistic environment can elicit relaxation and cognitive restoration effects and thus stress recovery.
- VR allows for representations of body own signals (biofeedback) embodied by the avatar (e.g., embreathment, cardio-visual full-body illusion). This enhances embodiment and possibly triggers self-referential processes that could support HRV biofeedback outcomes.

8 Chapter 8 – Towards the Use of Virtual Reality and Biofeedback to Study and Stimulate the Heart-Brain Axis



The previous chapters reviewed the body-mind connection, and in specific the heart-brain axis, the role of cardiac vagal control and HRV biofeedback for autonomic regulation and cognition. Furthermore, the usefulness of VR for HRV biofeedback and cognitive assessment was proposed. In the following, the previous chapters are synthesized and the methodology common to all experiments is presented. Notably, this includes the development of a new VR system integrating biofeedback and cognitive assessment.

8.1 Synthesis, Problematic, and Theoretical Hypotheses

In line with the idea that the mind and body are connected, the general introduction put forward the physiological connection between neural pathways innervating the heart and the brain and how their intricate interplay affects a number of cognitive functions. Considerations from psychophysiology theories, most notably the neurovisceral integration model, and neural structures underlying autonomic, cognitive, and emotional regulation as well as memory and future thinking lay the theoretical foundation that these cognitive faculties link to cardiac vagal control. Autonomic pathways deliver top-down and bottom-up informational streams between the brain and body periphery that can be assessed by HRV, providing insight into cognitive processes. Numerous studies among healthy adults have supported the neurovisceral integration (Thayer & Lane, 2000, 2009) model by demonstrating correlations between

vmHRV and cognitive functions involved in self-regulation, such as cognitive control and emotion regulation. However, these studies mainly interested in single-measure associations by assessing HRV during resting-state prior to the cognitive task. This suggests that resting HRV can be seen as a trait marker reflecting self-regulatory capacities, but it tells us little about the dynamic psychophysiological interaction as we experience the world. Specifically in regard to the rather low correlation strength that has been found (Holzman & Bridgett, 2017; Zahn et al., 2016), *in situ* measures of HRV during cognitive processing may clarify the interaction with the ongoing cognitive processes. The recent emergence of the Vagal Tank Theory (Laborde et al., 2018) and associated studies highlight this promising path by studying changes to specific phases instead of state measures in the context of self-regulation. However, the research field is still in its infancy but is expected to quickly evolve. Specificity. At present, substantial evidence has been put forward, using either state or phasic HRV measures, for cognitive performance linked processes that have the strongest backup by the neurovisceral integration model, namely inhibition and emotion regulation. Higher-order functions such as long-term memory and future-oriented thought of personal experienced episodes, which strongly rely on executive, emotional, and self-referential processing, had been of far less consideration, despite their crucial role in human behavior. Preliminary evidence indicates that the association of cardiac vagal control with cognitive and emotional control extends to thought processes such as suppressing irrelevant or unwanted memories. Interestingly, the link between cardiovascular adaptation and self-referential processes involved in higher mental processes had not been investigated at all, although both mechanisms have a strong association to the neuronally highly integrated ventromedial PFC which connects to emotional and executive hubs. Another limitation of existing studies is that they seem to be struggling to clarify the functional directionality of the heart-brain axis. Given that it constitutes of efferent and afferent with complex branches to different physiological systems, HRV may be reflective of body states affecting cognition or index cognitive processes that influence the heart. The answer is, probably both. However, it remains an important aspect to consider when studying the mind-body connection. Thus, it seems timely to investigate the implication of HRV on executive, emotional, and self-referential processing with special regard to higher-order cognition and directionally of the effect.

Moreover, very little research has been dedicated to tracking changes in HRV alongside changes in cognition, especially during interventions that affect HRV. In the introduction, physiological and cognitive foundations of HRV biofeedback were

reviewed, which support the idea that it could be a promising tool to study the mind-body interaction and to improve cognitive performance. HRV biofeedback has found its use in various clinical applications targeting stress reduction, but the literature on cognitive effects in healthy and clinical populations remains very sparse and lacks randomized control experiments and effect maintenance periods. These would help to determine if neurophysiological changes through the ANS drive behavior, which would corroborate a psychophysiological link infested in the heart-brain connection. First results from young, healthy adults presenting behavioral and neuroimaging data are very promising, demonstrating the benefits of HRV biofeedback to improve cognitive control and brain changes related to autonomic and cognitive processes. Recent analyses from a larger sample highlight that large oscillations in heart rate strengthen feedback loops in brain regions that can regulate brain activity associated with emotional and self-referential processes. Together with the theoretical groundings, it seems very promising to explore the autonomic link between HRV biofeedback and cognition and its potential effects to stimulate mind and body with important consequences on a range of health and well-being applications. Thus, this thesis aims to overcome the various pitfalls listed above by conducting experiments among young, healthy adults designed to answer the following questions:

- Does vmHRV reflect executive, emotional, and self-referential processes involved in long-term memory and episodic future thinking, and thus self-regulation in higher cognition?
- Does HRV biofeedback promote adaptive long-term memory and episodic future thinking through vagally mediated changes in executive, emotional, and self-referential processes?

To better study these questions the implementation of psychophysiological experiments in virtual reality (VR) was considered. The following section describes the rationale and development of a novel VR-HRV biofeedback system to foster experimental control and robustness.

8.2 Integrating HRV Biofeedback and Cognitive Assessment in Virtual Reality

Based on available material in the MC2 laboratory, a new system adapted to our experimental needs and incorporating gold-standard physiological recordings was developed.

Within the framework of this thesis, three experimental studies were carried out termed *BIOTRAC*, short for **BIO**feedback **TR**Aining & **C**ognition. The numbering corresponds to the order in which the experiments were conducted. To promote open science, all materials, including video recordings of the VR setup, supplementary results, and the research data are accessible on public project-specific online repositories (Table 3).

Table 3 – Promoting Open Science: Public Project Repositories

BIOTRAC-1 Persistent effects	https://osf.io/u4t7p/ (OSF link)
BIOTRAC-2 False memory	https://osf.io/593p6/ (OSF link)
Preregistration:	https://osf.io/edhpc/ (OSF link)
BIOTRAC-3 Mental time travel	https://osf.io/xgfdc/ (OSF link)

Note. Materials are uploaded on the Open Science Framework (OSF).

All three experiments described in this dissertation included the use of an immersive VR system that integrated real-time physiological measures. Common points between the similar setups are detailed below. HRV biofeedback training was implemented for each experiment in a VR environment depicting a naturalistic scene to increase motivation, exercise adherence, self-referential processing bias, and autonomic stress recovery (see Chapter 8.2). Furthermore, for study 2 and 3 the experimental procedure was also implemented in VR. The main reason was that in contrast to study 1, which was a longitudinal study with separate cognitive assessment and training sessions, study 2 and 3 were single-session investigations that intertwined cognitive processing and HRV biofeedback phases. Consequently, the whole experimental procedure was

realized in VR. The main advantages of this procedure were, firstly, participants had not to be de- and re-immersed into the VR environment (i.e., taking constantly the head-mounted display on and off) between cognitive task and HRV biofeedback phases, which would have caused large confounding effects on physiological and cognitive processes, increased experiment lengths and subjects' discomfort, and decreased the sense of presence. Secondly, the VR system provided a very high degree of experimental control since participants were shielded from external extractions (e.g., laboratory room, presence of the experimenter). In addition, it gave complete control over the coding of the VR environment and procedure, allowing for experimental fine-tuning (e.g., parametrization of visual/ auditory inputs, procedural timings, generation of data processing pipelines).

8.2.1 Material and software

The material comprised a VR system connected to a physiological data acquisition system. For the VR immersion, we used the HTC Vive ([study 1](#); [HTC & Valve, 2015](#)) and HTC Vive Pro ([study 2 and 3](#); [HTC & Valve, 2018](#)), including two hand controllers. Auditory signals were played either via external stereo speakers (study 1) or the headphones integrated in the VR headset (study 2 and 3). VR environments were designed and played using the VR-software platform SteamVR (Valve) and game engine Unity 3D version 2018.3.0 and higher (Unity Technologies, 2018), incorporating the object-oriented program language C#. Physiological recordings were obtained by the data acquisition system MP150 (BIOPAC Systems, Inc., 2015). This setup included the BioNomadix module BN-RSPEC (BIOPAC Systems, Inc., n.d.-b) for the wireless transmission of respiration and ECG data recorded by a respiration transducer BN-RESP-XDCR (BIOPAC Systems, Inc., n.d.-a) and 3-Lead Ag-AgCl surface electrodes (EL504 or EL258), respectively. A high-performance computer running on Windows 10 simultaneously played the VR, received the physiological data streams, and integrated these into the VR environment. Physiological recordings were displayed in real-time and saved by data acquisition and analysis software AcqKnowledge 5.0.4 (BIOPAC Systems, Inc., 2019). The latter included the network data transfer license ACK100W-NDT (BIOPAC Systems, Inc., 2010) for the transmission of the data to Unity 3D. The Unity Interface for AcqKnowledge plugin (BIOPAC Systems, Inc., 2017) facilitated the data stream between the two entities.

8.2.2 From recording to biofeedback

Throughout each experiment, participants sat, typically in an upright position, on a chair with armrests. A 3-Lead ECG and changes in thoracic-abdominal circumference (respiration amplitude) were recorded according to the manufacturer's guideline (BIOPAC Systems, Inc., n.d.-c, 2016). The ECG skin surface electrodes were placed on the torso based on Einthoven's triangle (i.e., right clavicle, lower left and right rib) that collected data from Lead II. Electrode cavities were filled with electrode gel (GEL100 for ECG, non-irritating, hypo-allergenic), which ensured electrical contact. The respiration belt transducer was placed on the level of the solar plexus to measure thoracic-abdominal circumference but was moved in case ceiling effects in the signal occurred (i.e., reaching sensor limits) upward (thoracic movements) or downwards (abdominal movements). The respiratory and cardiac sensors physically connected the BioNomadix transmitter for wireless transmission to the base station within a reach of 2m. Respiratory and ECG signals were received by the transmitter within a range of ± 10 V and 1 μ V to 10 mV peak to peak, and bandlimited between 0 and 10 Hz and 0.5 and 150 Hz, respectively. Further, the transmitter applied a notch filter at 50 Hz. ECG signal gain was kept fixed at 2000, and output signals ranged for both types at ± 10 V. Recordings were then transmitted at a rate of 2 kHz to the acquisition station. The data were subsequently sampled with an A/D resolution of 16 bits and an accuracy of $\pm 0.003\%$ of the full scale range before being forwarded via the crossover ethernet cable and ethernet adapter to the computer. Incoming online data were then registered by the AcqKnowledge software with a rate of 1 kHz, and a heart rate waveform was calculated online based on beat-to-beat (RR) time intervals. Recorded and calculated data channels were displayed during training in real-time via a monitor to the experimenter and saved on the local hard drive at the end of each session for later analyzation. Simultaneously, Unity retrieved data of all channels with a polling frequency of 50 Hz. Processing of the data in the VR was performed by means of customized scripts coded with C#. In this context, the change of physiological parameters evoked the modification of some characteristics of the VR environment, which was streamed from the computer to the VR display. Specific tests to measure the lag between physiological phenomena (e.g., heartbeat) and biofeedback appearance were not performed; however, numerous pilot tests confirmed that no delay was perceptible.

8.2.3 Virtual reality environment

One principal VR environment was designed where participants were immersed during self-regulation training (i.e., HRV biofeedback or the active control training) and during the memory and future thinking tasks in study 2 and 3 ([Figure 18](#)). In each case, participants were embodied by a human avatar in the first-person perspective sitting or lying on the beach of a small and isolated island. During their VR experience, the avatar remained in the sitting or semi-recumbent position, just like the real body, with the feet facing the sea so that the field of view was mainly focused on the water and on the avatar's body. Body-avatar motor synchronization was established for the head, arms, and partly for the torso and legs through the VR headset and controllers, except for study 1, where no movements and direct interactions with the environment were required. There were two avatar versions, a female and a male, which were roughly matched in terms of age to the sample population. The environment was kept simple to avoid distractions during the training and tasks. The only dynamic elements were the gentle movements of a palm tree, the waves with the wind, the circling of seagulls in the distance, and a turtle in the water. The speakers played calming sea sounds in congruence with the environment. HRV biofeedback was delivered in the VR environment through the modification of the color of the sea in accordance with the real-time heart rate signal. With increasing heart rate, the water became continuously brighter and light-bluish and turned to a darker and more violet color as it declined (green and orange respectively in study 1). Color coding was done by fitting the individual resting heart rate range to a RGB 1.0 scale. In this line, a 1-min calibration period shortly before HRV biofeedback during a resting-state period determined setpoints in the color scale, so that the sea reached normal (i.e., unchanged) or extreme colors when heart rate was at the median or 1.5 times the inter quartile range above/below the upper/ lower quartile, respectively. These setpoints were determined during pilot testing and evoked clearly distinguishable biofeedback during rest and HRV biofeedback for a range of participants with very low and high resting vmHRV (RMSSD from 10 to 120 ms). Besides the advantages mentioned in Chapter 7, we chose this particular setup and environment because it provides a large field of view for simple-to-interpret biofeedback. The sea stretches the entire horizontal line of the field of view, and the dichotomous meaning of colors can readily be interpreted through the visual periphery. This presumably facilitates the perceptual and cognitive processing compared to spatially restricted and complicated biofeedback, such as running graphs, especially when no covert attention is paid to the biofeedback. This is particularly useful when participants are (visually) defocused (e.g., during states of drowsiness or

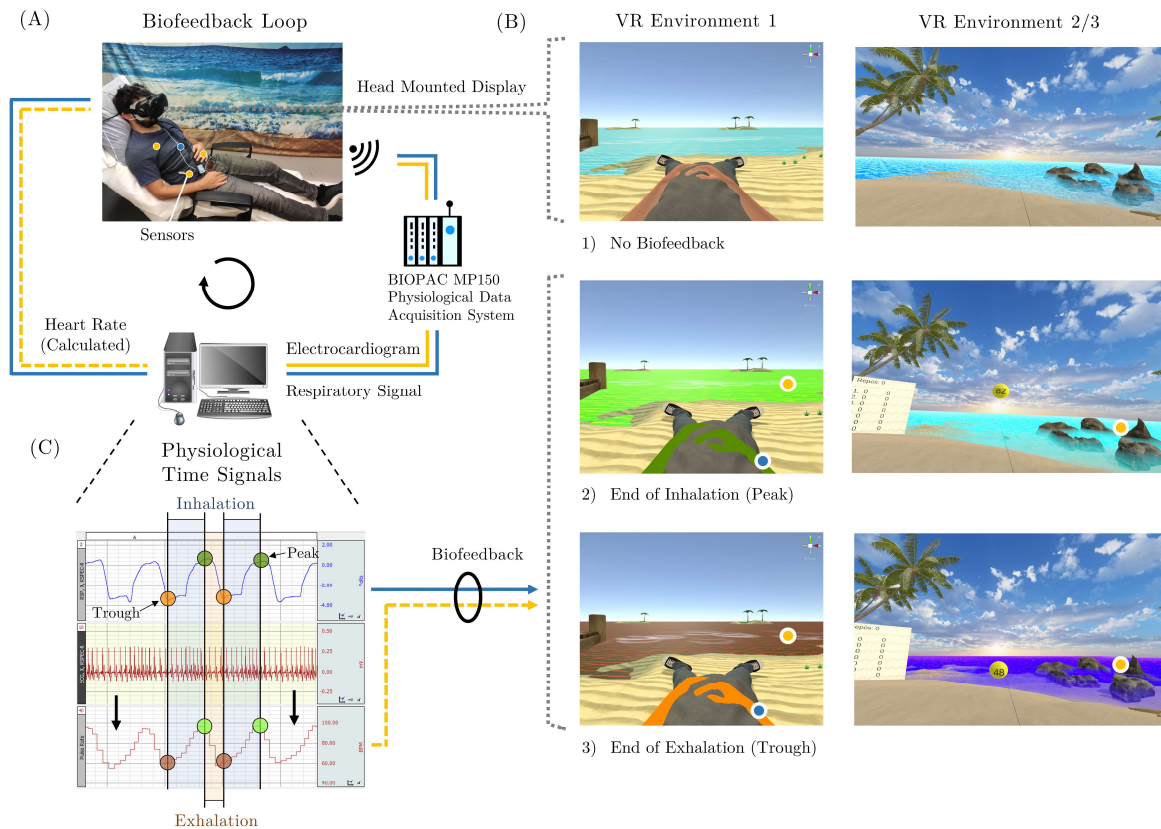


Figure 18 – Heart Rate Variability Biofeedback in Virtual Reality

A new virtual reality (VR) system was developed in which participants completed the heart rate variability (HRV) biofeedback training (study 1, 2, and 3) and the cognitive assessment (study 2 and 3). (A) Real-time physiological recordings from a 3-lead electrocardiogram (yellow) and respiration transducer (blue) were processed and fed to the VR system. (B) The color of the sea represented the heart rate calculated from each interbeat interval (study 1, 2, and 3) and the color of the avatar the respiration amplitude (study 1 only). HRV biofeedback was perceived as the gradual change in the sea color (from red/violet to green/light blue, at median heart rate level the sea color was natural). (C) During HRV biofeedback participants were asked to maximize cardiac oscillations (i.e., maximal color change) through slow breathing near the resonance frequency. In study 1, breathing was self-paced (focusing only on the biofeedback), whereas in study 2 and 3 it was paced by vertically shuttling sphere running at constant rhythm of 6 cycles per minute.

high eye strain) or concentrated on other things (e.g., interoceptive sensations, observing the avatar).

8.2.4 Experimental procedure

Throughout all experiments, including cognitive tasks and HRV biofeedback, participants remained seated upright with hands resting in the lap or on the arm rests (except in study 1 during HRV biofeedback where a semi-recumbent position facilitated

the training). We would have much liked to incorporate more interactive elements in the HRV biofeedback to increase user engagement to reduce potential negative effects of prolonged motor-skeletal quiescence, such as drowsiness and restlessness, e.g., asking participants to lift and raise their arms or perform slight yoga movements in congruence with the biofeedback. However, we chose the path of higher methodological rigor, as we judged that remaining in the same posture with no fluctuations in physical demands would provide the best comparability of physiological results within and between experiments. In addition, restricted movement and sitting during VR immersion are safer and reduce cybersickness (see Chapter 7.5).

After sensor application, signals were checked for irregularities (e.g., ectopic beats, inversed ECG, ceiling effects). A 5-minute resting-state preceded physiological recordings during any task or training. For these baseline measures participants were asked to sit comfortably, refrain from moving, talking, or sleeping, and to breathe naturally while keeping eyes open (except in study 3 due to the resting thought assessment). In line with the manufacturer's recommendations, the sensor application and resting-state measure were separated by at least 5 minutes, to leave time for the conduction gel to activate. Experimental procedures of the cognitive tasks and training in the VR were fully automatized. Experimenters had to start any tests with only one click in the user interface. Otherwise, the experimenters had only to monitor the procedure and intervene for unseen difficulties. In the same line, all events were marked, and all data were recorded, processed, and saved automatically. Cognitive task procedures and training in the VR were always preceded by a familiarization and coaching phase, respectively, which were partly automatized as well.

HRV biofeedback training was based on Lehrer's (Lehrer et al., 2000) Resonance Frequency Training. However, the resonance frequency was not determined a priori, but participants self-regulated their breathing along with sea-color biofeedback, for reasons as described in Chapter 2.2.1. During a separate coaching phase before the first training phase, the interpretation of the biofeedback signal was explained (natural sea color: the heart rate beats at the average speed; sea turns bright and bluish: the heart rate increases; sea turns dark and violet: the heart rate decreases). Biofeedback was presented for around 1 minute with the instruction to breathe naturally, so the participant could get a feeling of how their heart rate is fluctuating normally. Then, they were asked to take one long deep breath and to breathe slowly out. Since only young participants were recruited (18-35 years old), this typically evoked a stark increase and fall in heart rate and thus a change in color. At this point, the concepts

of HRV, HRV amplitude (i.e., change in color), RSA, and resonance breathing, and the goal of the training were explained (i.e., maximization of the HRV amplitude and RSA by evoking most extreme color changes as possible while keeping these changes in synchrony with the own breathing). Then, participants were given 1 to 2 minutes to follow a slow breathing pacer running at 6 cpm. We advised increased breathing amplitude but cautioned against possible hyperventilation due to exaggerated breathing. Training modalities slightly varied across the experiments. In the first study, only the experimenter orally paced the first two minutes of each training session. Afterwards, participants had to adapt their breathing rhythm and amplitude themselves to maximize HRV amplitude and RSA. In the second and third study, a 6 cpm breathing pacer was provided to facilitate the training because the training period was much shorter. Contrary to study 1, subjects did not have multiple sessions to optimize their breathing and were moreover constantly interrupted by the cognitive task. Furthermore, all studies included an active control group to control for potential confounding effects caused by placebos and self-regulation efforts. In this line, we wanted to rule out that cognitive effects were caused simply by breathing self-regulation that does not significantly simulate vmHRV.

8.3 Data Processing

During study 2 and 3, where cognitive tasks were implemented in VR, behavioral outcomes (e.g., participant responses, response reaction times) were all recorded and saved by the VR system. These were then processed and analyzed along with the physiological data using the statistical software R (R Core Team, 2023). Before analysis, physiological data were preprocessed using a customized version of the Neurokit2 Python package (study 1: version 0.0.18 from March 2020, study 2 and 3: version 0.2.3 from December 2022). Please note that Neurokit2 provides a comprehensive documentation about the open-access tool (Makowski, 2023). We opted to use Neurokit2 instead of AcqKnowledge's built-in analysis tools because it provides semi-automatized artefact correction pipelines, and its data processing methods are based on state-of-the-art approaches. Nevertheless, AcqKnowledge was due to its user-friendly interface used for visual inspection and segmentation of individual data recordings. Where possible, movement and signal artefacts were removed while preserving R peaks by flattening the signal between peaks. Segments were excluded if they were strongly affected by movement artefacts or ectopic beats, i.e., generally, $>2\%$ of the R peaks were undetectable or if multiple consecutive R peaks could not be

preserved. Globally, only a very few segments had to be excluded due to the movement restrictions and the robustness of the acquisition system against artefacts. Neurokit2 processed and then analyzed segments individually to obtain statistical measures of the ECG, HRV, and RSA (methods used: *ecg_process*, *rsp_process*, *ecg_analyze*, *hrv*, *hrv_rsa*). Neurokit2 offers an extensive output of over 90 HRV, 37 respiratory and 8 RSA indices that not only includes standard measures proposed by the TaskForce (Camm et al., 1996) but also a range of non-linear measures. All graph outputs were turned on (i.e., raw and corrected signal, heart rate, heart period, peak detection and correction, Poincaré Plot, power spectral distribution), and primarily default settings were used. Signals were filtered in accordance with BIOPAC's application note 233 (BIOPAC Systems, Inc., 2016) by a Butterworth high pass filter at 0.5 Hz and a notch filter at 50 Hz for the ECG as well as by a Butterworth bandpass filter between 0.05 and 1 Hz for the respiration signal. R peaks were detected and iteratively corrected based on the *Kubios* method (Lipponen & Tarvainen, 2019). Furthermore, we restricted during R peak detection heart periods not to be shorter than 500 ms (>120 cpm) and longer than 2000 ms (<30 cpm) as we expected no normal heart period in this range. Where a missing R peak was detected, the program inserted one in the middle between the adjacent R-peaks.

In all studies, where applicable, linear mixed effect regression models were applied for a statistically more robust analysis (Yang et al., 2014). These models allow for the modeling and correction of population or relatedness structure induced by random effects (e.g., random subject effects). Moreover, they show great robustness to distributional violation (Arnau et al., 2013; Schielzeth et al., 2020). Consequently, the advantages are enhanced statistical power, greater conformity to skewed data, and a reduction in Type-1 (false positive) errors. In addition, to further increase Type-1 error control (Luke, 2017) we calculated effects of type 3 and estimated degrees of freedom based on the Satterthwaite (or Kenward-Roger) approach and restricted maximum likelihood model. A mistake commonly committed by researchers when applying linear mixed effect models is to report standard error of the mean (SEM) alone as a measure of variability of the estimated marginal means. The obvious advantage is that this standard error appears small because it is calculated by the standard deviation divided by the square root of the sample size. However, standard error is an inferential and not a descriptive statistic. It describes the dispersion of sample means around the population mean and thus reflects the variability for a particular sample size.

Consequently, we reported 95% confidence intervals to describe the distribution of our results derived from mixed models.

In summary, data were processed using most up-to-date and highly adaptive analysis software allowing for an effective correction of signal errors and were analyzed based on robust linear mixed effect models.

8.4 Chapter Summary

- Previous chapters were shortly reviewed, and the following research questions were postulated that will be examined in three experimental studies:
 - Does vagally mediated HRV reflect executive, emotional, and self-referential processes involved in long-term memory and episodic future thinking and thus self-regulation in higher cognition?
 - Does HRV biofeedback promote adaptive long-term memory and episodic future thinking through vagally mediated changes in executive, emotional, and self-referential processes?
- A new virtual reality (VR) setup was presented that integrates HRV biofeedback in a naturalistic VR environment providing simple-to-interpret biofeedback.
- Furthermore, cognitive tasks assessing false memory production and mental time travel were integrated in VR for study 2 and 3, respectively. This allowed us to investigate, for the first time, immediate HRV biofeedback effects simultaneously on cognitive processes and autonomic regulation during cognitive activity.
- The integrated task and HRV biofeedback in VR were completely automatized to avoid susceptibility to experimentation errors.
- Automatized and semi-automatized data processing pipelines were implemented for a more robust processing of physiological data.
- Any material, such as VR video footage, is available in online repositories.

9 Chapter 9 – Exploring Persistent Cognitive Effects of Physiological Stimulation through HRV Biofeedback

This article has been published in *Frontiers in Neuroscience* (Bögge et al., 2022). The research data, details about the VR-HRV biofeedback system as well as supplementary materials and results not featured in publication are publicly available on the Open Science Framework online repository (OSF link: <https://osf.io/u4t7p/>).

9.1 Introduction

The first study in this thesis, termed BIOTRAC-1, aimed to corroborate and explore the psychological effects of repeated vmHRV stimulation through HRV biofeedback on cognitive control and self-referential episodic memory in a longitudinal experimental design.

At the time the study was designed, there had been few studies confirming HRVB-related cognitive benefits, mainly focusing on executive functions based on single-session experiments, and often lacking randomized control groups. Moreover, none of these studies directly related cognitive results to increases in vmHRV during training or studied outcomes on episodic memory and self-referential processing. Given the scarcity of research studies, especially longitudinal ones, a range of different executive control and subjective rating scales were assessed to determine the specificity of the HRV biofeedback effect. We were particularly interested in determining the variables for which vmHRV stimulation would have the greatest effect, thus providing promising venues for the following studies and future HRV biofeedback applications. In this context, effects that persisted one week after six training sessions and the association of pre-to-post-test differences with vmHRV during training were investigated. For this study, a novel VR-HRV biofeedback system as presented in Chapter 8 was developed. Different to the following two studies, the system included respiratory feedback reflected by the avatar color (i.e., “embreathment”; Monti et al., 2019), and participants were laying in a semi-recumbent position to enhance vagal activity (Kubota et al., 2013). The reason for VR implementation was generally to elicit greater vmHRV, motivation, and body self-referential processing (i.e., self-awareness, embodiment) during training. An active control group was included that followed the

same HRV self-regulation protocol (based on mindfulness) as the HRV biofeedback group, except that no biofeedback was presented. The target was to control for essential positive subject-expectancy (i.e., placebo) effects, as the main objective was to link cognitive outcomes to vmHRV. Furthermore, this allowed us to check the usefulness of the biofeedback signal during non-respiratory-paced HRV self-regulation training for vmHRV and cognitive stimulation. Scores of RMSSD and RSA measured vmHRV; however, psychophysiological associations were established with RSA since it best captures respiratory induced CVC during HRV biofeedback. It was assumed that variables that increased after HRV biofeedback and were associated with the degree of vmHRV stimulation would reflect long-term changes autonomic and brain functioning contributing to the psychological function measured.

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Respiratory sinus arrhythmia during biofeedback is linked to persistent improvements in attention, short-term memory, and positive self-referential episodic memory

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Background: Heart rate variability (HRV) biofeedback, an intervention based on the voluntary self-regulation of autonomic parameters, has been shown to affect prefrontal brain functioning and improve executive functions. The interest in using HRV biofeedback as cognitive training is typically ascribed to parasympathetic activation and optimized physiological functioning deriving from increased cardiac vagal control. However, the persistence of cognitive effects is poorly studied and their association with biofeedback-evoked autonomic changes has not yet been explored. In addition, no study has so far investigated the influence of HRV biofeedback in adults on long-term episodic memory, which is particularly concerned with self-referential encoding processing.

Methods: In the present study, a novel training system was developed integrating HRV and respiratory biofeedback into an immersive virtual reality environment to enhance training efficacy. Twenty-two young healthy adults were subjected to a blinded randomized placebo-controlled experiment, including six self-regulation training sessions, to evaluate the effect of biofeedback on autonomic and cognitive changes. Cardiac vagal control was assessed before, during, and 5 min after each training session. Executive functions, episodic memory, and the self-referential encoding effect were evaluated 1 week before and after the training program using a set of validated tasks.

Results: Linear mixed-effects models showed that HRV biofeedback greatly stimulated respiratory sinus arrhythmia during and after training. Moreover, it improved the attentional capabilities required for the identification and discrimination of stimuli ($\eta_p^2 = 0.17$), auditory short-term memory ($\eta_p^2 = 0.23$), and self-referential episodic memory recollection of positive stimuli ($\eta_p^2 = 0.23$). Episodic memory outcomes indicated that HRV biofeedback reinforced positive self-reference encoding processing. Cognitive changes

were strongly dependent on the level of respiratory sinus arrhythmia evoked during self-regulation training.

Conclusion: The present study provides evidence that biofeedback moderates respiration-related cardiac vagal control, which in turn mediates improvements in several cognitive processes crucial for everyday functioning including episodic memory, that are maintained beyond the training period. The results highlight the interest in HRV biofeedback as an innovative research tool and medication-free therapeutic approach to affect autonomic and neurocognitive functioning. Finally, a neurocognitive model of biofeedback-supported autonomic self-regulation as a scaffolding for episodic memory is proposed.

KEYWORDS

heart rate variability biofeedback, respiratory sinus arrhythmia, cardiac vagal control, self-regulation, virtual reality, cognitive training, executive functions, self-referential episodic memory

Introduction

Heart rate variability biofeedback (HRVB) is a training technique that relies on the self-regulation of autonomous nervous system (ANS) processes to optimize physiological functioning affecting cognition (Lehrer and Gevirtz, 2014). In this context, autonomic activity is indexed by the heart rate variability (HRV), i.e., the periodic change in the cardiac rhythm. HRV characterizes cardiac-brain interactions and has important implications for psychophysiological research. It is a recognized indicator of a person's physiological and behavioral regulatory capacities underlying physical and psychological resilience (Thayer and Lane, 2000; Andreassi, 2010; Holzman and Bridgett, 2017). Moreover, increased levels of HRV have been associated with beneficial effects for health (Gevirtz, 2013; McCraty and Shaffer, 2015; Lehrer et al., 2020) and cognitive performance (McCraty, 2003,

2016; Hansen et al., 2004; Thayer et al., 2009; Forte et al., 2019). Different theories suggest that the interaction between HRV and cognition is associated with cardiac vagal control (CVC), which is an index of the tonic and phasic parasympathetic activity that the vagus nerves exert to regulate the heart (Lehrer et al., 2000; Thayer and Lane, 2000, 2009; McCraty and Childre, 2010; Shaffer et al., 2014). In this context, the Neurovisceral Integration Model (Thayer and Lane, 2000; Thayer et al., 2009) assumes that a set of cortical-subcortical neural circuits, associated with cardiac as well as cognitive regulation, is modulated *via* an inhibitory pathway linked to the prefrontal cortex that can be interrelated with vagal traffic. Hence, the authors proposed that vagally mediated HRV reflecting CVC is positively correlated with prefrontal cortex performance, which in turn is linked to diverse cognitive functions.

Both the Psychophysiological Coherence model (McCraty and Childre, 2010) and the Resonance Frequency Training model (Lehrer et al., 2000) argue that stronger vagal afferent outflow and prefrontal cortex stimulation can be achieved by optimizing the dynamic structures and interplay of physiological rhythms. According to McCraty and Childre (2010), this optimization is achieved by creating physiological coherence, represented by orderly and stable rhythms, within and between regulatory systems through slow breathing and activation of positive emotions. The Resonance Frequency Training model theorizes that slow breathing at the individual resonance frequency of around one breathing cycle per 10 s (≈ 0.1 Hz) evokes an alignment of the respiration, heart rate, and blood pressure rhythms reflecting enhanced homeostatic regulation (i.e., baroreflex gain). The techniques involved in the two models both focus on a stable alignment of oscillatory systems driven by vagal influence of the parasympathetic branch (i.e., CVC) that produces auto-coherent (sinusoidal) heart rate

Abbreviations: HRVB, heart rate variability biofeedback; ANS, autonomous nervous system; HRV, heart rate variability; CVC, cardiac vagal control; RSA, respiratory sinus arrhythmia; VR, virtual reality; SRE, self-reference effect; EM, episodic memory; vmPFC, ventromedial prefrontal cortex; dlPFC, dorsolateral prefrontal cortex; BG, biofeedback group; CG, active control group; BMI, new body mass index; ECG, electrocardiogram; R/K/G, Remember/Know/Guess; NN, normal-to-normal: time interval between successive normal heartbeats; RMSSD, root mean square of successive heartbeat interval differences; SDNN, standard deviation of normal heartbeat intervals; pNN50, percentage of successive normal heartbeats that differ by more than 50 ms; lnLF, natural logarithm of absolute low frequency power of the heart rate signal; lnHF, natural logarithm of absolute high frequency power of the heart rate signal; normLF, relative power of the low frequency band; normHF, relative power of the high frequency band; LF/HF, absolute power ratio of the low frequency and high frequency band; P2T-RSA, natural logarithm of the RSA calculated by the peak-to-trough method; PB-RSA, natural logarithm of the RSA calculated by the Porges-Bohrer method; ANOVA, analysis of variance; EMM, estimated marginal mean; DV, dependent variable.

waveforms with greater amplitudes. Furthermore, both have in common that HRV is mainly driven by respiration *via* the vagus nerve, also referred to as respiratory sinus arrhythmia (RSA). The latter thus reflects respiration-related CVC which can be assessed by measuring the RSA amplitude (heart rate difference from peak to trough across the breathing cycle) which captures cardiac-respiratory synchrony and HRV amplitude. Another prominent marker of vagally mediated HRV that describes CVC is the root mean square successive difference in the heart period series (RMSSD; Laborde et al., 2017; Shaffer and Ginsberg, 2017). The difference between these two indices is that RSA amplitude reflects CVC which is more tightly linked to respiration and physiological coupling than RMSSD. Accordingly, RSA amplitude is more strongly affected during HRVB and may serve as a more precise indicator of training success whereas RMSSD may better capture overall influences on CVC.

The models presuppose physiological state awareness for voluntary autonomic control. Such awareness can be created through biofeedback, which refers to the measurement and feedback of endogenous physiological parameters. In this context, cardiac and often also respiratory responses, typically presented through the visualization on a screen, are utilized by the user to adapt the HRV regulation strategy (e.g., change in breathing rhythm). Previous HRVB procedures based on the Resonance Frequency Training model or the Psychophysiological Coherence model, also sometimes termed RSA biofeedback, showed positive effects on diverse cognitive functions in healthy adults (see Dessy et al., 2018 and Tinello et al., 2021 for a review), including acute improvements in inhibitory control and attention measured directly after only one session of training (Sherlin et al., 2010; Prinsloo et al., 2011, 2013; Blum et al., 2019) as well as improvements maintained for 1 week in verbal short-term memory, decision making, inhibitory control, and sustained attention (Sutarto et al., 2010, 2012, 2013). In clinical settings large gains in cognitive functions were also achieved, such as improvements in attention, short- and long-term memory (Ginsberg et al., 2010; Lloyd et al., 2010). Despite these first promising results, the relationship between biofeedback-induced changes in the ANS and cognitive improvements as well as the importance of the biofeedback signal remain unclarified. To the best of our knowledge, no previous HRVB study has so far quantified the relationship between autonomic and cognitive changes or included a control placebo condition. Previous findings indicated that when such a condition was included in a respiratory biofeedback study, no positive effect of the biofeedback component could be found (Kapitza et al., 2010; Tinga et al., 2019). Moreover, self-regulation training such as mindfulness and meditation practices are also known to increase HRV amplitude and coherence if they involve slow breathing or the evoking of positive emotions (Cysarz and Büssing, 2005; McCraty and Shaffer, 2015) and

may evoke similar levels compared to HRVB interventions (Brinkmann et al., 2020). In addition, none of the previous studies included blinded randomized control trials and an effect maintenance period between the training and post-training cognitive evaluation. Therefore, it remains unclear whether HRVB benefits cognition beyond the training period and whether these cognitive changes were mediated through physiological changes.

In addition, virtual reality (VR), an emerging tool in psychological research, has been used only very rarely for HRVB practices. The interest of an immersive VR-application is that it can introduce new ways in which the user is stimulated and how biofeedback is delivered during training. In this regard, VR can, compared to computer screens, increase the level of immersion, user engagement, sense of embodiment (Kilteni et al., 2012) and presence, i.e., the feeling of being located in and of responding to a virtual environment as if it were real (Fuchs, 2017; Armougum et al., 2019). These properties are particularly useful to increase the intensity of attentional commitment to the biofeedback (Sanchez-Vives and Slater, 2005) and to manipulate the emotional mode (Riva et al., 2007). Both a high level of attention and positive affectivity are crucial for HRVB task success and may positively influence training outcomes. The role of VR for biofeedback purposes to improve cognitive and emotional states supporting training has already been emphasized previously (Cho et al., 2004; Shaw et al., 2007; Repetto et al., 2009; Shiri et al., 2013; Gromala et al., 2015; Blum et al., 2019, 2020; Rockstroh et al., 2019, 2020). Furthermore, a stronger sense of presence has been associated with greater skill transfer to real life applications (Sanchez-Vives and Slater, 2005; Grassini and Laumann, 2020), highlighting the benefits of VR for biofeedback interventions.

The relevance of HRVB for cognition has been studied primarily for prefrontal cognitive functions involved in early stage information processing but never for long-term memory in adults and self-referential processing in general. Episodic memory (EM) is a unique memory system that records specific events experienced by oneself (Tulving, 1985, 2002). Self-focused experience during encoding is critical in determining the idiosyncratic nature of long-term memory (Hommel, 2004; Bergouignan et al., 2014; Makowski et al., 2017; Bréchet et al., 2018). Several paradigms have been developed to explore the role of the self in EM performance. The best-known paradigm for studying this relationship is self-reference manipulation (Rogers et al., 1977; Symons and Johnson, 1997; Klein, 2012). Self-reference processing consists in linking new to-be-remembered information to the self, either *via* its narrative component (e.g., pre-stored self-knowledge and autobiographical memories) or its minimal component (e.g., the “I” who is experiencing “here and now” or the body self) (Gallagher, 2000), that provides a memory advantage to the new information known as the self-reference effect

(SRE). Firstly, self-regulation training requires attentional focus to the self which is assumed to elicit self-awareness and self-reference processes (Vago and David, 2012). The self also extends to the embodied self, namely the virtual representation of the person's own body and physiological functions (Monti et al., 2019). In this regard, biofeedback may further support the stimulation of self-referential processing as it provides access to, and facilitates the monitoring of, self-related processes that normally go unnoticed (e.g., changes in the heart rate). Secondly, self-referential processing is characterized by a greater activation of the ventromedial prefrontal cortex (vmPFC; Northoff et al., 2006; D'Argembeau et al., 2007; Denny et al., 2012; Martinelli et al., 2013; Yaoi et al., 2015), a cortical area that is also involved in cognitive and physiological self-regulation processes (Hänsel and von Känel, 2008; Thayer et al., 2009; Maier and Hare, 2017). Initial evidence that HRVB alters brain functioning related to self-processing after training has been recently reported (Schumann et al., 2021; Bachman et al., 2022). Thus, we assume that VR-HRVB training may alter the mnemonic properties of self-reference through self-focused attention and ANS-mediated changes in the neurophysiological functioning related to the vmPFC.

The target of this study was to evaluate the lasting impact of increasing CVC during HRVB on the task performance of a wide range of cognitive functions in young healthy adults, including attention and executive functions, and for the first time, long-term EM and self-referential processes. The work investigated the specific effect of biofeedback during HRV self-regulation training on cognition as well the association between autonomic and cognitive changes. A novel system was developed coupling real-time biofeedback with immersive VR. Two randomized and blind groups were compared including a control placebo condition that differed from the HRVB intervention group by the absence of biofeedback. It was hypothesized that (1) young healthy adults practicing HRV self-regulation training stimulate more profoundly CVC indexed by RSA amplitude and RMSSD during training when biofeedback is provided with greater effects on RSA amplitude, (2) HRVB training sustainably improves executive and emotional control as well as EM compared to training without biofeedback, (3) increases in EM performance are greater for items encoded with self-reference due to changes in the SRE, and (4) improvements in behavioral functions are positively correlated with the level of respiration-linked CVC (i.e., RSA amplitude) during training.

Materials and methods

As part of this work, a public data repository (Bögge et al., 2021) was created that contains in addition to the datasets, the digital materials used and on materials and methods.

Participants and study design

A minimum sample size of 20 participants for the cognitive effects of HRVB was estimated before data collection based on the only available publications with similar protocols that also included a cognitive maintenance period and a control group (Sutarto et al., 2010, 2012, 2013). In this line, Sutarto et al. (2010) found significant group-by-time interaction effects on memory and attention using a sample of only 16 subjects. Furthermore, partial eta-square values greater than 0.16 were determined for group-by-test interaction effects on memory and attention measures reported by Sutarto et al. (2012), who replicated their previous study with a bigger sample size, by calculating the group difference between time effect sizes. Based on the assumption that partial eta-square values greater than 0.10 will be observed for interaction effects in this study, a minimum sample size of 20 participants was calculated using G*Power 3.1.9.4 (Faul et al., 2009) with alpha = 0.05, power = 0.80, and correlation among repeated measures = 0.5. For the physiological measures a minimum sample size of 90 (15 participants × 6 repeated measures) was determined with alpha = 0.05 and power = 0.80. The corresponding power analysis was performed for an independent *t*-test with nested data (repeated measures per participant). One sample corresponds to the measure of a single session. Each participant had to pass six training sessions. Therefore, 90 samples correspond to the sum of all sessions of 15 participants (6 sessions × 15 participants). We assumed moderate-to-strong group differences (Cohen's *d* > 0.6) as HRVB affects CVC very strongly in young healthy adults (Lehrer et al., 2003; Prinsloo et al., 2013; Blum et al., 2019; Rockstroh et al., 2019) whereas effects in the control group were expected to be at best modest (Krygier et al., 2013; Léonard et al., 2019).

Participants were recruited through an online application form that was accessible *via* an online platform communicating experiment offers and hangouts in the university building. In total, 25 young healthy adults were enlisted for a series of six self-regulation training sessions that was preceded and followed by a cognitive assessment session. All the following inclusion and exclusion criteria in this section were established prior to data collection. The study included only 20- to 30-year-old native French speakers who reported not being concerned by any of the following conditions: history or treatment for psychiatric, neurological, cardiac, or severe respiratory disorders, treatment with a cognitive impact, chronic pain, frequent dizziness or nausea, vertigo, impaired but not corrected visual or auditory capabilities, substance abuse. Further, participants were required to have completed at least 12 years of education and be novices in meditation, as regular mindfulness practice could impact self-regulation capabilities. Finally, the analysis took account only of participants who attended each session and whose test scores

(see below) did not indicate high levels of anxiety or depression. After enrollment, participants were divided pseudo-randomly into a biofeedback group (BG) and an active control group (CG). In total 22 subjects were included for the data analysis, of which 12 were in the BG (8 women, mean age 24 ± 2.48 years) and 10 in the CG (6 women, mean age 26.88 ± 3.93 years). Three participants were excluded because two exhibited high anxiety scores and one did not show up for the last assessment session.

Experiments were conducted individually between April 2019 and March 2020 at the Institute of Psychology of the Université Paris Cité, with participants being blind to the group assignment and existence of two different experimental conditions (with and without biofeedback). Informed and written consent was obtained at the beginning of the first session. At the end of the last session participants were compensated with a gift voucher. All procedures performed in studies involving human participants were in compliance with the ethical standards according to institutional guidelines and national legislation (Jardé law, 2016). Data privacy protection, collection, and processing were in accordance with the 2018 reform of Eu data protection rules (2018).

Cognitive evaluations and training were conducted in two different experimental rooms. To keep the instructions and information given equal between groups and to circumvent differences in subject-expectancy, it was mentioned to each participant during recruitment and at the beginning of the first assessment that training might improve health as well as cognitive functions in general. Demographic details, the new Body Mass Index (BMI) for the measure of body fat, and hours of sport per week were recorded at the beginning of the first session. Furthermore, all participants reported being right-handed and having no prior experience of biofeedback training. Levels of anxiety and depression were assessed at the beginning of the first and last session with the score-based validated French version of the State-Trait Anxiety Inventory (Spielberger, 1983; Schweitzer and Paulhan, 1990) and the shortened and validated French version of the Beck Depression Inventory (Beck and Beamesderfer, 1974; Collet and Cottraux, 1986). According to the manual of the State-Trait Anxiety Inventory and Beck Depression Inventory, the severity of the syndromes was classified as high when scores were above 55 and 15, respectively. Measures of participant characteristics did not significantly differ at a significance level of $\alpha = 0.05$ between groups except for the BMI (Table 1). It was therefore added as a control variable in the HRV analysis. Anxiety and depression scores did not change from pre- to post-test and did not differ between groups at post-test ($ps > 0.527$). Further, participants were asked to refrain from smoking and consuming caffeinated or alcoholic substances during training days until the end of the sessions. After the end of the study, participants had 1 week in which to complete, if they wished, an anonymized online follow-up questionnaire that assessed their subjective feeling about training effects on their cognition and wellbeing.

Training system

A new VR biofeedback system was developed for the self-regulation training of HRV. The novelty compared to conventional HRVB training systems is that cardiac as well as respiratory responses are embodied in an immersive VR environment displayed *via* a head mounted display (Vive; HTC and Valve, 2015; Figure 1). In this virtual world, created with the computer software Unity 3D (Unity Technologies, 2018), the user takes on the form of a human avatar (first-person body view) half-reclining on a lonely beach gazing at the open sea. Changes in thoracic or abdominal circumference and an electrocardiogram (ECG) are recorded wirelessly by the BIOPAC data acquisition system MP150 (Biopac Systems, Inc., n.d.a,b,c,d,e,f) including surface electrodes and a respiratory belt transducer. Signals are then processed by customized scripts embedded in Unity 3D that allow the data stream to be coupled with the VR environment. In this way, HRV and respiration can be embodied in real time by the change of color of the sea and the avatar, respectively. Consequently, the visual biofeedback can be used in combination with a training method, e.g., a breathing exercise, to regulate the heart and respiratory functions in a targeted manner. A more detailed account of the setup as well as of the following training procedure is provided in the public data repository (Bögge et al., 2021).

Training procedure and physiological recordings

Each participant of the BG and CG attended individually six training sessions over a period of 3 weeks. For each week, two sessions had to be scheduled on different days that lasted around 1 h including 25 min of training in VR. Participants of both groups followed the same self-regulation training (i.e., regulation of the respiration and heart rate) specified below during which only the BG received biofeedback. Physiological parameters were recorded each session following guidelines of the manufacturer's application note 233 (Findlay and Dimov, 2016). For the HRV study design, processing, analysis, and report we followed the guidelines of the Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology (1996) and recommendations for HRV in psychophysiological research (Laborde et al., 2017).

At the beginning of each session participants were seated on a reclining chair where they remained seated throughout the session in a Fowler position with a whole trunk inclination at 45° and knees slightly bent. Both groups were provided with similar instruction sheets that included information about the principles of HRV, RSA, Resonance Frequency Training, mindfulness, meditation, and HRV training techniques (see repository Bögge et al., 2021). Only the BG received extra

TABLE 1 Participant characteristics.

Control variable	Mean (SD)		Group effect	
	BG (n = 12)	CG (n = 10)	F (1,20)	p
Proportion of females ^a	66%	60%	0.11	0.746
Proportion of subjects regularly playing video games ^a	34%	20%	0.49	0.484
Current Years of Education	14.17 (1.70)	14.50 (1.51)	0.23	0.635
BDI (Depression)	3.67 (3.70)	4.50 (3.92)	0.26	0.614
STAI-Y1 (State Anxiety)	30.67 (8.29)	28.50 (6.72)	0.44	0.515
STAI-Y2 (Trait Anxiety)	35.08 (9.19)	34.58 (7.76)	0.03	0.874
Hours of sport per week ^b	2.00 (2.25)	2.00 (2.5)	236	0.932
New Body Mass Index (BMI) ^b	20.85 (2.30)	23.64 (7.80)	132	0.011

BG, biofeedback group; CG, active control group; BDI, beck depression inventory; STAI, state trait anxiety inventory.

^aGroup effect is represented by $X^2(1, N = 22)$.

^bDue to violation of normality distribution the median, inter-quartile-range (in parenthesis) and results from the Mann-Whitney-Wilcoxon test ($U[24,20]$) are reported.

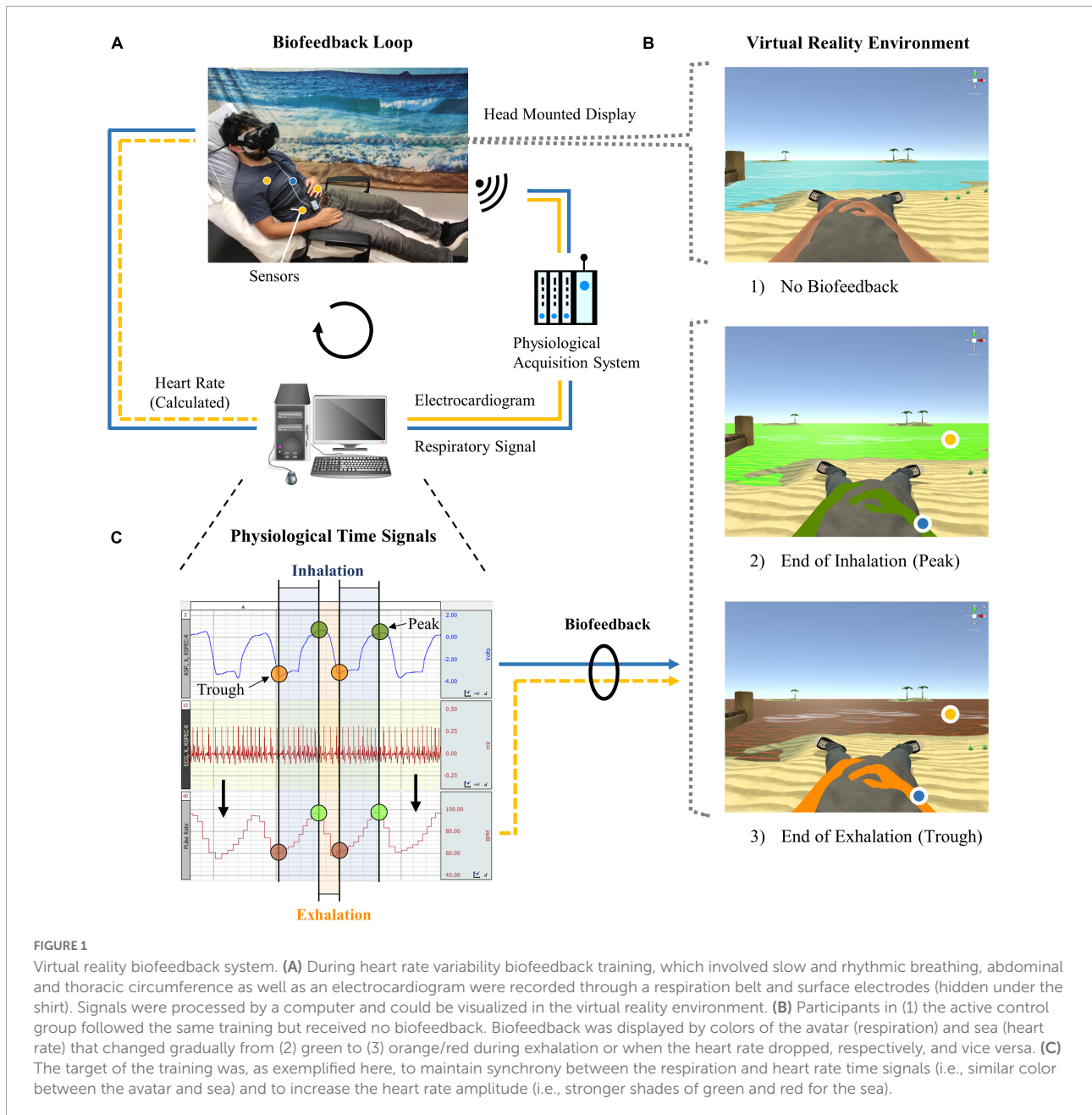
specifications for the biofeedback signals. The given objective was the same for both groups, i.e., to increase levels of HRV and synchrony between heartbeat and respiratory oscillations. To ensure that the participants felt at ease and complied with the instructions, they were also orally briefed and debriefed before and after each training session, respectively, with questions being clarified. Additionally, instructions were recapitulated during a 5-min habituation period in VR prior to starting training in the first session. During this period, subjects were free to explore and familiarize themselves with the VR environment and biofeedback. Otherwise, participants were immersed in VR only during the training phase. For the duration of the training, participants were instructed to place their hands on their belly to mimic the posture of their avatar, to restrict their movements except for the head, and to refrain from talking.

Self-regulation training was based on the Resonance Frequency Training protocol of [Lehrer et al. \(2000\)](#). Participants were asked to breathe rhythmically at around one cycle per 10 s, inhaling diaphragmatically and exhaling through pursed lips at equal intervals. Shallow and natural inhalation was advised to prevent hyperventilation. No pacer was provided; instead, participants of both groups were instructed to adjust the respiratory rate that elicited the largest heart rate oscillations. However, for the first 2 min of each training session, the rhythm (i.e., 1 cycle per 10 s) was dictated to help the subjects get a better sense of timing. Moreover, in order to facilitate the monitoring and control of the HRV, participants were instructed to conduct a body scan ([Ditto et al., 2006](#)), a common meditation practice involving the focalization of attention on the sensations of respiration and heartbeat in a certain part of the body. Attention had to be directed to five different body parts successively for 5 min each. The only difference between groups was that the BG received visual biofeedback. Consequently, they were free to choose whether to concentrate on body sensations or on the colors in the VR environment for information on their own HRV, whereas the CG had to rely solely on body perception. For the BG, the body part displaying biofeedback changed

automatically and indicated the locus on which the user should focus. Contrary, the CG was instructed orally to shift their attention each 5 min. During training, a running ventilator was placed 1.5 m in front of the participant and sea sounds were played to increase feelings of immersion. Furthermore, the physiological recordings included two 5-min resting-state measures to determine the baseline and recovery level; one shortly before the VR immersion and one starting 5 min after the training. In addition, the participant and experimenter were separated by blinds during recordings to reduce distractions and increase levels of comfort.

System assessment

In order to explore VR and attention related characteristics of the present system, self-report evaluations of a subsample of 16 Participants (9 in the BG) were recorded. Participants were asked to rate their sense of presence and embodiment (i.e., body ownership, agency, location of the body, and external appearance) in the VR after each second training session using adapted versions of the Slater-Usuh-Steed questionnaire ([Slater and Steed, 2000](#); [Usuh et al., 2000](#)) and the embodiment questionnaire proposed by [Gonzalez-Franco and Peck \(2018\)](#), respectively. Participants were assessed either at session 1, 3 and 5 (A) or at session 2, 4 and 6 (B). The assessment sequence A or B was randomized among participants. Half of the participants were assessed in sequence A (5 in the BG) and the other half in sequence B (4 in the BG). Furthermore, subjects were asked after each training session to estimate the amount of time they felt attentive to the task and the amount of time they felt drowsy during self-regulation training (see repository [Bögge et al., 2021](#)). In addition, subjects reported the level of fatigue they were feeling at the moment before and after each session. This item was based on the Right Now item from the Brief Fatigue Inventory ([Mendoza et al., 1999](#)) with “problems thinking clearly” added so that mental fatigue was also reflected



in the score (Guidelines, 1998). Recordings of one session in the CG had to be excluded due to technical problems. In total there were 47 samples for the presence and embodiment scales each and 95 samples for the attention and fatigue scores each.

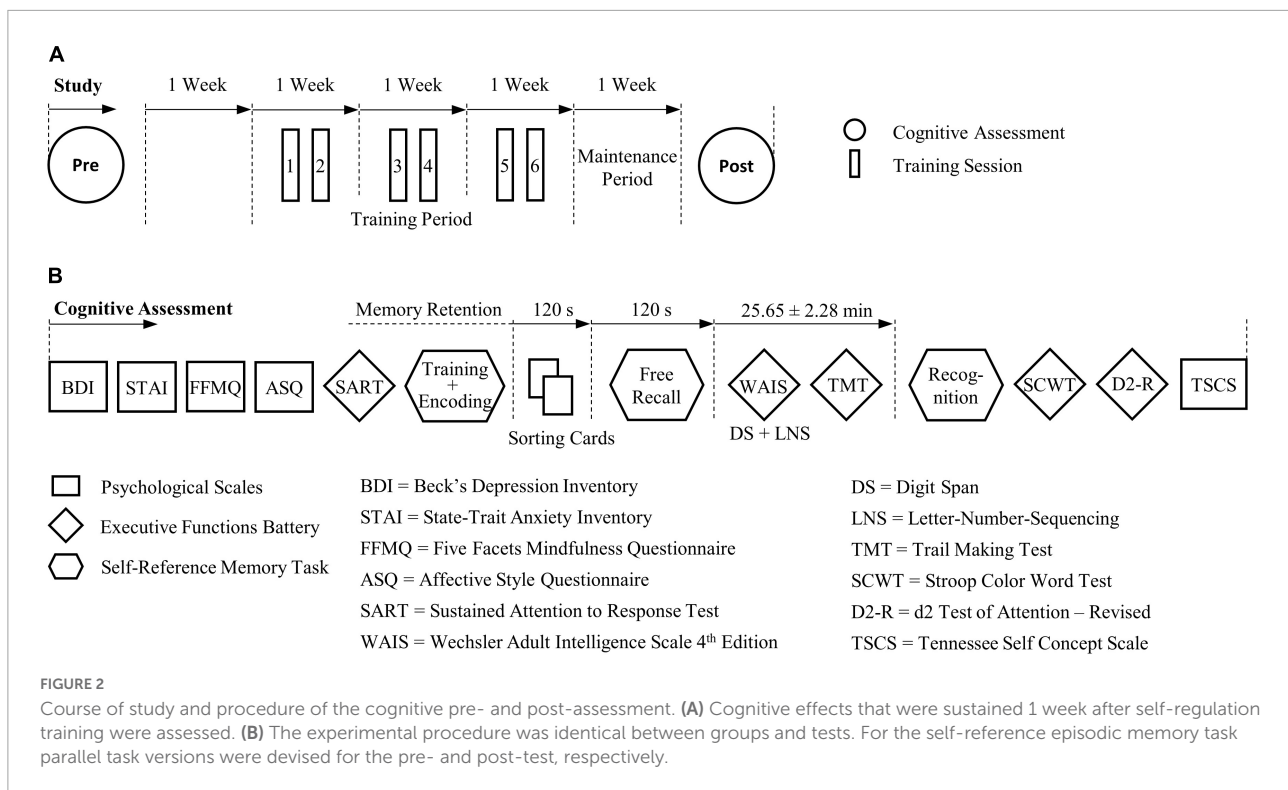
Cognitive assessment

Standard and validated tests and scales including measures of memory, executive and affective control, mindfulness, and self-concept were administered with a pretest-posttest experimental design. Participants were individually assessed

with an identical procedure between tests and groups around 1 week before and around 1 week after the training period (Figure 2). Pre- and post-assessments were carried out by two different experimenters, with the posttest being performed blind.

Psychological scales

At the beginning of each assessment, participants were asked to complete four computerized self-administered questionnaires, including the Beck Depression Inventory (Beck and Beamesderfer, 1974; Collet and Cottraux, 1986) and State-Trait Anxiety Inventory (Spielberger, 1983;



Schweitzer and Paulhan, 1990) that were used for screening (see 2.1). Additionally, the state of mindfulness and emotional regulation capabilities were assessed using the French translation of the Five Facet Mindfulness Questionnaire (Baer et al., 2006; Heeren et al., 2011) and a shortened and validated French version of the Affective Style Questionnaire (Hofmann and Kashdan, 2010; Makowski et al., 2018), respectively. Questionnaires were administered and scores calculated with the Python module Neuropsychia (Makowski and Dutriaux, 2016) in WinPython64 version 3.7.2 (Raybaut and 2014–2019+ The WinPython Development Team, 2019) based on Python version 3.7. Assessments were concluded with a self-assessment scale of the subjective perception of the self-concept by means of three shortened French versions of the Tennessee Self-Concept Scale (Fitts and Warren, 1996; Duval et al., 2007; Compère et al., 2018). While all three forms comprised the same 21 items of the original Tennessee Self-Concept Scale, they evaluated the self-concept in different time dimensions (i.e., past, present, future). Global scores were retrieved for each form with higher scores indicating a more positive self-perception.

Executive functions

Executive functions including sustained attention, processing speed, cognitive flexibility, inhibition, as well as short-term and working memory were evaluated by means of six cognitive tests (Figure 2). Sustained attention and inhibitory control were checked before the memory task by a computerized version of the Sustained Attention to Response

Task (Robertson et al., 1997; Makowski and Dutriaux, 2016) which is a Go/No-Go task with a majority of Go stimuli (89%). The mean reaction time as well as the rate of correct Go and No-Go responses were determined. Attention and concentration capabilities were also evaluated at the end of the assessment by the French revised version of the d2 Test of Attention (Brickenkamp et al., 2015). Norm-referenced scores of the Processed Target Objects, Percentage of Errors (or Error Rate) and the Concentration Performance were derived. Cognitive interference involving inhibition processes was investigated using the Stroop Color and Word Test (Stroop, 1935). In line with recommendations of Scarpina and Tagini (2017), a new global score was introduced, representing the interference effect that incorporated the processing time and the corrected as well as uncorrected errors of each subtest (see repository Bögge et al., 2021). Further, abilities of cognitive flexibility were assessed by the Trail Making Test (Reitan, 1958). For the analysis, the completion time of part A and part B and the difference between the Trail Making Test parts (B-A) in seconds were included. For the Stroop Color and Word Test and Trail Making Test the French translations from the GREFEX test battery (Godefroy et al., 2010) were used. Working memory capabilities were assessed by the Digit Span and Letter-Number Sequencing tests from the French translation of the fourth edition of the Wechsler Adult Intelligence Scale (Wechsler, 2010) that tested the immediate recall of series of digits and letters. Norm scores were derived for all digit spans in the Digit Span (i.e., forward, backward,

sequencing, and total) and Letter-Number Sequencing tests as well as for the Working Memory Index.

Self-reference episodic memory task

To test EM, in particular recollection memory, involving self-reference processes, we adhered to validated protocols that investigated the mnemonic SRE in healthy young and older subjects and in pathological condition (Lalanne et al., 2013; Compère et al., 2016). All materials, stimuli, and the procedure used for this task derived from the latter two studies which assessed EM using the Remember/Know/Guess (R/K/G) paradigm (Gardiner et al., 2002). Memory probes (see repository Bögge et al., 2021) were personality trait adjectives (e.g., “optimistic” and “malicious”) originating from Anderson’s personality-trait word list (Anderson, 1968). The number of positive and negative items was balanced within and among all lists. Two parallel task versions were used for the pre- and post-test with an identical procedure and different word lists. The task was divided into three phases: (1) encoding, (2) free recall, and (3) recognition (Figure 3).

Encoding

Following a short familiarization phase, participants were presented item by item with 48 adjectives of four different conditions which they were instructed to memorize. For every adjective, participants had to make a yes-or-no decision to decide, depending on the condition, whether (a) its first and last letters were in alphabetical order (perceptive condition), (b) it was considered as socially desirable in general (semantic condition), (c) it described them (semantic self-reference condition), or (d) it could be associated to a memory of a personal event (episodic self-reference condition).

Free recall

After a short memory retention period they were asked to retrieve without any aid as many adjectives as possible within 2 min. Subsequently, memory was further retained for a second period of around 25 min during which the memory task was interrupted by part of the executive functions test battery (Figure 3).

Recognition

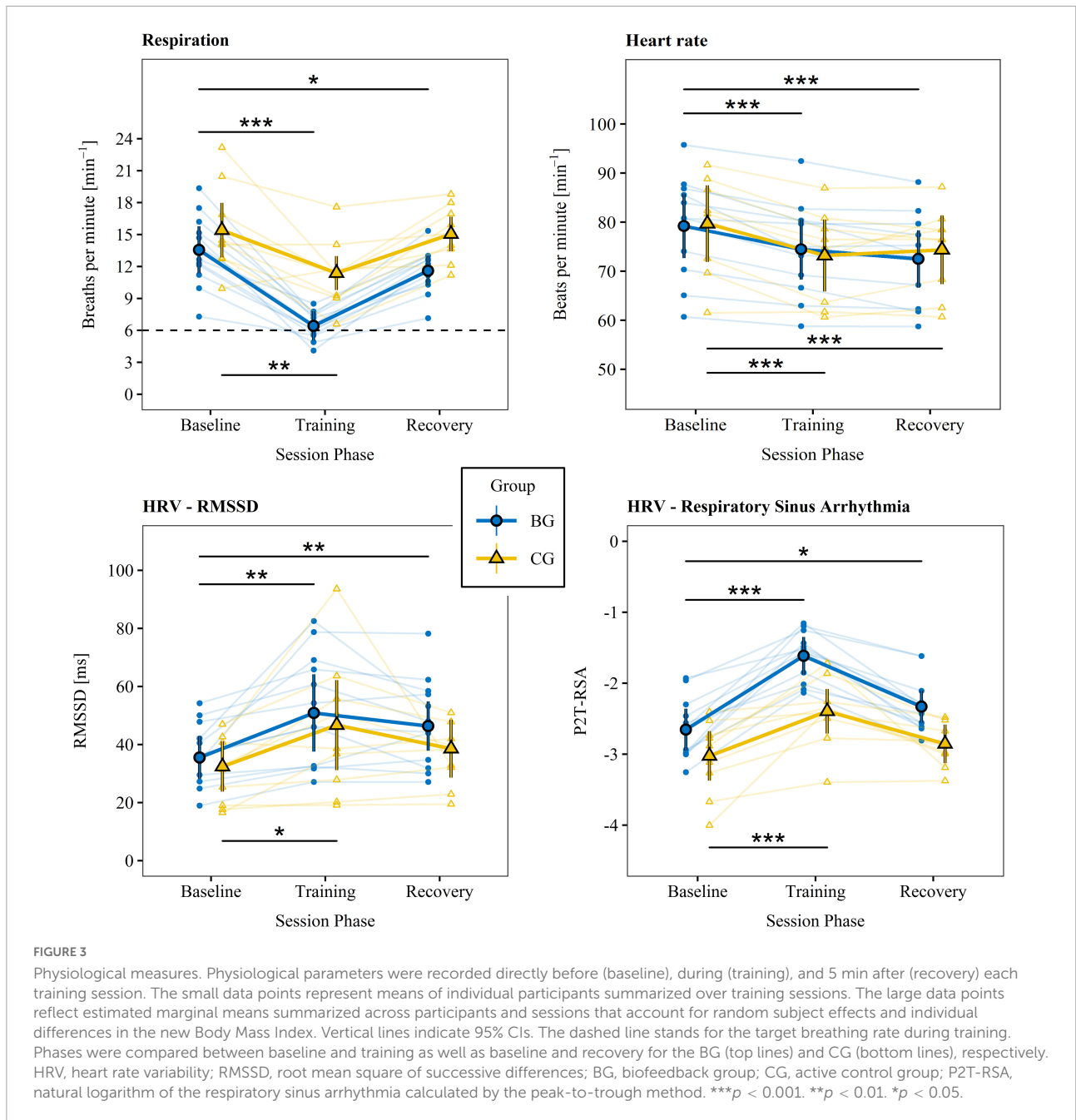
Participants were presented with a list of 48 adjectives, half of which (24 items) derived from the encoding conditions while the other half were novel distractor items. The content of the recognition lists was equal between participants and in random order. For each word the participants had to decide whether they had seen it during encoding or not. If the answer was “yes,” an additional question addressed the presence of memory recollection using the R/K/G paradigm (Gardiner et al., 2002). In this line, the participants had to decide whether they remembered (R) in which context the word occurred (they could mentally experience the encoding again), or whether they knew

(K) with certainty that the adjective appeared before, but they did not remember encoding details, or whether they guessed (G) its previous presence. Each R response was checked by asking the participant to indicate the corresponding condition.

Recordings included the response decisions and response reaction time during the encoding and recognition phase as well as the adjectives recalled. Measures of memory performance were the proportions of correct free recalls, subjective remembering (correct R responses), and objective source recollections (R responses correctly associated with the encoding condition) among the studied items. Furthermore, the performance of discriminating studied from distractor items was determined by calculating the sensitivity index d' (or d'). All measures were retrieved in dependence of the encoding condition and the valence of the adjectives.

Data processing of physiological recordings

Physiological recordings from the training sessions were preprocessed semi-automatically to generate measures of HRV and RSA in accordance with established guidelines, norms, and metrics (Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology, 1996; Laborde et al., 2017; Shaffer and Ginsberg, 2017). Recordings of the 25-min training phase were split into five non-overlapping 5-min segments per session to match the length with the baseline and recovery phases. Segments of the baseline, training, and recovery phases were then processed and analyzed individually using an adapted version of the Python package NeuroKit2 (Makowski et al., 2020). Based on recommendations by BIOPAC (Biopac Systems, Inc., n.d.f) and the application note 233 (Findlay and Dimov, 2016), preprocessing included a bandpass filter of 0.5–35 Hz for the ECG and a bandpass filter of 0.025–1 Hz for the respiratory signal. In the ECG signal QRS complexes were automatically identified and the timing of the R-peaks within each QRS complex was determined following the *NeuroKit* method. QRS complexes that were shorter than 0.4 or longer than 1.25 times the median of all QRS intervals were rejected. Additionally, any R-peak that occurred less than 500 ms after the preceding R-peak was excluded (i.e., maximum threshold of 120 Hz between two heartbeats). The timing of R-peaks and therefore the heart period series (i.e., R-R intervals) was then corrected based on the algorithm of Lipponen and Tarvainen (2019). The algorithm identified R-peaks that were missing, superfluous, or misplaced, causing very rapid changes in successive R-R intervals that are typical of ectopic beats. In the correction phase, R-peaks were then respectively either deleted, inserted, or moved to the center between the directly adjacent R-peaks. R-peak correction was iterated so that R-peaks were corrected one-by-one starting from the beginning of the time series. To handle the correction of



multiple adjacent R-peaks that were missed (e.g., rejection of R-peaks due to movement artifacts) the number of missing R-peaks was estimated whenever a missing R-peak was detected. Equal R-R intervals between inserted and adjacent R-peaks were assumed (i.e., constant heart rate) that were no longer than the 95th percentile plus the standard deviation of R-R intervals in the complete time series. The number of inserted R-peaks was increased until this threshold was undershot. For further details please consult the NeuroKit2 documentation (Makowski, 2021). Raw signals as well as graphical outputs generated from the analysis (e.g., original and corrected RR

period, heart rate, and respiration time series) were sighted individually for measurement errors, artifacts, and ectopic beats. The prevalence of ectopic beats in the general adult population is 1–4% and at the median they amount to around 0.01% of all heartbeats (Simpson et al., 2017; Marcus, 2020). It is normal, however, for some humans to experience higher numbers of ectopic beats; excessive numbers are generally defined as >10% of all heartbeats.

Complete sessions were discarded if one or more segments met one of the following exclusion criteria that were established prior to data collection: (1) the raw signal was strongly artifacted

or exhibited a high number of ectopic beats (i.e., proportion to total beats >2% or occurrence of more than two consecutive ectopic beats), (2) the analysis repeatedly failed to correct artifacts (e.g., large and abrupt changes visible in the heart period after correction), or (3) respiration cycles could not be properly detected. Recordings of 119 from a total of 132 training sessions were included for further statistical analysis. Eight sessions were excluded because too many ectopic beats were detected, four due to technical problems during data saving, and one because of the occurrence of large movement artifacts.

Measures of HRV were calculated for each 5-min segment. Time domain variables were based on time intervals between normal successive heartbeats (NN). Those included the square root of the mean of the squares of the successive differences between adjacent NNs (RMSSD), the standard deviation of the successive differences between adjacent NNs (SDNN) and the percentage of number of pairs of successive NNs that differed by more than 50 ms (pNN50). In the frequency domain, power spectral density was calculated for three frequency ranges: very low frequency (<0.04 Hz), low frequency (0.04–0.15 Hz), and high frequency (0.15–0.40 Hz). Spectral measures included the natural logarithm of absolute low frequency and high frequency power (lnLF and lnHF) as well as their normalized values. Further variables determined were the absolute power ratio of low frequency to high frequency and ln-transformed measures of the RSA using the Peak-to-Trough (P2T-RSA) and Porges-Bohrer (PB-RSA) method (Lewis et al., 2012).

Statistical analyses

The statistical analysis was carried out with R 3.6.2 (R Core Team, 2019) using the *rstatix* (v0.5.0; Kassambara, 2020), *lmerTest* (v3.1–2; Kuznetsova et al., 2017), and *emmeans* (v1.4.6; Lenth, 2020) packages. The analyses were performed separately for each dependent variable (DV). Statistical assumptions were checked according to instructions proposed by Kassambara (2019). Linear regression models including within-subject factors were developed based on mixed effect models including random subject effects (blocking factor). These models accounted for random intercepts and slopes along repeated measures of time. Main and interaction effects were calculated from the analysis of variance (ANOVA) or analysis of covariance when covariates were included. Effects of Type 3 are reported here due to the imbalance in group sizes. Following recommendations of Luke (2017) that produce most optimal Type 1 error rates for multiple factors mixed effect models, especially for smaller and unbalanced sample sizes (12–24 subjects), degrees of freedom were calculated using the Kenward-Roger method and unbiased estimates of variance and covariance parameters were determined using the restricted maximum likelihood. Factor effect sizes were based on partial eta-square values and interpreted as small, medium, and large

for values of 0.01, 0.06, and 0.14, respectively (Cohen, 1988). Further, group and test comparisons were always concerned with pre-to-post-test and CG-to-BG differences. Estimated marginal means (EMMs) were computed and compared using the *emmeans* package (v1.4.6; Lenth, 2020). Effect sizes derived from EMMs pairs were based on the parameter d_m which is determined analogously to Cohen's d . Values of 0.25, 0.5, and 0.85 were interpreted, based on recommendations of a HRV distribution analysis (Quintana, 2016), as small, medium, and large, for measures of HRV. EMMs and effect sizes are reported along with the 95% CI. Monotonic correlations were based on Spearman's rank-order correlation. All significance tests were based on $\alpha = 0.05$ and were two-tailed.

Repeated measures from the training phase were averaged within each session to balance the number of samples between the baseline, training, and recovery phase. Linear regression models were devised with group (BG, CG) as between-subject factor and session phase (baseline, training, recovery) as within-subject factor. Since group means of the BMI differed significantly (see 2.1), the mean-centered BMI was added as a covariate for cardiac measures [DV ~ new BMI + group * session phase + (1 + session phase | subject)]. EMMs were identified in each group for each session phase. EMMs of the training and recovery measures were then compared with the baseline within groups. Additionally, EMMs for the training and recovery phase were compared between groups using a model that adjusted means for baseline values (DV ~ baseline + group * session phase).

Behavioral outcomes were each analyzed with a factorial design including the between-subject factor group (BG, CG) and within-subject factor test (pre, post). Average values and group \times test interaction effects were determined for the measures apart from the EM task (DV ~ group * test). EM task variables additionally included the encoding condition (perceptive, semantic, semantic self-reference, episodic self-reference) and valence (positive, negative) as fixed factors. Memory performance scores were controlled for the number of responses and reaction time during encoding. Effects involving the interaction of group and test were checked for every encoding condition separately. If significance was observed for any effect in any condition, the variable was added as a covariate to the following analysis of memory responses. Likewise, effects on the memory retention period between the encoding and recognition phase were tested by means of 2 (BG, CG) \times 2 (pre, post) ANOVA. Since we were interested in EM performance in both reference conditions (self, non-self), regression models were devised separately for items with self-reference (semantic self-reference and episodic self-reference conditions) and without self-reference (perceptive and semantic conditions) [DV ~ (covariate) + group * test * encoding condition * valence + (1 + test | subject)]. Effects involving group \times test interaction and EMMs for each group-test combination were determined. Moreover, differences between

reference conditions were characterized by the calculation of the SRE. The latter can be described by the difference in memory performance for items encoded with self-reference compared to items encoded in general semantic context (Glisky and Marquine, 2009; Lalanne et al., 2013; Compère et al., 2016). To this effect, group \times test \times valence interaction effects were identified for encoding condition differences (semantic-to-semantic-self and semantic-to-episodic-self). Where a statistically significant involvement of the encoding condition or valence was detected, group \times test interaction effects on each level of the respective variable were determined. For all significant group \times test interaction effects, EMMs or average scores were compared between pre- and post-recordings. Furthermore, the effect of the other cognitive measures on significant memory outcomes was controlled for. To do so, variables that exhibited a significant group \times test interaction effect were added separately as covariates to the regression model. Finally, to study the relationship between physiological and behavioral results on a participant level, a correlation analysis was conducted for every behavioral variable. Pre- to-post differences of each participant were correlated with the baseline-adjusted EMM of P2T-RSA of the training. The P2T-RSA was chosen as the main indicator of vagally mediated HRV because it better captures vagal influences on a wide range of breathing frequencies compared to lnHF and lnLF and is less disturbed by sympathetic influences than the RMSSD. For significant correlations, the P2T-RSA \times test interaction effect (groups combined) was determined [DV \sim (covariate) + P2T-RSA * test (1 | subject)].

Results

System assessment

Separate mixed model analyses including random subject effects revealed no group differences for the sense of presence, sense of embodiment, or for any of its subcategories. However, compared to the CG the BG felt more attentive, $t(14) = 3.89$, $p = 0.002$, $d_m = 1.01$, and less drowsy, $t(14.1) = -3.41$, $p = 0.004$, $d_m = -0.53$, during the training phase. Self-reported fatigue did not differ between groups before, but after training, $t(14.2) = -2.39$, $p = 0.031$, $d_m = -0.73$. Only the CG felt significantly more fatigue after training. Further details are provided in the [Supplementary material A Table A1](#).

Maintenance and retention periods

In average 6.50 ($SD = 1.83$) and 6.20 ($SD = 2.74$) days passed between the last training session and post assessment in the BG and CG, respectively. No differences were found between group means, $t(20) = 0.31$, $p = 0.762$, $d = 0.13$. In the BG

the retention period from encoding to the recognition phase was in average 27.08 ($SD = 2.49$) min during pre-assessment and 24.58 ($SD = 1.16$) min during post-assessment, while in the CG it was 26.05 ($SD = 2.05$) and 24.80 ($SD = 2.49$) min, respectively. A significant main effect of test was identified, $F(1,20) = 8.79$, $p = 0.008$, $\eta_p^2 = 0.19$, because participants performed the tests during the retention period more rapidly in the post-assessment. No significant group effect, $F(1,20) = 0.407$, $p = 0.531$, $\eta_p^2 = 0.01$, nor interaction effect $F(1,20) = 0.976$, $p = 0.335$, $\eta_p^2 = 0.02$, was observed.

Physiological measures

Estimated marginal means derived from linear mixed models of the respiration rate, heart rate, and primary HRV variables indexing CVC and training success (i.e., RMSSD and P2T-RSA; Laborde et al., 2017; Shaffer and Ginsberg, 2017) as well as statistics of the within- and between group comparisons are given in [Tables 2, 3](#) and are illustrated in [Figure 3](#). The supplementary indices are presented in the [Supplementary material B \(Supplementary Tables B1, B2\)](#). There were no significant group differences between baseline measures for any of the physiological parameters.

The findings indicate that both groups successfully and to a great extent slowed their breathing and increased levels of RMSSD and P2T-RSA during training. However, only the BG came close to the target value of 6 breaths per minute (0.1 Hz). A training effect was present for some but not for all participants in the CG. For the respiration rate, RMSSD, and P2T-RSA, effect sizes were persistently higher in the BG. In addition, aftereffects (i.e., difference between baseline and recovery) on respiration rate, RMSSD, and P2T-RSA were observed only in the BG. Group comparison of the baseline adjusted training and recovery phases revealed significant large differences in the respiration rate and P2T-RSA for both phases and a moderate difference for RMSSD during recovery ([Table 3](#)). Heart rate dropped in both groups below baseline value during training and recovery and was slightly but significantly higher in the BG during training. Inversely, heart rate tended to be lower in the BG during recovery. A *post hoc* mediation analysis of the effects of respiration rate and heart rate on HRV is presented in the [Supplementary material C](#).

Psychological measures and executive functioning

Average scores and results of the group \times test interaction effect derived from the mixed model ANOVAs as well as correlations with P2T-RSA are reported for each score of the psychological scales and executive function test battery in [Table 4](#). Groups did not differ during pretest ($ps > 0.15$)

TABLE 2 Within-group comparisons of physiological measures.

Measure	Biofeedback group							Active control group						
	Baseline (n = 68)	Training (n = 68)	Recovery (n = 68)	Training-baseline		Recovery-baseline		Baseline (n = 51)	Training (n = 51)	Recovery (n = 51)	Training-baseline		Recovery-baseline	
	<i>EMM</i>	<i>EMM</i>	<i>EMM</i>	<i>t</i> (19.0), <i>p</i>	Effect size <i>d_m</i>	<i>t</i> (19.0), <i>p</i>	Effect size <i>d_m</i>	<i>EMM</i>	<i>EMM</i>	<i>EMM</i>	<i>t</i> (19.0), <i>p</i>	Effect size <i>d_m</i>	<i>t</i> (18.9), <i>p</i>	Effect size <i>d_m</i>
Respiration rate [min ⁻¹]	13.56 [11.34, 15.78]	6.42 [5.04, 7.80]	11.59 [10.18, 13.01]	-7.33, <0.001	-2.89 [-4.48, -1.31]	-2.79, 0.012	-0.80 [-1.50, -0.09]	15.41 [12.84, 17.98]	11.38 [9.79, 12.97]	15.05 [13.42, 16.68]	-3.58, 0.002	-1.63 [-2.86, -0.41]	-0.45, 0.659	-0.15 [-0.84, 0.55]
Heart rate [min ⁻¹]	79.20 [72.73, 85.68]	74.42 [68.33, 80.52]	72.48 [66.69, 78.26]	-4.62, <0.001	-0.81 [-1.34, -0.28]	-6.18, <0.001	-1.14 [-1.80, -0.48]	79.68 [72.01, 87.35]	73.19 [65.95, 80.43]	74.36 [67.46, 81.25]	-5.43, <0.001	-1.10 [-1.77, -0.43]	-4.24, <0.001	-0.90 [-1.52, -0.29]
RMSSD [ms]	35.50 [28.23, 42.76]	50.86 [37.55, 64.16]	46.35 [37.92, 54.77]	3.52, 0.002	1.14 [0.28, 2.01]	3.38, 0.003	0.81 [0.18, 1.43]	32.39 [23.83, 40.95]	46.65 [31.19, 62.11]	38.55 [28.68, 48.43]	2.83, 0.011	1.06 [0.13, 1.99]	1.67, 0.113	0.46 [-0.16, 1.07]
P2T-RSA	-2.65 [-2.95, -2.36]	-1.61 [-1.88, -1.35]	-2.33 [-2.56, -2.11]	7.70, <0.001	2.94 [1.34, 4.54]	2.73, 0.013	0.92 [0.09, 1.74]	-3.02 [-3.37, -2.68]	-2.40 [-2.71, -2.08]	-2.85 [-3.12, -2.59]	4.03, <0.001	1.78 [0.53, 3.03]	1.24, 0.229	0.48 [-0.37, 1.32]

Physiological measures recorded during training were compared with measures of the resting state before (baseline) and 5 min after training (recovery) using robust linear mixed-effect models. The 95% CIs and measurement units, if present, are presented in square brackets. *P*-values below 0.05 are displayed in bold font. The results show that training stimulated cardiac vagal control in both groups. Effects were greater when biofeedback was used and even persisted after the training. CI, confidence interval; *d_m*, effect size calculated by the *emmeans* R package analogous to Cohen's *d*; *EMM*, estimated marginal mean; RMSSD, root mean square of successive heartbeat interval differences; P2T-RSA, natural logarithm of the respiratory sinus arrhythmia calculated by the peak-to-trough method.

TABLE 3 Between-group comparisons of physiological measures.

Measure	Training (n = 119)				Recovery (n = 119)			
	Difference	z ratio	p	Effect size d_m	Difference	z ratio	p	Effect size d_m
Respiration rate [min^{-1}]	-4.47 [-5.46, -3.48]	-8.859	<0.001	-1.81 [-2.70, -0.92]	-2.87 [-3.86, -1.88]	-5.687	<0.001	-1.16 [-1.81, -0.52]
Heart rate [min^{-1}]	1.65 [0.15, 3.15]	2.155	0.031	0.280 [0.00, 0.56]	-1.46 [-2.96, 0.04]	-1.909	0.056	-0.25 [-0.53, 0.03]
RMSSD [ms]	4.84 [-1.67, 11.35]	1.457	0.145	0.36 [-0.15, 0.87]	7.06 [0.55, 13.57]	2.126	0.034	0.53 [-0.01, 1.06]
P2T-RSA	0.71 [0.55, 0.87]	8.913	<0.001	2.01 [1.02, 2.99]	0.42 [0.27, 0.58]	5.318	<0.001	1.20 [0.51, 1.88]

Comparisons are based on the differences of baseline adjusted estimated marginal means between groups (active control to biofeedback group) derived from robust linear mixed-effect models. The 95% CIs and measurement units, if present, are presented in square brackets. *P*-values below 0.05 are displayed in bold font. The results indicate that the use of biofeedback had a significant positive effect on respiratory-linked cardiac vagal control and parasympathetic activation during and after training. CI, confidence interval; d_m , effect size calculated by the *emmeans* R package analogous to Cohen's *d*; RMSSD, root mean square of successive heartbeat interval differences; P2T-RSA, natural logarithm of the respiratory sinus arrhythmia calculated by the peak-to-trough method.

for any measure. Notable group \times test interaction effects and correlations with HRV below or close to the significance level were found only for indicators of attention (Error Rate) and short-term memory (Digit Span Forward), but not of processing speed (Processed Target Objects of the revised d2 Test of Attention, Trail Making Test part A, Reaction Time in the Sustained Attention to Response Task), cognitive flexibility (Trail Making part B and B-A), inhibition (Interference Score of the Stroop Color Word Test and Rate of Correct No-Go Response of the Sustained Attention to Response Task), and working memory (Digit Span Backward, Sequencing, Total; Letter Number Sequencing; Working Memory Index Norm Scores). Pre-post comparisons revealed significant and large improvements only in the BG for the Error Rate score, $t(11) = 2.92, p = 0.014, d = 0.84, 95\% \text{ CI } [0.27, 2.14]$, and Digit Span Forward score, $t(11) = 3.45, p = 0.005, d = 1.00 [0.48, 1.79]$. Linear regression models verified that the pre-to-post-test effect was strongly dependent on the baseline-adjusted P2T-RSA score for the Error Rate, $F(1,19) = 5.60, p = 0.029, \eta_p^2 = 0.23$, and Digit Span Forward score, $F(1,19) = 8.19, p = 0.010, \eta_p^2 = 0.30$.

Episodic memory responses

Encoding phase

Results for measures of the encoding phase (i.e., the number of responses and the response reaction time to stimuli) are presented in the [Supplementary material D Table D1](#). Reaction time values were ln-transformed prior to linear regression due to violations of the normality assumption. No statistically significant effect involving the interaction of group \times test was observed for the number of correct responses, self-attributed adjectives, and autobiographical memories recalled. Contrary, the group \times test interaction was found to influence the reaction time in each condition. Generally, the BG took more time to respond in the post- than in the pre-assessment, whereas the CG took less time. Consequently, the ln-transformed reaction time was included as a covariate for the analysis of the subsequent memory results.

Episodic memory performance

Estimated marginal means and correlations with P2T-RSA of proportions of correct free recalls, subjective R responses, and correct source recollections to studied items (i.e., hits) as well as the discrimination performance between old and new items are listed in [Table 5](#). Groups did not differ significantly for any of the pre-test measures. Moreover, no significant group \times test interaction effects, group differences during pre-test measures, or time differences within groups were present for any reference condition for proportions of R responses to unstudied items and incorrect source recollections to studied items (i.e., false alarms). Therefore, R response and source recollection hits were not corrected for false alarms and were treated as indicators of

TABLE 4 Psychological scales and executive functions.

Psychological scales and executive functions tests	Biofeedback group		Active control group		ANOVA: Group × test effect			Spearman correlation with P2T-RSA	
	Pre-test (n = 12)	Post-test (n = 12)	Pre-test (n = 10)	Post-test (n = 10)	F(1,20)	p	η_p^2	r(19)	p
ASQ (0 to 7)									
Concealing	4.34 (1.39)	4.42 (1.40)	4.46 (2.03)	4.52 (1.71)	0.00	0.978	0.00	−0.24	0.290
Adjusting	4.73 (1.33)	4.64 (1.67)	4.77 (1.72)	4.01 (2.12)	0.93	0.348	0.04	0.06	0.802
Tolerating	4.50 (1.28)	5.30 (0.99)	4.79 (1.45)	5.02 (1.41)	0.62	0.441	0.03	0.23	0.317
FFMQ (1 to 5)									
Non-judging	3.23 (0.60)	3.35 (0.92)	3.64 (1.09)	3.62 (0.75)	0.08	0.787	0.00	−0.03	0.887
Non-reacting	3.30 (1.01)	3.60 (0.52)	3.71 (0.67)	3.51 (0.97)	2.12	0.161	0.10	0.12	0.619
Acting with Awareness	3.13 (0.68)	3.64 (0.76)	3.05 (0.74)	3.09 (0.70)	0.92	0.349	0.04	0.37	0.100
Observing	3.35 (0.90)	3.18 (0.95)	3.51 (0.85)	3.86 (0.51)	1.80	0.195	0.08	0.03	0.873
Describing	3.14 (0.90)	3.27 (0.79)	3.53 (0.71)	3.57 (0.75)	0.03	0.864	0.00	−0.01	0.975
TSCS (21 to 105)									
Past Total ^a	86.00 (19.50)	89.00 (17.50)	91.50 (2.75)	91.00 (8.25)	0.00	0.971	0.00	0.22	0.347
Present Total ^a	91.00 (8.70)	91.00 (7.25)	91.50 (2.75)	93.00 (7.00)	1.87	0.187	0.09	−0.22	0.334
Future Total ^a	92.50 (7.50)	94.50 (3.25)	96.00 (4.25)	96.00 (6.25)	0.01	0.940	0.00	0.27	0.235
SART									
Reaction Time [ms]	345.70 (34.81)	347.72 (35.43)	364.64 (33.18)	375.82 (45.68)	0.29	0.599	0.01	0.19	0.399
Correct No-go Responses [%]	76.24 (12.38)	75.31 (15.82)	73.70 (16.05)	73.33 (13.04)	0.01	0.909	0.00	0.15	0.519
Correct Go Responses [%] ^a	98.38 (2.08)	98.38 (2.32)	97.92 (8.45)	97.45 (8.10)	0.40	0.537	0.02	0.15	0.512
Revised d2 Test of Attention									
POT Norm Score	103.42 (12.42)**	110.33 (14.37)**	100.40 (17.23)**	106.60 (16.31)**	0.08	0.776	0.00	−0.19	0.404
E% Norm Score	102.33 (12.74)*	108.58 (11.80)*	95.90 (17.31)	93.60 (15.97)	4.16	0.055	0.17	0.52	0.015
CP Norm Score	103.83 (12.39)**	113.08 (13.35)**	96.70 (11.61)**	103.30 (10.76)**	0.85	0.369	0.04	−0.09	0.971
Stroop Color and Word Test									
Interference Score [s] ^b	33.35 (15.28)	32.00 (8.38)	42.40 (11.40)	41.75 (11.45)	0.50	0.490	0.02	0.12	0.608
Trail Making Test									
Part B—Part A [s] ^a	25.00 (14.83)	32.00 (19.88)	29.50 (9.45)	32.00 (16.25)	0.23	0.636	0.01	0.33	0.140
Part A [s]	31.25 (15.05)*	21.54 (5.11)*	30.95 (11.45)*	25.00 (7.32)*	0.63	0.436	0.03	0.04	0.873
Part B [s] ^a	52.50 (20.70)	52.00 (18.00)	59.95 (5.50)	57.50 (13.75)	0.02	0.884	0.00	0.33	0.145
WAIS-IV									
DS Forward Norm Score	9.67 (2.84)**	11.17 (3.01)**	9.80 (2.39)	9.30 (1.77)	6.10	0.023	0.23	0.48	0.027
DS Backward Norm Score	11.58 (3.29)	12.42 (2.43)	9.60 (3.24)	10.90 (1.66)	0.19	0.668	0.01	−0.05	0.817

(Continued)

TABLE 4 (Continued)
Psychological scales and executive functions tests

	Biofeedback group (n = 12)		Active control group (n = 10)		ANOVA: Group × test effect		Spearman correlation with P2T-RSA		
	Pre-test (n = 12)	Post-test (n = 12)	Pre-test (n = 10)	Post-test (n = 10)	F(1,20)	p	η_p^2	r(19)	p
DS Sequencing Norm Score	11.92 (2.28)*	13.25 (2.01)*	10.60 (2.27)**	11.90 (2.64)**	0.00	0.954	0.00	-0.07	0.766
DS Total Norm Score	11.17 (2.79)*	12.58 (2.84)*	10.00 (2.21)	10.70 (1.34)	1.14	0.298	0.05	0.35	0.123
LNS Norm Score	11.75 (3.02)	11.67 (3.73)	10.30 (2.41)	11.00 (3.06)	0.50	0.486	0.03	-0.32	0.152
WMI Norm Score	108.17 (15.11)	112.08 (17.45)	100.80 (12.65)	104.70 (11.53)	0.00	0.997	0.00	-0.06	0.809

Mean scores, the group × test interaction effect, and the correlation with baseline-adjusted level of HRV during training are presented for each behavioral variable. Standard deviations are presented in parenthesis and measurement units, if present, in square brackets. Value ranges in parenthesis indicate the possible numeric outcomes of the corresponding scale. Mean scores in each group that exhibited significant pre-to-post-test differences and exact p-values below 0.05 are displayed in bold font. The results show that episodic memory improvements related to biofeedback-induced parasympathetic stimulation occurred in scores of attention and short-term memory. ANOVA, analysis of variance; P2T-RSA, natural logarithm of the respiratory sinus arrhythmia calculated by the peak-to-trough method; ASQ, Affective Style Questionnaire; η_p^2 , partial eta square; FEMQ, Five Facets Mindfulness Questionnaire; TSCS, Tennessee Self-Concept Scale; SART, Sustained Attention to Response Test; PTO, Processed Target Objects; E%, Percentage of Errors; CP, Concentration; Performance; WAIS-IV, Wechsler Adult Intelligence Scale—Fourth Edition; DS, Digit Span; LNS, Letter-Number-Sequencing; WMI, Working Memory Index.

^aThe median and the inter-quartile-range (in parenthesis) are reported when values were found not to be normally distributed in one of the groups.

^bThe interference score was calculated based on recommendations of Scarpina and Tagini (2017) and included the processing time, corrected, as well as uncorrected errors of all subtests.

**p < 0.01. *p < 0.05.

subjective and objective recollection, respectively (c.f., Duarte et al., 2008).

A statistically significant group × test × valence effect was present only for the subjective probability estimates of self-referential items, $F(1, 139.3) = 5.06, p = 0.026, \eta_p^2 = 0.04$. None of the measures exhibited a group × test × encoding condition × valence or group × test × encoding condition interaction effect. As subjective and objective recollection are closely related, interaction effects in each level of valence were checked for both variables. Significant group × test interaction effects occurred only in the subjective and objective recollection (see Figure 4) of positive self-referential items. Significant large sized pre-to-post increases were verified only in the BG, $t(101) = 2.68, p = 0.009, d_m = 0.80, 95\% \text{ CI } [0.09, 1.51]$ (subjective recollection), $t(138) = 3.40, p < 0.001, d_m = 0.98, 95\% \text{ CI } [0.24, 1.72]$ (objective recollection). Moreover, both scores (groups combined) as well as old/new discrimination of self-referential items correlated significantly or by trend with P2T-RSA. Scores of d' improved only in the BG, $t(19.9) = 2.26, p = 0.035, d_m = 0.61, 95\% \text{ CI } [-0.02, 1.25]$. The pre-to-post-test effects were moderately-to-strongly but not statistically significantly dependent on the baseline-adjusted P2T-RSA score for measures of subjective recollection, $F(1,19.3) = 3.92, p = 0.062, \eta_p^2 = 0.17$; objective recollection, $F(1,19.3) = 1.35, p = 0.260, \eta_p^2 = 0.07$; and $d', F(1,19.8) = 1.59, p = 0.223, \eta_p^2 = 0.07$.

To control whether group × time interaction effects were related to changes in other cognitive faculties, previous behavioral measures that exhibited a significant group × test interaction effect (i.e., Error Rate and Digit Span Forward norm scores) were added separately as covariates to the regression model. No effect was observed on any EM variable.

Self-reference effect

The follow-up analysis looking at the SRE (i.e., semantic-to-self-episodic differences) revealed no significant group × test but did reveal group × test × valence interaction effects, except for the free recall hit rate, for any EM variable. Group × test interaction effects, EMMs of pre-to-post changes, and their correlation with P2T-RSA are presented for positive and negative stimuli in Table 6. A significant interaction effect and correlation were observable only for subjective and objective recollection of positive stimuli. Pre-to-post comparisons revealed moderate-to-large increases in the BG for subjective recollection, $t(39.8) = 1.51, p = 0.140, d_m = 0.78, 95\% \text{ CI } [-0.29, 1.85]$, and objective recollection, $t(46.7) = 2.75, p = 0.008, d_m = 1.27, 95\% \text{ CI } [0.18, 2.36]$, for positive stimuli. Also, a moderate but statistically not significant increase occurred in the SRE based on negative items assessed by d' , $t(74.9) = 1.87, p = 0.072, d_m = 0.78, 95\% \text{ CI } [-0.12, 1.68]$. The pre-to-post-test effects were strongly dependent on the baseline-adjusted P2T-RSA score for measures of subjective recollection, $F(1,18.4) = 6.03, p = 0.024, \eta_p^2 = 0.25$; objective recollection, $F(1,18.4) = 4.97, p = 0.038, \eta_p^2 = 0.21$; and d' ,

TABLE 5 Episodic memory performance.

Memory measures	Biofeedback group		Active control group		ANCOVA: Group × test effect				Spearman correlation with P2T-RSA	
	Pre-test (<i>n</i> = 12)	Post-test (<i>n</i> = 12)	Pre-test (<i>n</i> = 10)	Post-test (<i>n</i> = 10)	<i>df</i>	<i>F</i>	<i>p</i>	η_p^2	<i>r</i> (19)	<i>p</i>
Non-self-referential items										
Free recall hit rate	0.14 (0.03)	0.18 (0.03)	0.18 (0.03)	0.17 (0.03)	1, 24.2	0.57	0.457	0.02	0.24	0.293
Subjective recollection hit rate	0.41 (0.06)	0.46 (0.06)	0.38 (0.07)	0.48 (0.07)	1, 24.7	0.31	0.584	0.01	−0.03	0.899
Objective recollection hit rate	0.28 (0.04)	0.33 (0.06)	0.13 (0.05)	0.24 (0.06)	1, 24.2	0.43	0.518	0.02	−0.09	0.686
Old/new discrimination (<i>d'</i>)	1.07 (0.12)	1.17 (0.15)	1.09 (0.14)	1.16 (0.17)	1, 24.3	0.01	0.935	0.00	0.20	0.377
Self-referential items										
Free recall hit rate	0.16 (0.03)**	0.27 (0.03)**	0.13 (0.03)	0.20 (0.04)	1, 21.4	0.61	0.442	0.03	−0.07	0.776
Subjective recollection hit rate	0.51 (0.08)	0.60 (0.06)	0.53 (0.09)	0.51 (0.07)	1, 21.9	1.43	0.245	0.06	0.33	0.146
Positive items	0.49 (0.09)**	0.71 (0.07)**	0.53 (0.10)	0.45 (0.08)	1, 22.4	6.90	0.016	0.24	0.57	0.008
Negative items	0.54 (0.09)	0.50 (0.07)	0.53 (0.10)	0.57 (0.08)	1, 21.0	1.05	0.319	0.05	−0.06	0.789
Objective recollection hit rate	0.30 (0.07)**	0.48 (0.07)**	0.22 (0.07)	0.24 (0.08)	1, 22.0	3.89	0.061	0.15	0.38	0.092
Positive items	0.27 (0.08)***	0.52 (0.08)***	0.23 (0.08)	0.21 (0.09)	1, 22.6	6.79	0.016	0.23	0.43	0.055
Negative items	0.33 (0.07)	0.43 (0.08)	0.21 (0.08)	0.26 (0.08)	1, 21.0	0.05	0.833	0.00	0.22	0.343
Old/new discrimination (<i>d'</i>)	1.50 (0.12)*	1.79 (0.11)*	1.26 (0.14)	1.34 (0.13)	1, 21.4	1.15	0.296	0.05	0.48	0.031

EMMs of pre-to-post changes, their correlation (groups combined) with baseline-adjusted level of HRV during training, and the group × test interaction effect are presented for each memory variable. Statistics were derived from robust linear mixed-effect models. The behavior at encoding was controlled for. Standard deviations are presented in parenthesis. 95% CIs are presented in square brackets. EMMs in each group that exhibited significant pre-to-post-test differences and exact *p*-values below 0.05 are displayed in bold font. Subjective and objective recollection reflect the proportions of correct remember responses and source recollections to studied items, respectively. The results show that episodic memory improvements related to biofeedback-induced parasympathetic stimulation occurred in the recollection of positive items encoded with self-reference. P2T-RSA, natural logarithm of the respiratory sinus arrhythmia calculated by the peak-to-trough method; EMM, estimated marginal means; ANCOVA, analysis of covariance; η_p^2 , partial eta square.

****p* < 0.001. ***p* < 0.01. **p* < 0.05.

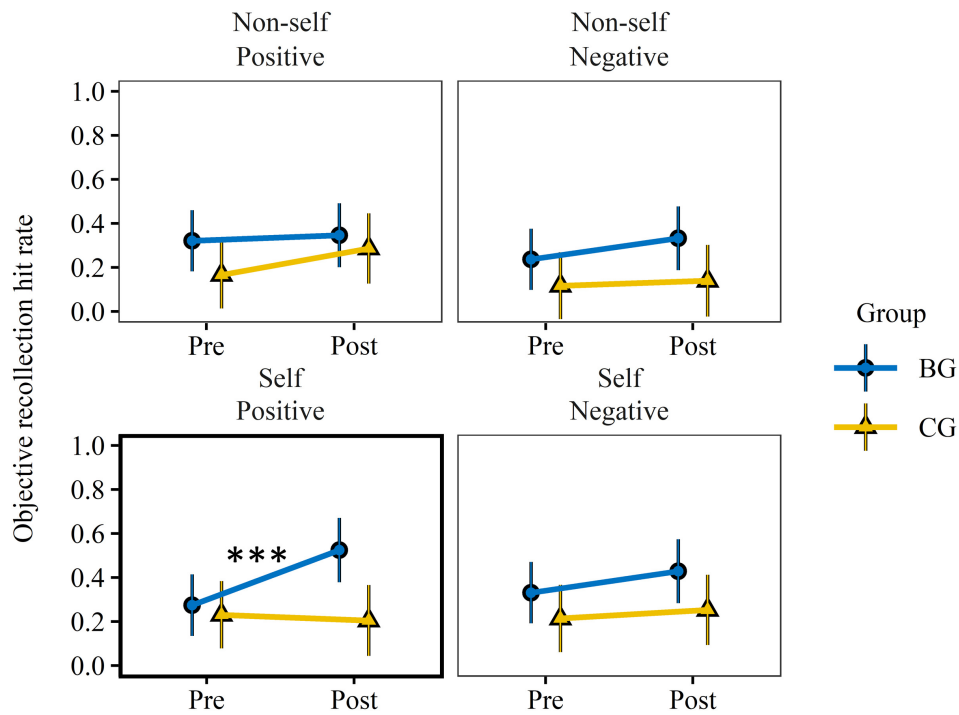


FIGURE 4 Training effect on objective memory recollection. Objective recollection hit rate was assessed by the proportion of correct source recollection of studied words. EMMs and 95% CIs, derived from robust linear mixed effect models, are presented per group, reference condition, valence, and test. EMMs accounted for inter-participant differences in response reaction time at encoding and random subject effects. Pre-test values did not differ significantly ($p > 0.14$) between groups. Only recollections of positive items encoded with the self-reference condition (bold frame) revealed a significant group \times test interaction effect. Training related improvements were found only in the BG. BG, biofeedback group; CG, active control group; EMM, estimated marginal means. *** $p < 0.001$.

$F(1,18.4) = 4.61, p = 0.045, \eta_p^2 = 0.20$. For both positive and negative items, there was no effect of the Error Rate or Digit Span Forward norm score on the SRE. In comparison, when the SRE was defined as semantic-to-self-semantic differences, the results showed the same trend, but effects were less pronounced (c.f. [Supplementary material D Table D2](#)).

$p = 0.025$; Describing score of the Five Facets of Mindfulness Questionnaire, $r(19) = -0.44, p = 0.025$, and the correct free recall rate of positive self-referential items, $r(19) = 0.67, p = 0.001$.

Exploratory analysis

Previous psychophysiological research has linked cognitive processes typically to resting-state measures of vagally mediated HRV. In the framework of an unplanned analysis, the monotonic relationship between vagally mediated resting-state HRV indexed by lnHF with behavioral results was investigated. Scores of lnHF and respiration rate that affect to which degree vagal influences are captured by lnHF, did not exhibit any group, session, or group \times session effects. Therefore, physiological baseline indicators were grouped by participants and EMMs were correlated with the pre-test scores using the Spearman and two-sided hypothesis tests. None of the psychological, executive functions, EM or SRE measures correlated with lnHF with the exception of the Stroop global interference score, $r(19) = -0.49,$

Discussion

The objective of this study was to determine the placebo-controlled and 1-week lasting effect of HRVB on executive functions and self-referential EM in young healthy adults. Beyond that, it was investigated whether changes in cognitive performance were linked to RSA amplitude during training as a measure of respiratory-related CVC and training success. The results show that biofeedback had a large effect on RSA amplitude during and after training and some cognitive functions. Group \times test interaction effects were found for measures of attention, short-term memory, and self-referential EM of positive stimuli. VR-related properties were controlled for. Moreover, findings indicated that RSA amplitude mediated cognitive improvements, thus confirming our hypotheses. However, some scores of affective and executive control were not affected by HRVB, including working memory and inhibitory

TABLE 6 Self-reference effect (SRE).

Variable	Pre-to-post change in SRE		ANCOVA: Group × test effect				Spearman correlation with P2T-RSA	
	Biofeedback group (<i>n</i> = 12)	Active control group (<i>n</i> = 10)	<i>df</i>	<i>F</i>	<i>p</i>	η_p^2	<i>r</i> (19)	<i>p</i>
Negative items								
Free recall hit rate	0.18 (0.10)	−0.03 (0.11)	1, 19.5	2.37	0.140	0.11	−0.04	0.850
Subjective recollection hit rate	−0.07 (0.20)	−0.04 (0.22)	1, 19.6	0.02	0.896	0.00	−0.02	0.942
Objective recollection hit rate	0.04 (0.16)	0.10 (0.17)	1, 19.6	0.08	0.783	0.00	0.18	0.423
Old/new discrimination (<i>d'</i>)	0.49 (0.27)	−0.40 (0.29)	1, 19.6	4.90	0.039	0.20	0.37	0.094
Positive items								
Free recall hit rate	0.08 (0.10)	0.12 (0.11)	1, 19.2	0.22	0.642	0.01	−0.27	0.236
Subjective recollection hit rate	0.30 (0.20)	−0.37 (0.22)	1, 19.4	6.88	0.017	0.26	0.45	0.038
Objective recollection hit rate	0.43 (0.16)**	−0.25 (0.17)	1, 19.4	8.49	0.009	0.30	0.47	0.031
Old/new discrimination (<i>d'</i>)	0.31 (0.27)	0.51 (0.29)	1, 19.4	0.24	0.627	0.01	0.09	0.696

EMMs and group differences of pre-to-post changes in the SRE. The SRE is defined here for each variable as the episodic memory score difference from the semantic to the self-episodic condition. EMMs of pre-to-post changes, their correlation (groups combined) with baseline-adjusted level of HRV during training, and the group × test interaction effect are presented for each memory variable. Statistics were derived from robust linear mixed-effect models. The behavior at encoding was controlled for. Standard deviations are presented in parenthesis. 95% CIs are presented in square brackets. EMMs in each group that exhibited significant pre-to-post-test differences and *p*-values below 0.05 are displayed in bold font. Subjective and objective recollection reflect the proportions of correct remember responses and source recollections to studied items, respectively. The results showed that increases in the SRE related to biofeedback-induced parasympathetic stimulation occurred in the recollection of positive items, confirming previous results. EMM, estimated marginal means; ANCOVA, analysis of covariance; η_p^2 , partial eta square.

***p* < 0.01.

control. Neural structures that underlie the implication of HRVB on self-reference processing are discussed.

Physiological outcomes

Physiological outcomes were in line with the Psychophysiological Coherence (McCraty and Childre, 2010) and Resonance Frequency Training (Lehrer et al., 2000) models. The training program proved effective for both groups, with a clear difference in training effect. The results showed, as hypothesized, that HRV self-regulation training evoked greater RSA amplitude during and even after the training when biofeedback was provided. Consistent with our assumption, the biofeedback effect was higher on RSA amplitude than RMSSD during training. In fact, biofeedback did not influence RMSSD during training, only afterward. These findings indicate that the biofeedback effect on CVC during training was strongly related to changes in respiration eliciting physiological coupling between respiratory, blood pressure, and cardiac phases. *Post hoc* analyses confirmed that slower respiration, along with lower heart rate, mediated to the greatest part the training and aftereffects on RSA amplitude. On the other hand, RMSSD was influenced by heart rate but not by respiration rate (Supplementary material C). While physiological coupling may be assumed during HRVB due to breathing near the resonance frequency, it remains unclear whether aftereffects on respiration rate and RSA amplitude were also linked due to increases in coherence. Besides, stronger ventilation (i.e., tidal volume), which is typical for HRVB, might have affected

RSA amplitude but RMSSD less so. The observation that no significant group difference was demonstrated for RMSSD during training may be inferred from three assumptions. Firstly, as demonstrated by the mediation analysis, RMSSD is relatively unaffected by changes in respiration. Secondly, RMSSD was biased due to *cycle length dependence* (i.e., dependence of HRV on the heart rate; McCraty and Shaffer, 2015): higher heart rate reduced RMSSD in the BG. Thirdly, biofeedback evoked greater attention-driven sympathetic activation. With respect to the latter two points, we assume that biofeedback triggered greater motivation toward the engagement in voluntary control of the respiration during training. Evidence supporting this claim was provided by group differences in breath control and self-reported attentional commitment to the task that were higher in the BG. In turn, directing attention to a task is linked to increased arousal and sympathetic activation which decreases RMSSD and increases heart rate. We suppose that, mediated by attention, voluntary breath control, and tidal volume, biofeedback stimulated sympatho-vagal efferent cardiac inputs for both branches of the nervous system. In this line of thought, sympathetic activation during training partly counterbalanced the vagally mediated influence on RMSSD. This assumption is supported by the finding that RMSSD values between groups did differ after training. This suggests that in the BG the completion of the task was accompanied by sympathetic deactivation and thus a greater parasympathetic shift in the sympatho-vagal balance. The same pattern was reflected by the mean heart rate which reflects mean efferent vagal and sympathetic effects. Heart rate was higher during training in the BG, despite greater parasympathetic-mediated HRV (RSA

amplitude, SDNN), and continued to drop after training only in the BG.

Conclusively, the outcomes demonstrate for the first time the moderating effect of biofeedback signals on the autonomic changes elicited by HRV self-regulation during and beyond the moment of self-regulation training. We therefore assume that biofeedback supported parasympathetic activation through increases in respiratory-linked CVC.

Executive functioning

In accordance with previous HRVB studies, the outcomes indicate that HRVB improves attentional capabilities required for the identification and discrimination of external stimuli and auditory short-term memory but not cognitive flexibility (Pop-Jordanova and Chakalaroska, 2008; Jester et al., 2019) and working memory (Lloyd et al., 2010) in young healthy adults. Moreover, these cognitive changes could be linked to ANS processes during training. This suggests that neurophysiological stimulation and not any placebo effect triggered cognitive enhancement. This idea is in line with previous findings that demonstrated a link between vagally mediated HRV and selective attention (Giuliano et al., 2018) as well as with the discrimination performance of false from true memories (Feeling et al., 2021). A change of response strategy that may change the interpretation of these results seems unlikely as speed and accuracy with respect to go-/no-go responses during the Sustained Attention to Response Task did not change from pre- to post-test in either group. Moreover, EM results support the idea that parasympathetic stimulation improved discrimination performance, not only of external stimuli, but also of internal thought processes as HRV significantly correlated with old/new memory discrimination performance. Future studies should check other types of working memory such as visuospatial span.

Notable consideration has been given to the association of resting-state vagally mediated HRV and HRVB with inhibition processes on neurophysiological and behavioral levels. In accordance with previous findings (Gillie et al., 2014; Feeling et al., 2015; Bernardi et al., 2016), results of the exploratory analysis showed a positive link between vagally mediated resting-state HRV and inhibitory control. Consequently, one would expect that, as for the identification and discrimination performance, stimulating physiological coherence and CVC would lead to greater inhibition. Yet, contrary to previous literature (Sherlin et al., 2010; Sutarto et al., 2010, 2013; Prinsloo et al., 2011; Blum et al., 2019), no training effects on inhibitory control were observed in either group, irrespective of whether the task required motor components (Sustained Attention to Response Task) or not (Stroop Color and Word Test). However, as in this investigation, studies controlling for the biofeedback training effect failed to report any significant interaction effects or group differences (Sherlin et al., 2010; Sutarto et al., 2010, 2013; Prinsloo et al., 2011). Hence, the lasting benefits of

HRVB on behavioral inhibitory control mechanisms remain unsubstantiated. One probable criterion might be insufficient sample size, which ranged from 9 to 60 in previous studies, or training intensity.

Episodic memory and self-reference

Memory performance outcomes of the self-reference episodic memory task suggest that vagally mediated effects of HRVB can improve recognition-based verbal EM through the strengthening of the SRE. On the one hand, placebo-controlled training benefits in the BG were present only when recollecting self-referentially encoded positive items. On the other hand, memory recollection and discrimination scores correlated moderately-to-strongly with HRV. In addition, advantages in memory retention of self-referential stimuli did not come at the cost of reduced memory performance of non-self-referential stimuli. Another indicator of the involvement of the self-processing system is the discrepancies between memory measures. Of all memory variables here, recollection success relies the most on self-referential memory because it requires the episodic recollection of information associated with the stimulus during encoding. To this effect, Conway and Dewhurst (1995) and Conway et al. (2001) even introduced the term self-reference recollection effect (SRRE) that comprises the SRE on the subjective and objective recollection measures. In addition, there are differences between the two recollection measures. True recollection can be assured for the measure of objective recollection (i.e., source retrieval) but not always for subjective recollection. Subjective remembering is often confused with high-confidence recognition, which does not necessarily rely on the recollection of qualitative properties of the memory (Yonelinas, 2001; Rotello et al., 2005). Discrepancies in the biofeedback effect (i.e., group \times test interaction effect) and correlation results between memory measures of self-referential items might therefore stem from different degrees of dependence on self-reference processes.

The importance of the self-processing system for the memorial training effect is further stressed by the findings related to the SRE. On the one hand, the presence of biofeedback had a large promoting effect on the SRRE (SRE on subjective or objective recollection) on both scales, providing evidence for the interaction between biofeedback and self-reference processing. On the other hand, results of the SRE reflected the same characteristics as those of the memory results discussed above: firstly, changes in the SRRE were linked to HRV; secondly, differences occurred between memory variables with effect sizes and correlations that were markedly larger for the recollection measures.

Remarkably, training effects on the SRRE concerned only positive items. This is an indication that affective biases played a role in the influence of biofeedback and HRV self-regulation training on SRRE. Indeed, it is a well-documented phenomenon

that self-relevant stimuli produce a bias in positivity, such that people tend to make flattering self-evaluations and to hold more positive memories (see [Cunningham and Turk, 2017](#), for a review on self-referencing biases). Furthermore, memory improvements were not mediated by changes in any other cognitive function assessed in this study. These results suggest that vagal stimulation and increased physiological coherence also mediated an effect of HRVB on cognitive processes beyond executive functioning associated with improved objective memory recollection and discrimination performance. Moreover, it supports the notion of a direct relationship between autonomic control and the self-reference processing system that may be based on a common set of neural structures. We propose a chain mediation model explaining the effect of HRV self-regulation training on the memory retrieval of self-referential encoded information ([Figure 5](#)).

Self-referential episodic memory and autonomic control

Within the central nervous system, there are several brain structures that are commonly engaged in autonomic control, self-reference, and emotional processing such as the vmPFC, dorsolateral prefrontal cortex (dlPFC), or cingulate cortex. The former is particularly noteworthy due to its central role in brain networks orchestrating autonomic and self-reference processes. On the one hand, the vmPFC as well as several other prefrontal regions including the dlPFC, cingulate cortex, and left anterior insula function as nodes of the central autonomic network ([Benarroch, 1993](#); [Sklerov et al., 2019](#)) at the highest level of a top-down chain to control autonomic functions such as cardiac regulation. On the other hand, the vmPFC, as part of the Self-Attention Network (SAN; [Humphreys and Sui, 2016](#)), has been firmly linked to self-reference processes ([Kelley et al., 2002](#); [Macrae et al., 2004](#); [Northoff et al., 2006](#); [Martinelli et al., 2013](#)). The SAN is believed to be responsible for self-biases in perception and attention through the activation of the vmPFC which is moderated by a control network involving the dlPFC. Moreover, the dual role for self-reference and autonomic processes is further underlined by the functioning of the default mode network (DMN; [Uddin et al., 2009](#)). The DMN is typically associated with self-referential cognition ([Buckner et al., 2008](#)) as it is active at moments of rest when attention is not directed to the exterior environment but to the self. Besides, the DMN is constituted mainly of brain regions involved in autonomic processing, with the vmPFC as one of its core centers, and is in direct relationship with autonomic control ([Beissner et al., 2013](#); [Bär et al., 2015](#)).

Consequently, within the autonomic nervous system, it seems possible that cardiac regulation during HRVB training influenced the functional dynamic of the vmPFC and related pathways. Indeed, the vmPFC is linked to antisympathetic and parasympathetic ANS activity, whose elicitation was the

aim of the training. In this context, biofeedback acts as a moderator that supports physiological change. The existence of a reciprocal interaction between the autonomic nervous system and forebrain in the context of cognition, memory, and emotion that strongly relies on central autonomic network elements has also been emphasized earlier ([Thayer and Lane, 2000, 2009](#); [Thayer et al., 2009](#); [Critchley et al., 2013](#)). Direct evidence that HRVB training increases resting state functional connectivity in the forebrain and between regions of the central autonomic network was recently demonstrated by [Schumann et al. \(2021\)](#). They showed that HRVB intervention compared to a control group increased connectivity between vmPFC and several forebrain structures, including the cingulate cortex, left anterior insula and dlPFC. They also found that the effect was mediated by elements of the central autonomic network in the brainstem. Hence, it can be assumed that repeated HRVB training may have a sustained impact on the dynamism of the self-reference system due to surges in functional connectivity between forebrain structures (i.e., vmPFC, dlPFC, etc.) and activity in the vmPFC which in turn can be ascribed to the promotion and inhibition of pathways involved in parasympathetic and sympathetic autonomic regulation, respectively.

In this context, we theorize that these functional changes (see [Figure 5](#) “CNS”) evoked by HRV self-regulation training (see [Figure 5](#) “ANS”) facilitated the processing of self-referential information at (1.1) or after initial encoding (2), which leads to the inflation of the SRE and self-related memory retrieval (3). According to the neurophysiological assumptions postulated here, there is also an alteration in the functionality between the vmPFC and limbic structures involved in affective processing and reward circuitry (e.g., cingulate cortex, insula, and amygdala). Moreover, vmPFC activity has been linked to affective meaning and positive valence ratings ([Wincoff et al., 2013](#); [Kim and Johnson, 2015](#)). Hence, we postulate that functional changes were also responsible for changes in affective processing (1.2), explaining the positivity bias in the presented results. This is in line with previous literature that repeatedly linked HRVB to changes in emotional processing ([McCraty et al., 2009](#); [Lehrer et al., 2020](#)). According to the Psychophysiological Coherence model ([McCraty and Childre, 2010](#)), activating positive emotions harmonizes bodily processes that shift an “inner baseline reference” ([McCraty and Zayas, 2014](#)) related to alterations in information processing. So, following the HRVB training, which likewise stimulated physiological coherence, may have also resulted in such a baseline shift, biasing information processing toward positive stimuli. In this regard, HRV self-regulation training influences affective arousal elicited by positive stimuli when PFC is engaged in self-reference processes impacting subsequent information processing (1.3).

Previous literature suggests that the SRE is primarily related to processes at encoding ([Morel et al., 2014](#); [Kalenzaga et al., 2015](#)) (2.1 and 3.1). Moreover, following our assumptions, biofeedback can also be surmised to affect DMN functionality,

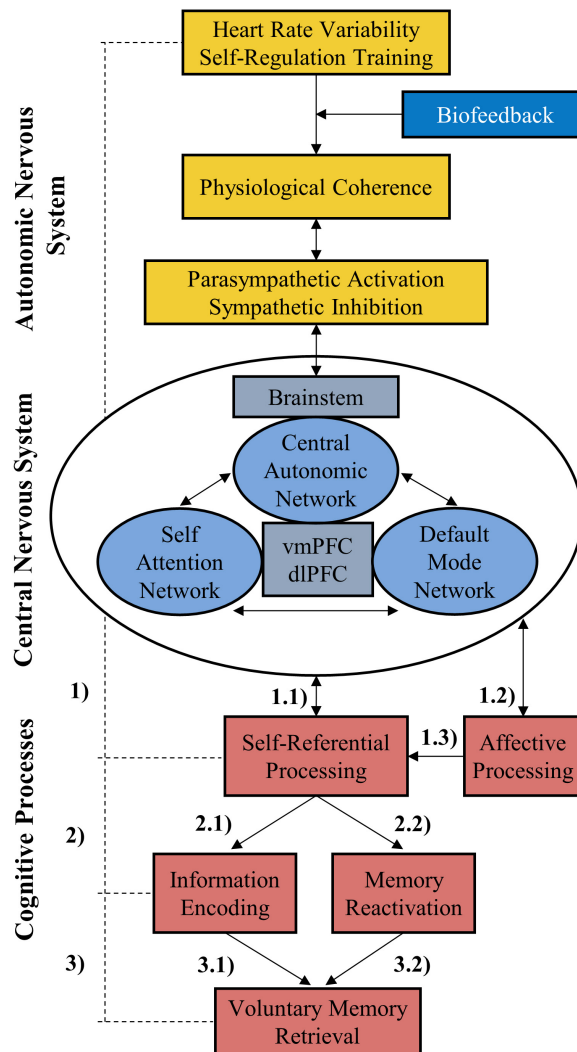


FIGURE 5

The self-regulation-self-referential-memory (SR-SRM) model. Autonomic control can be exercised through HRV self-regulation training and thus affects pathways of the autonomic nervous system which reach the central nervous system. These pathways connect via the brainstem with several forebrain structures in the central autonomic network. Due to shared structures (most notably the vmPFC) further brain networks are influenced down the line which are involved in self-referential information processing (1.1). Likewise, affective processing is affected by functional changes related to limbic structures (1.2) which in turn influence self-referential processing (1.3). Firstly, self-referential encoding (2.1) provides a memory advantage to the encoded information (3.1). Secondly, self-referential processes are associated with the internal focus on thoughts that can trigger reactivation of a new memory or add novel associations to it, especially when the memory is related to the self (2.2), supporting its consolidation and retrieval (3.2). Consequently, strengthening self-referential processing via HRV self-regulation training may support voluntary retrieval of memory. In this context, biofeedback acts as a moderator because it facilitates self-regulation. vmPFC, ventromedial prefrontal cortex; HRV, heart rate variability.

impacting information processing related to our default mode. Besides the inherited central aspect of self-reference, the default mode is also concerned with a range of self-relevant cognitive processes such as mind wandering, recalling memories, simulating, or planning the future (Mooneyham and Schooler, 2013). Hence, the training may also have important consequences on the behavior related to the default mode. For instance, subjects might be more prone to engage in self-referential cognition or to be more concerned by affective

biases. In this regard, an alternative interpretation of our memory results is that training affected self-referential thought processes occurring after the initial encoding during the consolidation or retrieval phase (2.2). It might be that the training success was associated with a greater propensity to engage in retrospection or prospection whose content was linked to the learned self-referential memory probes triggering memory reactivation and reassociation. Consequently, these processes could have facilitated access to the memory trace at

retrieval (3.2). Previous findings underline that post-encoding memory consolidation can occur at rest (Axmacher et al., 2008; Tambini and Davachi, 2013) and when engaged in a task with high frontal related processing demands but low hippocampal related processing demands (Varma et al., 2017, 2018). One indicator to verify whether HRVB promoted self-reference processes occurring after encoding, and thus after post-encoding memory consolidation, may be the comparison of pre-to-post changes in the SRE between the recollection measures and free recall success for positive items. Based on the assumption that an essential part of the memory consolidation took place during the long retention period between the free recall and recognition phases, one would expect in the BG a higher pre-to-post-increase in the SRE for the measure of objective recollection than for free recall success, which was the case in this work. It is thus likely that improvements in EM retrieval were mediated by altered processes at both stages, during encoding and after encoding. Though the influence of encoding processes on the SRE is scientifically more founded, it remains unclear to what extent HRVB related memory improvements can be attributed to these two stages, respectively.

Covariates

In the current study the influence of HRVB on various measures of psychological trait characteristics including emotional regulation, mindfulness, or self-concept was checked. Neither the HRVB training nor the mindfulness training in the CG showed an influence on any score. Accordingly, contrary to previous assumptions, no biofeedback-related changes in affective control or self-awareness were verified. One likely explanation is that the scales used were not sensitive enough to capture any changes as they assessed stable traits rather than reactional states. Furthermore, it is possible that the intervention period and/or the intensity was not long enough or high enough to produce trait changes that could be perceived by the participant.

Experimental biases exhibited by behavioral changes at encoding in terms of response reaction time and number of adjectives associated with the self-concept or autobiographical memories can be excluded since measures were added as covariates to the statistical models when necessary. Furthermore, one might argue that the training affected interoceptive awareness that mediated the impact of the bodily state on memory. In other words, participants were more conscious of autonomic processes causing additional information to be linked to memory. Therefore, additional qualitative properties or cues that had been deeply encoded *via* integration with autonomic control (Critchley et al., 2013) may have been available, facilitating retrieval. The moderate correlation found between HRV and the measure of awareness supports this claim. Also, Blum et al. (2019) found that a

VR-immersion with a natural scene during HRVB increases aspects of a mindfulness state. However, given the statistical insignificance of the correlation and the fact that no effects were observed for any of the mindfulness trait scales, the outcomes did not confirm that self-awareness was related to memory encoding. Nevertheless, it cannot be ruled out that measures of mindfulness state or interoceptive awareness instead of general trait features might have accounted for variations within the results.

In the present study it has been shown that the VR setup used evoked comparable levels of sense of embodiment and presence between groups. We therefore suspect that these characteristics did not moderate group differences in instantaneous and potential long-term psychophysiological changes. Especially self-ownership, which can also extend to the avatar and embodied biofeedback, is known to affect the SRE through the activation of brain networks involved in self-processing (Cunningham et al., 2011; Cunningham and Turk, 2017). However, we do not exclude the possibility that the use of VR moderated HRVB effects through other VR-related mechanisms. For instance, it is possible that the VR implementation increased bodily self-consciousness (Blanke, 2012) during HRVB, and therefore supported self-processing, through greater attention to the biofeedback signal. Though the direct effect of the VR on HRVB outcomes was not assessed in this study, the large effect sizes indicate that the use of VR enhanced cognitive improvements when compared to standard-HRVB, especially regarding the SRE. This effect might be corroborated by more frequent training and will be the subject of future studies which contrast VR-HRVB with a classical HRVB intervention.

Another important factor for the mediation of assessment score changes was participants' expectations about the training efficacy. Subject-expectancy effects are known to contribute to HRVB outcomes (Khazan, 2013) and were therefore controlled through blinding and introduction of an active placebo-control group. Furthermore, it has been argued that subject-expectancy effects may be influenced by the perception of control over physiological parameters (Weerdmeester et al., 2020). The finding that groups did not differ in terms of agency, however, is suggestive that participants receiving biofeedback did not expect their training to be more beneficial due to a stronger perception of any changes that their self-regulation training evoked. In addition, results of the online follow-up questionnaire (Supplementary material E) hinted that expectations about cognitive training effects did not differ between groups.

Implications and perspectives

One of the strengths of the current work is that contrary to most HRVB studies, post-evaluations were not carried out immediately after the last training session. It is therefore

probable that certain training effects were not observable due to their ephemerality. This might also explain why here no effect was reported on several executive functions, specifically inhibitory control, whereas it was reported in studies with comparable sample size and that did not include a maintenance period. Additionally, in contrast to other studies, a statistical approach was adopted that is robust against group differences and violations of distributional assumptions, that accommodates for random subject and time effects (Schielzeth et al., 2020), providing reliable Type 1 error rates for small samples. Consequently, the findings emphasize that instant effects cannot be simply extrapolated, and that caution should be exercised when interpreting such results. Further, this underlines the importance of including a maintenance period in experimental paradigms that investigate the effect of biofeedback on cognition.

Moreover, previous HRVB studies investigated mainly (young) adults who were susceptible to or experienced high levels of work-related stress. Those studies postulated that through the reduction of stress, cognitive performance increases. The present work shows that improvements can also be evoked in young adults without any specified pre-condition and that no experience in self-regulation training is required. The findings also demonstrate for the first time that only six 25-min sessions of HRVB training can be sufficient to provoke changes in the self-referential EM system and discrimination performance that are sustained beyond the training period. Thus, the present study stresses the importance of VR-HRVB interventions in yielding potential long-term advantages for cognition and well-being, especially in regard to short- and long-term memory and committing errors. However, these results have yet to be corroborated by protocols including longer training and maintenance periods, samples of different age segments, and clinical populations. Moreover, the influence of VR-related effects needs to be further investigated.

Heart rate variability biofeedback appears as a promising application for a wide range of fields that are concerned with the peak performance, maintenance, or recovery of cognitive functions. For example, HRVB may prove useful as a therapeutic tool to treat patients suffering from impaired cognition or to combat neurocognitive decline. Specifically, those with conditions that distort self-reference and affective processing, such as schizophrenia, may benefit from HRVB. Further, we recommend considering the implementation of biofeedback also for other self-regulation training programs as state-awareness proved to be advantageous for training outcomes.

In addition, if HRVB indeed has a long-lasting effect on the self-reference system and DMN functionality, training programs could have meaningful implications on a wide range of behaviors, such as those related to self-regulation, body self, mind wandering, prospection-based cognition, and social behavior. Besides the demonstrated leads, further investigation is required to ascertain the relationship of

changes in HRV with self-referential cognition, short-term memory and the identification and discrimination of stimuli. It would also be interesting to explore whether cognitive processes associated to HRVB can impact memory at later memory phases (i.e., beyond encoding). We encourage future HRVB studies to include resting state or phasic HRV measures shortly before or during cognitive assessment that could explain training related effects. Moreover, multimodal neuroimaging approaches are needed to comprehensively explore the neural dynamism underlying the relationship between HRVB-stimulated autonomic activity and cognition.

Conclusion

In the framework of this study, a new cognitive training system was developed that allows for human immersion in a naturalistic VR environment in which HRV and respiratory biofeedback can be visualized. For the first time, two randomized and blind groups were compared that trained HRV self-regulation either with or without VR-HRVB. Statistically significant cognitive effects that persisted 1 week after participation in an HRV self-regulation training program were assessed. Findings demonstrate for the first time the essential role of HRVB to drive cognitive improvement through physiological change. Biofeedback improved aspects of attention, short-term memory, and self-referential EM but not inhibitory control, processing speed, working memory and non-self-referential EM. Furthermore, biofeedback greatly strengthened the SRE for positive stimuli. Cognitive improvements could be linked to the level of the respiratory sinus arrhythmia during training which is associated with physiological coherence, baroreflex gain, and CVC. The presented results are in accordance with the neurovisceral integration model providing additional evidence that parasympathetic activation improves cognitive functioning involving the identification and discrimination of stimuli and self-referential processing. It is conjectured that changes in neural pathways and structures related to autonomic control affected brain networks involved in attentional control, affective processing, and self-referential processing. The results provide reasons to direct further research toward the influence of HRVB on the mind-body complex, as it could reveal important implications for neurocognitive functioning and behavior.

Data availability statement

The datasets presented in this study and details about the virtual reality biofeedback training can be found in the Open Science Framework (osf.io) online repository (doi: [10.17605/OSF.IO/U4T7P](https://doi.org/10.17605/OSF.IO/U4T7P)).

Ethics statement

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The participants provided their written informed consent to participate in this study.

Author contributions

LB contributed to conceptualization, methodology, software, validation, formal analysis, investigation, resources, data curation, writing—original draft preparation, writing—reviewing and editing, visualization, and project administration. IC-B contributed to investigation and writing—reviewing and editing. PP contributed to conceptualization, methodology, resources, writing—reviewing and editing, supervision, and funding acquisition. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fnins.2022.791498/full#supplementary-material>

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9.2 Conclusion

The main results of this first study can be summarized as follows:

- The VR-coupled HRV biofeedback training strongly increased vmHRV (i.e., RMSSD, RSA) during and 5 minutes after training.
- HRV biofeedback, compared to the control group, improved attentional capabilities required for identification and discrimination of stimuli, auditory short-term memory, and self-referential episodic memory recollection of positive stimuli.
- Episodic memory outcomes indicated that HRV biofeedback reinforced positive self-reference encoding processing but did not improve episodic memory *per se*.
- No effects were found on cognitive interference, working memory, cognitive flexibility and subjective ratings of affective control, mindfulness, or the self-concept.
- There was a strong and positive association between cognitive pre-to-post-test changes and baseline-adjusted RSA evoked during training for outcomes that were significantly improved by HRV biofeedback.

The findings confirmed the hypotheses that HRV biofeedback enhances mnemonic self-referential processing and certain assets of cognitive control and that this effect is linked to vmHRV. Results showed, in line with previous findings applying a similar protocol (Sutarto et al., 2010, 2012, 2013), that HRV biofeedback evoked large improvements in sustained attention and short-term memory but not in cognitive flexibility or in cognitive inhibition (Stroop effect). Given the robust association of vmHRV with inhibition and working memory, one might have expected such an effect. However, to this end, the study was very likely not powered enough. The effect on attention was specific to the avoidance of errors in a visual discrimination task during high mental load. It seems thus that vmHRV stimulation through HRV biofeedback has great effect on cognitive control functions involved in identifying and discriminating irrelevant from relevant information. A significant association between RSA and the capability to discriminate self-referential episodic memories from distractor items underlines this assumption. In addition, HRV biofeedback improved the self-reference effect for positively valenced but not for negatively valenced items. This suggests that HRV biofeedback reinforces the self-positivity bias. Summarized, these findings propose in concordance with the neurovisceral integration model that cardiac vagal controlled is tied to the activity of brain networks involved in cognitive and emotional control as

well as self-referential processing and that increasing phasic vagal activity can persistently change their neural correlates. Departing from these results, we first assumed that if vmHRV is linked to the discrimination performance of external stimuli, it might also support the discrimination of internal stimuli such as memories. Secondly, we theorized if the vmHRV is related to positive self-referential bias during memory encoding it would also be presented during mental time travel into the past and future.

10 Chapter 10 – HRV Biofeedback Effect on Cognitive Control over Long-Term Memory and its Association to Autonomic Regulation during Memory Processing

This article is currently under revision in *Psychophysiology* (Journal ISSN: 1469-8986, Manuscript ID: PsyP-2023-0370). The below article features the manuscript at the time of submission, which has been published as a pre-print by the journal (Bögge et al., 2023). Review reports have been received shortly before the thesis manuscript submission and primarily concern the separation of confirmatory and exploratory results. The research project, including the research data, all supplementary materials and results, as well as video material of VR environment will be made publicly available upon article acceptance on the Open Science Framework online repository (OSF link: <https://osf.io/593p6/>).

10.1 Introduction

The second article of the thesis, termed BIOTRAC-2, aimed at extending previous results from BIOTRAC-1 by demonstrating that cardiac vagal control mediates cognitive control processes involved in long-term memory.

The first study showed that HRV biofeedback improves cognitive control related to the discrimination of similar stimuli and that this effect is related to the level of vmHRV during training. Consequently, we asked ourselves if this effect was due to neurophysiological changes reflected in vmHRV during cognitive processing and whether this effect would also extend to discrimination performance in the long-term memory domain. The primary interest was to replicate and expand on the results of Feeling et al. (2021) by showing that vmHRV measured as RMSSD during rest and during memory processing (i.e., encoding, retrieval) links to true-to-false memory discrimination and metamemory of false memories (i.e. confidence in response choices) as proxies of cognitive control over memory. At the same time, we wanted to test for the first time whether HRV biofeedback can instantaneously increase vmHRV during subsequent memory processing phases. Since cognitive control over memory and vmHRV have been previously associated (Feeling et al., 2021; Gillie et al., 2014, 2015), it was assumed that by experimental manipulating vmHRV during memory processing,

the potential mediation effect on cognitive processes could be studied. In this line of thought, we sought to corroborate the notion that cognition depends on autonomic regulation in response to a situation and, with such, the representation of internal states of the body. To this end, a single-session experiment was designed during which participants completed twice, similar to the study of Feeling et al. (2021), the Deese-Roediger-McDermott for assessing false memories based on neutral items. Before and between memory phases, participants completed either HRV biofeedback or a paced-breathing exercise that did not stimulate vmHRV. The complete procedure was implemented in VR to increase higher experimental control and the degree of automatization and task flow continuity. We abandoned the longitudinal approach, mainly due to COVID restrictions but also to increase sample size and statistical power. The work was divided into a pre-registered confirmatory analysis (OSF link: <https://osf.io/edhpc/>) as well as an exploratory analysis. The confirmatory analysis examined tonic values as it was assumed that the psychophysiological association found for tonic resting-state vmHRV would also be reflected during memory processing. However, in the pre-registration, we already considered adding an investigation of phasic vmHRV along with the idea of the Vagal Tank Theory that reactivity values will provide a deeper insight into the relationship between cardiac vagal control and cognitive self-regulation.

10.2 Reviewed Article (Bögge et al., *IN REVIEW*)



Autonomic and cognitive control in memory: Investigating the psychophysiological link using heart rate variability biofeedback

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Manuscript ID	PsyP-2023-0370
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Complete List of Authors:	Bögge, Lukas; Université Paris Cité, Memory, Brain & Cognition Laboratory Colás-Blanco, Itsaso; Université Paris Cité, Memory, Brain & Cognition Laboratory Ferragu, Juliette; Université Paris Cité, Memory, Brain & Cognition Laboratory Gaston-Bellegarde, Alexandre; Université Paris Cité, Memory, Brain & Cognition Laboratory La Corte, Valentina; Université Paris Cité, Memory, Brain & Cognition Laboratory; Institut Universitaire de France Piolino, Pascale; Université Paris Cité, Memory, Brain & Cognition Laboratory; Institut Universitaire de France
Keywords:	Biofeedback < Content/Topics, Cognitive Control < Content/Topics, Memory < Content/Topics, Heart Rate Variability < Methods, Young Adults < Groups Studied, Respiration < Methods
Abstract:	Vagally-mediated heart rate variability (vmHRV) at resting-state has been associated to cognitive functions dependent on cognitive control, such as memory. However, little is known about the phasic interaction between cognitive and autonomic control. In a pre-registered within-between-subject designed experiment, the potential of vmHRV biofeedback to simultaneously stimulate vmHRV during memory processing and cognitive control over memory was tested, along with investigating psychophysiological association. 71 young healthy adults completed (twice) a false memory task in virtual reality. Immediately before memory encoding and retrieval, participants practiced either vmHRV biofeedback or a control breathing exercise. Cognitive control over memory was assessed as the confidence towards false memories and the capability to discriminate them from true memories. Resting-state vmHRV before each test and phasic vmHRV during memory encoding and retrieval was measured as the root mean square differences (RMSSD) in heart period. vmHRV biofeedback had neither an immediate effect on cognitive control over memory nor on phasic RMSSD. Both metrics were associated only under consideration of the resting-state and heart rate values. Cognitive control over memory was positively predicted by parallel reactivity (i.e., change from baseline) in heart rate ($\beta = .333$) and RMSSD ($\beta = .238$) at memory retrieval. In

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	consistence with previous psychophysiological models, the findings demonstrate a link between cognitive and phasic vagally-mediated autonomic control which extends to higher-level cognitive functions such as long-term memory. In this context, memory performance seems to be dependent on tonic and phasic (frequency) components of parasympathetic modulation in response to memory processing.

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Autonomic and cognitive control in memory: Investigating the psychophysiological link using heart rate variability biofeedback

1 Impact statement

2 The results add a nuanced view on the psychophysiological relationship between autonomic and
3 cognitive control. We provide evidence that instead of HRV state measures, parallel changes in heart
4 rate and HRV in response to cognitive processing better predict cognitive performance. The results
5 are not only consistent with previous psychophysiological models, but also suggest that memory
6 performance depends on a dual process of parasympathetic regulation that is revealed when HRV is
7 adjusted for heart rate.

Autonomic and cognitive control in memory: Investigating the psychophysiological link using heart rate variability biofeedback

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Keyword: heart rate variability, biofeedback, autonomic control, cognitive control, long-term memory, virtual reality.

Impact statement

The results add a nuanced view on the psychophysiological relationship between autonomic and cognitive control. We provide evidence that instead of HRV state measures, parallel changes in heart rate and HRV in response to cognitive processing better predict cognitive performance. The results are not only consistent with previous psychophysiological models, but also suggest that memory performance depends on a dual process of parasympathetic regulation that is revealed when HRV is adjusted for heart rate.

Abstract

Vagally-mediated heart rate variability (vmHRV) at resting-state has been associated to cognitive functions dependent on cognitive control, such as memory. However, little is known about the phasic interaction between cognitive and autonomic control. In a pre-registered within-between-subject designed experiment, the potential of vmHRV biofeedback to simultaneously stimulate vmHRV during memory processing and cognitive control over memory was tested, along with investigating psychophysiological association. 71 young healthy adults completed (twice) a false memory task in virtual reality. Immediately before memory encoding and retrieval, participants practiced either vmHRV biofeedback or a control breathing exercise. Cognitive control over memory was assessed as the confidence towards false memories and the capability to discriminate them from true memories. Resting-state vmHRV before each test and phasic vmHRV during memory encoding and retrieval was measured as the root mean square differences (RMSSD) in heart period. vmHRV biofeedback had neither an immediate effect on cognitive control over memory nor on phasic RMSSD. Both metrics were associated only under consideration of the resting-state and heart rate values. Cognitive

control over memory was positively predicted by parallel reactivity (i.e., change from baseline) in heart rate ($\beta = .333$) and RMSSD ($\beta = .238$) at memory retrieval. In consistence with previous psychophysiological models, the findings demonstrate a link between cognitive and phasic vagally-mediated autonomic control which extends to higher-level cognitive functions such as long-term memory. In this context, memory performance seems to be dependent on tonic and phasic (frequency) components of parasympathetic modulation in response to memory processing.

1 Introduction

1.1 Autonomic and cognitive control

According to psychophysiological models relying on the body-brain interaction, bodily states and processes are associated to cognitive functioning (Critchley et al., 2013). In this light, embodied approaches to cognition emphasize the role of the interacting body in cognition (Hommel, 2004; Varela et al., 2017; Versace et al., 2014), also with regard to memory functions (Bréchet, 2022; Iani, 2019; Tuena et al., 2019). The role of the body in cognition not only encompasses sensorimotor aspects but also physiological variables reflecting autonomous nervous system (ANS) activity, which is now recognized to play an important role in cognition (Critchley, 2009; Critchley et al., 2013; Damasio et al., 1997).

The ANS is divided, besides the enteric division, into the parasympathetic nervous system (PNS) and sympathetic nervous system (SNS) that regulate the cardiac activity in a reciprocal, coactive, or independent manner (Berntson et al., 1991). In this line, the heart rhythm slows down under increasing efferent input from the PNS via the vagus nerves, whereas vagal withdrawal or an increase in SNS activity accelerates the heart. Thus, ANS activity is reflected in the fluctuations in the heart period that are described as the heart rate variability (HRV). The neurovisceral integration model posits that HRV is regulated by a top-down control system involving forebrain structures such as the prefrontal cortex, cingulate cortex, insula, and amygdala as well as brainstem nuclei (Smith et al., 2017; Thayer et al., 2009; Thayer & Lane, 2000). The heart-brain connection embeds a set of cortical-subcortical neural circuits that is associated with cardiac as well as cognitive regulation and which links prefrontal cortex activity to vagal modulation. Hence, it was proposed that vagally-mediated HRV (vmHRV) is correlated with activity of executive brain regions, most notably the prefrontal cortex (Thayer et al., 2012). Executive function (or also referred to as cognitive control) is the process by which behavior is adapted according to goals, plans, and contextual knowledge. Some authors have claimed it is divided into three core functions (Lehto et al., 2003; Miyake et al., 2000): inhibition [including inhibitory control over responses and interference control (selective attention and cognitive inhibition)], working memory (updating), and cognitive flexibility (shifting). Indeed, greater resting-state vmHRV has been related to better cognitive control (Forte et al., 2019, 2022; Holzman & Bridgett, 2017; Zahn et al., 2016). Moreover, there is emerging evidence that vmHRV also relates to higher-level cognitive function that is supported by cognitive control such as memory. In this line, it has been demonstrated that resting-state vmHRV is positively correlated with inhibitory control processes involved in the voluntary suppression of memory and thought (Gillie et al., 2014, 2015), memory discrimination between items with low visual distinctiveness (Magnon, Mille, et al., 2022), and the reduction of false memories (Feeling et al., 2021). Memory is essential in everyday life. For instance, being able to distinguish between true and false long-term memories is important for autonomy, self-confidence, and the reliability of testimonies. Therefore, studying the brain-body interactions underlying memory is of crucial importance to understand and promote healthy behavior.

1.2 False memory as a measure of cognitive control over memory

False memory is a form of memory distortion and describes the erroneous retrieval of an event that did not occur or that is remembered differently in contrast to the actual event (Abichou et al., 2020; Roediger et al., 1998; Schacter, 1999, 2021). These commission errors are often held in memory with high level of confidence (Dehon, 2012) what makes them difficult to be detected or eradicated. False memory arises from memory interference when correct retrieval of stored information is hindered because the true memory is competing with other memories for cognitive resources. High relatedness between competing memories favors false memory production, a circumstance that is used by the Deese-Roediger-McDermott (DRM) paradigm (Deese, 1959; Roediger & McDermott, 1995) to assess false memory. In this paradigm, participants are instructed to memorize several lists of items during an encoding phase. The items in each list may either be strong semantical associates (e.g., “sit”, “table”; associative list) of a not listed item (e.g., “chair”) or be members (e.g., “kiwi”, “orange”; categorical list) of the same category (e.g., “fruits”), excluding the most prototypical item (e.g., “apple”). During a later recognition phase, additional, previously unseen lure items are presented that are either semantically related to learned list items (i.e., critical lures, e.g., associative list: “chair”, categorical list: “fruits” or “apple”) or semantically weakly to unrelated (i.e., distractors, e.g., “car”). Critical lures are much more likely believed to be truly memorized than distractors and thus their false recognition is considered a false memory.

Different explanations for the formation of false memories have been proposed, of which some (e.g., the fuzzy trace theory; Reyna & Brainerd, 1995) bring the semantic-level similarity to the fore, arguing that false memories are a result of overreliance on gist (i.e., essential meaning) and familiarity due to a lack of episodic details and distinctiveness at retrieval (possibly from stronger encoding of gist than verbatim information) and the existence of shared features between the false memories and recently encoded information. Another model, the Activation Monitoring Theory (Gallo, 2010; Roediger et al., 2001; Roediger & McDermott, 2000) proposes that false memories derive from implicit associative activation of non-presented critical lures during the processing of list items and errors in determining the source of the information (e.g., perceptual details). In this regard, the activation of an information, for example at encoding or retrieval, also strengthens the representation of associated items (e.g., the critical lures) facilitating their false recognition. For these activated lures to be detected as false memories, source monitoring processes must be engaged to disentangle their origin from those of true memories, i.e., the perceptual details and spatiotemporal context in which they were previously encoded (Abichou et al., 2021, 2022)

Therefore, false memory can be considered a measure of cognitive control over memory which supports the selection of the true memory and suppression of competing memories mainly at the encoding and retrieval phases. The association of cognitive control with the production of false memories has been mainly verified for cognitive functions that are typically linked to vmHRV such as working memory (Abadie & Camos, 2019; Holden et al., 2020; Mirandola et al., 2017; Peters et al., 2007; Ruffman et al., 2001) and inhibition (Alberts, 2010; Colombel et al., 2016; Howe, 2005; Lövdén, 2003; Ruffman et al., 2001) in children, young, and old adults. Overall, results showed that better inhibition and working memory abilities predict lower false memories and that increases in false memories formation in ageing could be explained by a decline in cognitive control (Abichou et al., 2020; Colombel et al., 2016; Lövdén, 2003; Sommers & Huff, 2003), mainly attributed to age-related decline in the prefrontal cortex functioning (Craik & Grady, 2002). Furthermore, neuroimaging studies have highlighted the existence of cerebral characteristics that distinguish, in part, between true and false memories, especially an increase in the activity of the prefrontal cortex

126 during false recognition, compared to the activity associated with true memories (Kim & Cabeza,
127 2007; Kurkela & Dennis, 2016).

128 Consequently, based on theoretical and structural ties, cardiac vagal control indexed by vmHRV
129 should be associated with cognitive control over memory. One study recently demonstrated such a
130 link between resting-state vmHRV with the production of false memories using the DRM task
131 (Feeling et al., 2021). However, like in most psychophysiological studies, the correlation between
132 cognitive functioning and vmHRV was established for physiological measures recorded only at
133 resting-state. Little is known about the influence of phasic vmHRV assessed during task
134 performance, when cognitive control is engaged, on cognitive functioning. In this line of thought,
135 phasic measures could provide new insight into the interaction between autonomic processes and
136 memory control at different memory processing stages (i.e., from encoding to retrieval).

137 **1.3 vmHRV stimulation through biofeedback**

138 As cognitive control is positively linked to vmHRV, it seems interesting to study the plausible causal
139 relationship and to improve cognitive functioning by stimulating vmHRV. vmHRV can be increased,
140 and thus autonomic processes modulated non-invasively through HRV biofeedback (Lehrer &
141 Gevirtz, 2014). HRV biofeedback relies on the observation of body-own physiological signals
142 derived from cardiac and often also respiratory measures which serve to up-regulate vmHRV, mostly
143 through slow and rhythmic breathing. Such training entrains physiological coupling between
144 respiratory, blood pressure, and heart rate functions that are believed to optimize body functioning
145 and to stimulate vagal afferent outflow as well as prefrontal cortex activity (Lehrer et al., 2000;
146 McCraty & Childre, 2010). Physiological changes can be induced within a minute and can last 10 or
147 more minutes after training (Bögge et al., 2022; Lehrer et al., 2003). First studies demonstrated that
148 executive functions, especially inhibition, are improved after HRV biofeedback training (Bögge et
149 al., 2022; Dessy et al., 2018; Nashiro et al., 2022; Tinello et al., 2021). Prinsloo et al. (2013) showed
150 that even a single session was associated with neural changes suggestive of increased attention during
151 and shortly after training. Neuroimaging data further underlined that repeated training increases
152 prefrontal activity and functional connectivity between forebrain structures and autonomic control
153 centers that are also involved in cognitive control (Nashiro et al., 2022; Schumann et al., 2021; Yoo
154 et al., 2022).

155 **1.4 Objectives and hypotheses**

156 Based on theoretical models as well as neurophysiological and behavioral evidence supporting the
157 link between cardiac vagal control and cognitive control, we assume an association between resting-
158 state as well as phasic vmHRV and cognitive control underlying memory processing. Instead of
159 simply studying the relationship of state indicators, we propose a vmHRV stimulation study that tests
160 the relationship between individual changes in vmHRV and changes in memory. On the one hand,
161 results may provide fundamental insights into the mechanisms of HRV stimulation on true and false
162 memory. On the other hand, we target to explore the possibility of HRV biofeedback to stimulate
163 vmHRV during cognitive processing and to improve cognitive control over term memory in young
164 healthy adults. Findings might provide the groundwork for HRV-based cognitive training
165 approaches. For this pre-registered study (registration DOI: <https://osf.io/edhpc>, associated project:
166 https://osf.io/593p6/?view_only=07d070654c12467cb8c509f6e175a029, private view link only) a
167 2x2 within-between subject design was implemented that compared the immediate effect of HRV
168 biofeedback on false memory retrieval to a control breathing exercise. We formulated the following
169 confirmatory hypotheses:

- 1
2 170 **H1)** Resting-state vmHRV is positively correlated to working memory and interference inhibition.
3 171 **H2)** Short-term HRV biofeedback increases vmHRV during subsequent memory processing (i.e.,
4 172 encoding or retrieval).
5 173 **H3)** Short-term HRV biofeedback prior to memory encoding and retrieval improves cognitive
6 174 control over memory.
7 175 **H4)** Resting-state and phasic vmHRV during memory processing (i.e., encoding or retrieval) are
8 176 positively correlated to cognitive control over memory.
9 177 **H5)** Changes in cognitive control over memory are partially mediated by changes in vmHRV
10 178 during encoding or retrieval.

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13 179 Moreover, we extended the results by a planned exploratory analysis that investigated the association
14 180 between vmHRV reactivity (i.e., change from baseline in response to memory processing) and
15 181 cognitive control over memory.

16 182 **2 Materials and Methods**

17 183 **2.1 Participants**

18 184 We used the software program G*Power 3.1.9.4 to conduct two separate power analysis to determine
19 185 the required minimum target sample size. Our goal was to obtain at least .90 power to detect effects
20 186 at .05 alpha error probability. The first analysis concerned the group-by-test interaction effect on
21 187 measures of vmHRV and cognitive control over memory. Given the lack of comparable studies, we
22 188 estimated a sample size that would allow for the detection of even small effects. In this line, we
23 189 assumed an effect of partial eta square = 0.04 and a repeated measures correlation coefficient of .50.
24 190 The second analysis concerned the correlation between vmHRV and memory measures for which we
25 191 assumed a moderate effect of .35 based on previous findings (Feeling et al., 2021; Gillie et al., 2014).
26 192 The first and second analysis provided estimates of 66 samples (i.e., 66 participants) and 81 samples
27 193 (i.e., 41 participants as repeated measures [T1, T2] will be grouped together), respectively.
28 194 Consequently, the target sample size was set at 66 participants.

29 195 83 volunteers were recruited via proposals distributed via social media, an experiment dissemination
30 196 platform, and a course platform accessible by psychology students of the Université Paris Cité.
31 197 Participants were paid 30€ in gift-cheques or received course credits for agreeing to participate. The
32 198 study was conducted in compliance with the ethical standards according to national legislation (Jardé
33 199 law) and with the 1964 Helsinki Declaration and its later amendments. Ethical approval to conduct
34 200 the study was obtained from the Université Paris Cité institutional review board (N° IRB: 00012021-
35 201 123). All participants provided their informed and written consent right before the experiment start.
36 202 They were then assigned to either a biofeedback group (BG) or an active control group (CG) using
37 203 block randomization stratified by sex (male, female). Parallel task versions, designed to
38 204 counterbalance stimuli presentation order, were assigned using dynamic randomization. In this line,
39 205 participants were assigned in ascending order in blocks of 16 depending on their group assignment
40 206 and sex (e.g., first and second female participants in BG are assigned to task version 1 and 2,
41 207 respectively). During the experiment subjects were blind to the group assignment, hypotheses, and
42 208 study design.

43 209 Participants were required to be healthy adults between 18 – 35 years old that are native French
44 210 speakers and that have acquired university entrance qualification. Subjects were excluded from
45 211 participation if they reported to be concerned by at least one of the following conditions: history or
46 212 treatment for psychiatric, neurological, cardiac, or severe respiratory disorders, treatment with a
47 213 cognitive impact, chronic pain, frequent dizziness or nausea, vertigo, impaired but not corrected

visual or auditive capabilities, reading problems, substance abuse, medication that affects the cardiac activity. In addition, high scores of anxiety and the subjective feeling of pain and being sick led to exclusion (see “Participant characteristics”). Inclusion and exclusion criteria were checked at the beginning of the experiment. Due to ethical reasons, all participants that registered via the course platform to earn course credits were eligible to participate. Their data were excluded afterwards if found to be ineligible for data analysis. Furthermore, participants were asked not to smoke or vaporize two hours preceding the experiment, not to consume caffeinated substances or alcohol or any other stimulative or sedative substances (e.g., medicaments, drugs) at the experiment day, and not to exercise intense physical activity 24 hours preceding the experiment. In total 12 participants were excluded: five due to medical conditions, three due to high trait anxiety, two due to medication use, and two because they did not meet the age or language requirements.

2.2 Procedure

2.2.1 Overview

All participants were assessed individually in an experimental room of our laboratory within a single session of around 3 hours (Figure 1). During the experiment participants remained, visually shielded from the experimenter, seated in front of a desk equipped with a monitor, keyboard, and a virtual reality (VR) setup. Control variables including measures of working memory and interference inhibition were assessed at the beginning of the experiment. Thereafter, both groups completed two parallel versions of the Deese-Roediger-McDermott (DRM) task (Deese, 1959; Roediger & McDermott, 1995; Stadler et al., 1999), (first test: T1, second test: T2) integrated in VR for the assessment of cognitive control over memory. During the DRM task participants exercised either HRV biofeedback or variable breathing as a control exercise that does not stimulate vmHRV. Physiological recordings were taken during the DRM task and during a 5-minute resting-state period (i.e., baseline) preceding the task. During the pauses participants were free to drink water or go to the toilettes. However, to reduce differential effects and fatigue effects on physiological recordings, all participants were asked to stand up and, if possible, to remain standing or to walk. The procedure was kept generally identical between tests and groups except for the HRV biofeedback in the BG at T2. Subjects were notified about the second DRM test and the exercise type (i.e., HRV biofeedback or variable breathing) first during familiarization at T2 to reduce motivational biases. This design was

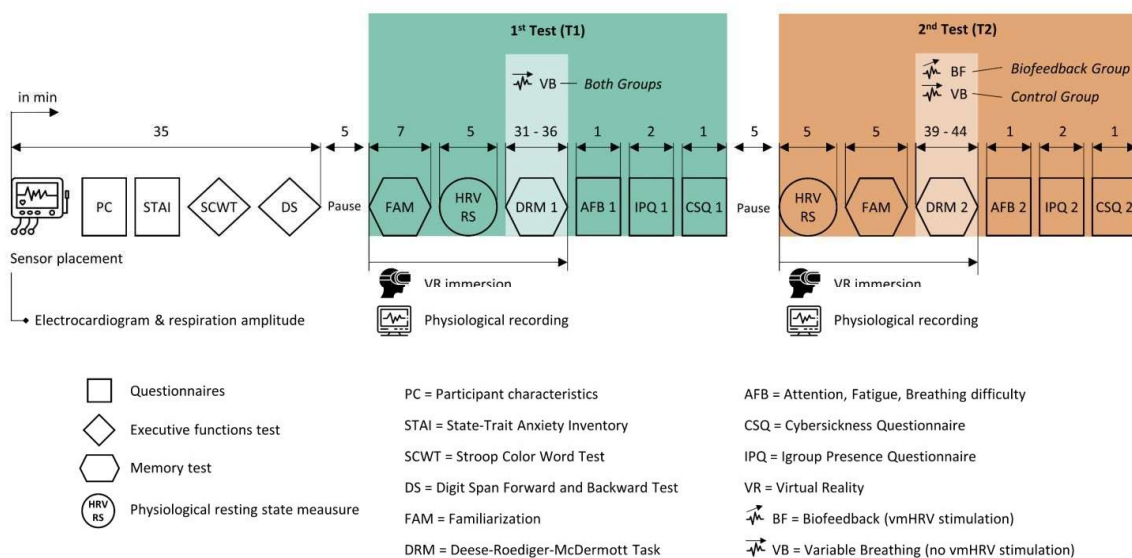


Figure 1 – General Procedure

Note. Participant characteristics were recorded at the beginning of the experiment. Afterwards, all participants passed twice the same test (T1, T2) including two parallel versions of a false memory task (i.e., DRM). During the DRM at T1, both groups performed a control breathing exercise that was designed not to stimulate vmHRV before memory encoding and retrieval. During T2, the control group repeated the procedure from the T1 whereas the biofeedback group exercised HRV biofeedback to increase vmHRV. Physiological recordings at resting-state and task control measures were taken before and after the false memory task, respectively. Participants were familiarized with the task procedure at the beginning of T1 and with the HRV biofeedback (only biofeedback group) first shortly before the second false memory test in order not to bias the resting-state recording. This figure has been designed using images from Flaticon.com.

chosen to assess if vmHRV stimulation through HRV biofeedback evokes changes in cognitive control over memory while controlling for re-test and respiratory self-regulation effects.

2.2.2 Participant characteristics

Participants characteristics were assessed at the beginning of the experiment through digitalized questionnaires, scales, and cognitive tasks that were presented on the computer screen using customized Python scripts and the Python package Neuropsychia (Makowski & Dutriaux, 2017). Variables of the first questionnaire are described in the supplementary material SM1. In addition, levels of state and trait anxiety were determined by means of the French translation of the State-Trait Anxiety Inventory (STAI; Schweitzer & Paulhan, 1990; Spielberger, 1983). Participants were excluded if according to the manual either of the tests indicated either a high or very high score (>55) or if any of the pain or sickness scores was higher than 5. Executive functions (working memory and inhibition) were evaluated by means of the Stroop global interference score and digit span standard score derived from the Stroop Color and Word Test (Stroop, 1935) and the Digit Span test (in the fourth edition of the Wechsler Adult Intelligence Scale; Wechsler, 2010), respectively. The Stroop global interference score was calculated based on recommendations of Scarpina & Tagini (2017) and included the processing time, corrected, as well as uncorrected errors of all subtests (Bögge et al., 2022).

2.2.3 Technical setup

A 3-Lead electrocardiogram and changes in thoracic-abdominal circumference (respiration amplitude) were obtained with the MP150 data acquisition system (BIOPAC Systems, Inc., 2015) according to the manufacturer's guideline (BIOPAC Systems, Inc., n.d., 2016). Surface electrodes were placed on the torso based on Einthoven's triangle that collected data from Lead II. A heart rate waveform was calculated online based on beat-to-beat time intervals. All signals were acquired with a sampling rate of 1000 Hz. During the recording, participants were asked to sit upright, to rest the arms in the lap, refrain from moving and talking, and to breath naturally if not instructed otherwise.

The VR system and integration of the physiological system was based on our previous study (Bögge et al., 2022). VR allows an embodied immersion very close to daily life situations with a high self-presence and thereby ecological and controlled setups (Slater et al., 2022). Participants were immersed in a VR environment using a head mounted display including headphones and two hand controllers (HTC Vive Pro). In the environment, they were embodied by a human avatar of the same gender and age in the first-person perspective sitting on a lonely beach and gazing at the open sea. The headset and controllers established visuomotor correlations between the real and artificial avatar body for the head, arms, hands, and legs. The following DRM task was incorporated by displaying instructions, cues and response options on a marble wall appearing in front of the user. The right

287 controller recorded the users' responses. Physiological signals were fed to the VR system allowing
288 for their online display (i.e., biofeedback).

289 **2.2.4 Training**

290 During the DRM task participants exercised either HRV biofeedback or a variable breathing exercise.
291 HRV biofeedback was based on the resonance frequency training (Lehrer et al., 2000, 2013) to
292 stimulate vmHRV. Variable breathing was based on the control breathing task presented by Leganes-
293 Fonteneau et al. (2021) and implemented as an active control exercise which also requires effort to
294 regulate the breathing but does not increase vmHRV. During both exercise types, a vertically shuttling
295 sphere appeared in front of the avatar that moved at a constant rhythm of 6 cycles per minute (HRV
296 biofeedback) or at a variable rhythm of 12 to 16 (mean = 14) cycles per minute (variable breathing).
297 Participants were asked to follow the sphere with their breath by breathing either through the mouth
298 or nose. During HRV biofeedback the heart rate was represented numerically on the sphere and by
299 the color of the sea. In this context, changes in the heart rate were displayed by changes in the color
300 of the sea (i.e., sea turned gradually cyan/violet when the heart rate increased/decreased). Besides
301 following the pacer, participants were asked to adapt their breathing (i.e., velocity, volume) to
302 achieve high-amplitude fluctuations in the heart rate that were synchronized with the breathing
303 pattern. Furthermore, cardio-visual stimulation was provided by displaying heartbeat flashing
304 through the color intensity. This was done to help the subject with the interpretation of the
305 biofeedback. During variable breathing no biofeedback was given but instead the synchronicity level
306 between the pacer and the actual respiration. Synchronicity was calculated for each paced ventilation
307 cycle by determining the time interval proportions of real to paced inspiration and expiration. In turn,
308 inspiration and expiration time intervals were determined from the maximal and minimal respiration
309 amplitude within each paced ventilation phase. Synchronicity ranged from -100 (inversely phased) to
310 100 (completely in-phase). Participants were asked not to force deeper breathing and to maintain
311 maximal synchronicity during the whole exercise. Synchronicity was also calculated during HRV
312 biofeedback but was not displayed. During any exercise, if values dropped below 75 a beep was
313 played to remind the participant to focus on the task.

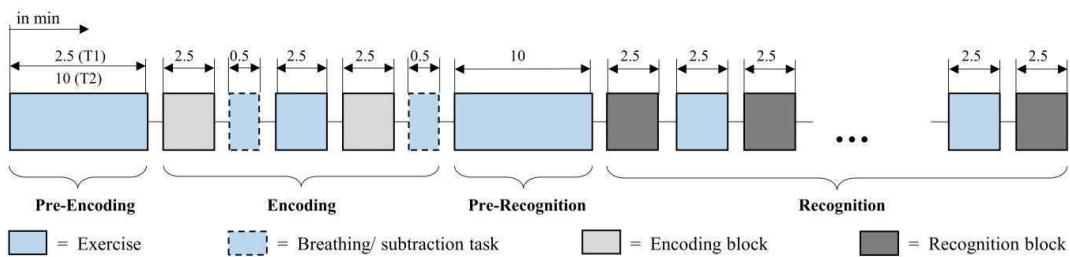
314 **2.2.5 Cognitive task**

315 To investigate the effect of HRV biofeedback on true and false memory retrieval as a proxy of
316 cognitive control over memory, a modified version of the DRM task was used (Deese, 1959;
317 Roediger & McDermott, 1995; Stadler et al., 1999). The task was divided into four phases (Figure
318 2A). Participants exercised either HRV biofeedback or variable breathing immediately before the
319 intentional learning (i.e., encoding) and recognition of word lists in order to manipulate vmHRV
320 during encoding and retrieval. The stimuli set used in this experiment was designed to increase the
321 sensitivity of the assessment in terms of false memory retrieval and to ensure minimum physiological
322 recordings lengths (supplementary material SM2 and SM3). During encoding participants were
323 required to memorize 120 words equally divided into 2 blocks of 4 lists each. Stimuli were
324 comprised of neutral common everyday words that were within each list (e.g., "thirst", "eat", "meal")
325 semantically associated to an unshown critical lure item (e.g., "hunger"). Stimuli were presented
326 sequentially in the fixed order of the list (Figure 2B). The order of the 16 associative word lists (T1
327 and T2) was counterbalanced through a 16x16 balanced Latin square design. After each encoding
328 block participants were asked to follow the pacer of the exercise on which a new random 2-digit
329 number appeared every 3 seconds. In addition, they had to subtract each number by two and to say
330 the result mentally. The subtraction task was implemented to limit immediate cue recall during the
331 following exercise. Words had to be kept in memory until the start of the recognition phase in
332 average for 14.2 (min = 10.5, max = 17.9) minutes. During recognition participants were individually

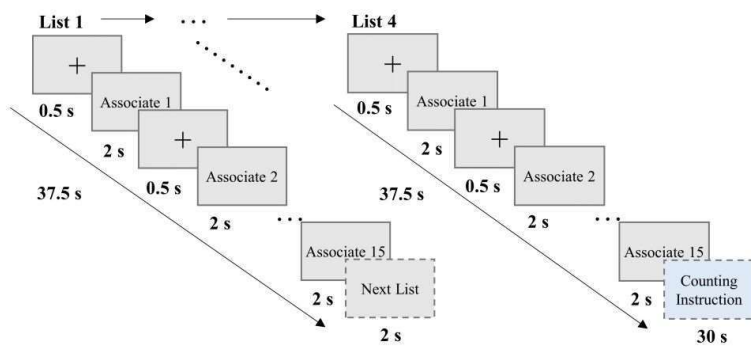
1
 2 333 presented with 24 of the learned items (i.e., targets, serial position 1, 3, 10 of each list) and 40 new
 3 334 words. The latter consisted of 8 semantically related critical lures corresponding to the learned lists
 4 335 and 32 unrelated distractors (e.g., “pocket”, “choice”). Distractors shared either no or only weak
 5 336 similarity with learned items in terms of semantic, lexical/associative, or structural properties. For
 6 337 each word, participants had to judge whether they recognized it from the encoding phase (“yes” or
 7 338 “no” response) and how confident they were in their choice on a scale from 0 to 100 (0 being “not at
 8 339 all confident”, 100 being “completely confident”), (Figure 2C). The erroneous recognition of critical
 9 340 lures (“yes” response) was considered a false memory. Items were presented in a randomized order;
 10 341 however, critical lures were equally distributed (i.e., one lure in every block of eight items).
 11 342 Recognition was divided into blocks so that no more trial was initiated after 2.5 minutes have passed.
 12 343 Between encoding and recognition blocks the exercise was performed. Thirty seconds before the end
 13 344 of each exercise block the pacer as well as the biofeedback disappeared, and spontaneous breathing
 14 345 was instructed to limit the effect on the respiration frequency during encoding and recognition
 15 346 blocks. In this context, pilot tests showed that deep breathing provoked subjects to stop breathing
 16 347 during subsequent encoding. The exercise was the same throughout the task depended on the group
 17 348 and test (Figure 1). The procedure at T1 and T2 was identical except for the exercise type and the
 18 349 length of the exercise before encoding. Regarding the latter, the first exercise block at T1 was set to
 19 350 2.5 (instead of 10) min to reduce the experiment duration and possible fatigue effects. This was
 20 351 assumed not to compromise the comparability between groups and tasks since variable breathing (no
 21 352 vmHRV stimulation) before encoding was not assumed to affect the DRM outcomes.

26 353

A) Modified Deese-Roediger-McDermott (DRM) Task



B) Encoding block



C) Recognition block

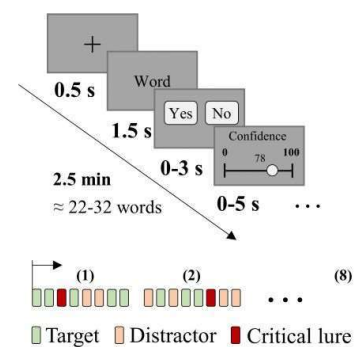


Figure 2 – Modified Deese-Roediger-McDermott task

Note. **A)** Participants were instructed to memorize as many of the 120 words presented during the two encoding blocks as possible and to recognize them (i.e., targets) among new words (i.e., lures) during the later recognition phase. Before each encoding and recognition block participants performed a breathing exercise which was implemented to increase vagally-mediated heart rate variability (heart rate variability biofeedback) or not (variable breathing) during subsequent memory encoding and recognition. Recognition blocks ended after 2.5 min have elapsed and a new exercise block started. Recognition ended generally during the third recognition block after all 24 targets and 40 lures had been presented. **B)** During each encoding block four associative word lists were presented by displaying words individually on a marble wall in front of the user in the virtual reality. Words in each list were associated to one unshown critical lure item. **C)** During recognition words and response choices were presented again on the marble wall. Following each word participants had to indicate whether they recognized the word from the encoding phase or not and the level of confidence in their choice on a continuous scale from 0 to 100 (0 being “not at all confident”, 100 being “completely confident”) by pointing on the response with the hand controller. The word order was randomized during recognition; however, critical lures were distributed such that only one critical lure occurred in each block of eight items.

2.2.6 Familiarization

At the beginning of the T1, all participants were familiarized with the task by completing a shortened version of the first DRM task including the variable breathing with a separate set of stimuli that contained no critical lures. Familiarization was repeated if participants struggled to perform the task (e.g., they did not correctly handle the controllers while responding or if the synchronicity level was repeatedly below 75). The familiarization was completed before the resting-state measure in order to reduce arousal effects which can be triggered by the initial VR immersion. Familiarization at T2 concerned the biofeedback procedure and was skipped in the CG. The biofeedback procedure was explained to the participants who then exercised HRV biofeedback under guidance of the experimenter until noticeable increases in cardio-respiratory synchrony and heart rate amplitudes were achieved for at least one minute.

2.2.7 Task control measures

Further control variables assessed directly after each DRM-test using a computerized visual analogue scale of 0-10 were the levels of perceived fatigue during the task (0 being “no fatigue”, 10 being “extreme fatigue”), interference of fatigue with concentration during the task (0 being “no interference”, 10 being “extreme interference”), difficulty to adapt the breathing during the exercise (0 being “not difficult”, 10 being “extremely difficult”), and attention to the task at encoding as well as recognition (0 being “not attentive at all”, 10 being “extremely attentive”). Moreover, the level of total presence in the VR and the degree of cybersickness (focus and dizziness) during the task were assessed by the Igroup Presence Questionnaire (IPQ; Schubert et al., 2001) and the 9-items Cybersickness Questionnaire (CSQ; Stone III, 2017). Finally, critical lure awareness was assessed by asking participants from which moment on they were aware that critical lures were implemented in the memory task (“before recognition in the first test”, “during recognition in the first test”, “before recognition in the second test”, “during recognition in the second test”, “after both tests”).

2.3 Physiological data processing

Physiological recordings were manually inspected, and artefacts removed using AcqKnowledge 5.0.4 Software (BIOPAC Systems, Inc., 2019). Recordings were then divided within each phase (i.e., baseline, pre-encoding, encoding, pre-recognition, recognition) into equally long non-overlapping segments of 150 seconds. Segments of the electrocardiogram and respiration amplitude were individually processed with the Python package NeuroKit2 (Makowski et al., 2021) at default settings, unless otherwise specified. Preprocessing included a Butterworth high pass filter at of 0.5

1
2 400 Hz as well as a notch filter at 50 Hz for the electrocardiogram and a bandpass filter of 0.05 – 1 Hz for
3 401 the respiration amplitude. Artefacts in the heart period signal were detected and corrected as
4 402 described by Lipponen & Tarvainen (2019). The root mean square successive difference in the heart
5 403 period series (RMSSD) was assessed as a measure of vmHRV following guidelines of Shaffer &
6 404 Ginsberg (2017) and the Task Force of the European Society of Cardiology and the North American
7 405 Society of Pacing and Electrophysiology (1996). Furthermore, the mean heart rate as well as the
8 406 mean respiration rate and mean respiration amplitude were derived as control variables. Further
9 407 information on the processing can be found in the NeuroKit2 documentation (Makowski, 2023).
10 408 Phase means were calculated per test. Consequently, for each phase at least two 150 seconds
11 409 segments were averaged. The complete physiological data set of a participant was excluded in the
12 410 case of a potential arrhythmia (i.e., proportion of ectopic beats to total beats >2%, average heart rate
13 411 <40 bpm or >100 bpm at both resting-state measures). Segments were excluded whenever R peaks
14 412 could not be properly detected or corrected (i.e., large and unexpected spikes in the heart rate signal).
15 413 From a total of 2059 segments, 2024 were included for the final analysis. 32 (i.e., 2 complete T2
16 414 recordings) were excluded due to technical problems during data saving and 3 due to R peak
17 415 correction failures. Finally, RMSSD values were transformed with the natural logarithm due to
18 416 violation of the normality assumption.

22 417 2.4 Cognitive control over memory

23
24 418 Scores of memory discrimination performance (d') and correct confidence (CC) were determined as
25 419 proxies of cognitive control over memory from the memory responses per subject and test. d' reflects
26 420 memory retrieval success that is free from response bias whereas CC approximates metamemory
27 421 (i.e., meta-awareness of own memory processes). Both scores were determined for critical lures and
28 422 distractors separately as the performance to discriminate targets from critical lures (d'_{critical}) or
29 423 distractors ($d'_{\text{distractor}}$) and the correct confidence score when responding to critical lures (CC_{critical}) or
30 424 distractors ($CC_{\text{distractor}}$). It is supposed that differences in cognitive control over memory will
31 425 specifically affect d'_{critical} and CC_{critical} because the correct and confident detection of critical lures
32 426 (i.e., avoiding false memories) compared to distractors requires a stronger engagement of cognitive
33 427 control. Therefore, d'_{critical} and CC_{critical} were the primary behavioral variables of the investigation.

34
35 428 Before computation, trials were dropped that contained either a missing recognition or confidence
36 429 response (i.e., time limit surpassed before response choice). The capability of discriminating targets
37 430 from distractors and targets from lure items was calculated based on signal detection theory as the
38 431 sensitivity index d' (Pallier, 2002). d' is the difference in the normal z-score distribution Z of
39 432 correctly recognized old items (hits) and wrongly recognized new items (false alarms), ($d' = Z_{\text{hit}} -$
40 433 $Z_{\text{false alarm}}$). Furthermore, CC was calculated from normalized confidence ratings following true
41 434 responses ($conf_T$) and false responses ($conf_F$) where n_T and n_F represent the number of true or
42 435 false responses, respectively:

$$43 436 \left(CC = \frac{\sum_{i=0}^{n_T} conf_{Ti} - \sum_{i=0}^{n_F} conf_{Fi}}{(n_T + n_F) * 2} + \frac{1}{2} \right)$$

44
45
46
47
48
49 437 In this context, CC is the normalized difference between true and false response number weighted by
50 438 the confidence which takes values from 0 (only completely confident false responses) to 1 (only
51 439 completely confident correct responses). Scores of two tests at T2 had to be excluded due to technical
52 440 problems during data saving.

2.5 Data analyses

The analysis was carried out with R 4.2.1 (R Core Team, 2022). Interference was based on the standard $p < .05$ criteria. All tests were two-tailed. The post-hoc Benjamini-Hochberg false discovery rate (FDR)-controlling procedure at $\alpha = 0.05$ adjusted for multiple comparisons. Uncorrected p -values are reported. Results that were significant after p -value correction were marked ($*p < .05$, $**p < .01$, $***p < .001$). Factor effect sizes were reported as partial eta-square values and interpreted as small, medium, and large for values of 0.01, 0.06, and 0.14, respectively (Cohen, 1988). Effect sizes derived from contrasts were based on the on Cohen's d and were interpreted as small, medium, and large for scores of 0.2, 0.5, and 0.8 (Cohen, 1988). Reference conditions were T1 for the test factor, CG for the group factor, and baseline (or encoding if baseline was excluded) for the phase factor.

2.5.1 Biofeedback effect

Behavioral and physiological variables were analyzed based on linear mixed effect models using the afex package 1.3.0 (Singmann et al., 2023). These models included the group (BG, CG) x test (T1, T2) factors and allowed for random coefficients across subjects. Degrees of freedom were determined using the Satterthwaite approach and restricted maximum likelihood model to increase Type-1 error control (Luke, 2017). The biofeedback effect on each variable was assessed as the group x test interaction effect. Estimated marginal means and 95% confidence intervals per group and test are reported.

Task control measures. Variables were analyzed separately, and main and interaction effects are reported. Additionally, T1 scores were contrasted between groups.

Baseline differences and manipulation check. To test further group differences that were present before the manipulation, RMSSD, heart rate, respiration rate, and respiration amplitude were analyzed separately at the T1 only. Linear mixed effect models including group (BG, CG), and phase (resting-state, pre-encoding exercise, encoding, pre-recognition exercise, recognition) as predictor variables were applied. Furthermore, a manipulation check was conducted by analyzing RMSSD during the exercise. RMSSD was grouped by phase (pre-encoding exercise, pre-recognition exercise) which was included as a factor in the model. The manipulation was considered successful if at least moderate interaction effect could be observed.

Heart rate variability. RMSSD scores measured during memory processing were investigated. RMSSD was grouped by phase (encoding, recognition) which was included as a factor in the model. The biofeedback effect on RMSSD and its interaction with phase was investigated. T1 scores were contrasted to T2 scores in each group and phase.

Cognitive control over memory. The biofeedback effect on d'_{critical} , CC_{critical} , $d'_{\text{distractor}}$, $CC_{\text{distractor}}$ was determined. In case a significant interaction was detected, scores at T1 and T2 were contrasted within each group.

2.5.2 Psychophysiological analysis

H1) Executive functions. To test the hypothesis H1) correlations were performed between resting-state RMSSD at T1 and executive functions (i.e., digit span standard score, Stroop global interference score) using the Pearson approach.

H4) Correlation Analysis. To check for correlations between physiological and behavioral measures and potential confounders in the following mediation analysis a heatmap representing Pearson

482 correlations was created (tests combined). Significance was tested for correlations between memory
 483 measures concerning critical lures (d'_{critical} , CC_{critical}) and RMSSD during the resting-state and
 484 memory processing phases ($RMSSD_{\text{baseline}}$, $RMSSD_{\text{encoding}}$, $RMSSD_{\text{recognition}}$). Hypothesis H4) was
 485 considered confirmed if d'_{critical} or CC_{critical} correlated with $RMSSD_{\text{baseline}}$ and $RMSSD_{\text{encoding}}$ or
 486 $RMSSD_{\text{recognition}}$.

487 *H5) Mediation Analysis.* The mediation of the test effect on primary memory variables (d'_{critical} and
 488 CC_{critical}) via $RMSSD_{\text{encoding}}$ and $RMSSD_{\text{recognition}}$ was tested for both dependent variables separately.
 489 $RMSSD_{\text{baseline}}$ was additionally added to control for baseline variations. Since scores of RMSSD
 490 largely correlated between phases, they were included as three distinct mediators in the same model.
 491 Moreover, fatigue interference assessed after each task was included as a covariate. Mediation
 492 analysis was performed based on structured equation models using the lavaan 0.6.15 package
 493 (Rosseel, 2012) allowing for covariance between mediators. All variables except the dependent
 494 variable were standardized before model entry. We tested the significance of direct and indirect
 495 effects using bootstrapping procedures. Standardized effects were computed for each of 2000
 496 bootstrapped samples, and the 95% confidence interval was computed by determining the effects at
 497 the 2.5th and 97.5th percentiles. Rows with missing values were dropped before analysis. In total,
 498 138 out of 142 samples were included.

499 3 Results

500 3.1 Sample characteristics and task control measures

501 Table 1 – Sample characteristics

502 *Note.* Mean values and standard deviations are presented per group. Groups were compared using
 503 Student's t-test if not indicated otherwise. If applicable, units or the scale range are given in
 504 parentheses after each variable. Uncorrected p-values are reported.

505 ^a The variable is not normally distributed. The median, inter-quartile-range (in parenthesis) and
 506 results of the Mann-Whitney U test are reported.

507 ^b Groups were compared using the Fisher's Exact test.

508 ^c A smaller value indicates greater cognitive inhibition.

Variable	Mean values		Group comparison			
	Biofeedback Group (<i>n</i> = 35)	Active Control Group (<i>n</i> = 36)	Estimate	Statistic	<i>p</i>	Effect size
Demographics						
Age (years) ^a	22.14 (4.19)	24.26 (10.71)	1.342	710	0.236	0.142
Sex (% female) ^b	57.1%	66.7%	0.671	-	0.469	-
Laterality (% right-handed) ^b	94.3%	97.2%	2.100	-	0.614	-
Psychology students (%) ^b	37.1%	36.1%	0.957	-	0.999	-
Higher education (years)	3.37 (1.83)	3.53 (2.42)	-0.153	-0.306	0.760	-0.073
Compensation (% course credits) ^b	17.1%	16.7%	1.034	-	0.999	-
Neuropsychological assessment						
State Anxiety – STAI-Y1 (20-80)	30.54 (6.81)	29.31 (6.07)	1.237	0.809	0.421	0.192
Trait Anxiety – STAI-Y2 (20-80)	39.47 (8.48)	37.83 (9.41)	1.637	0.763	0.448	0.183
Inhibition – Stroop global interference score ^c	7.91 (8.90)	8.03 (8.35)	-0.116	-0.057	0.955	-0.014

Autonomic and cognitive control in memory

Working Memory – Digit span standard score (1-19)	12.71 (3.60)	12.83 (3.40)	-0.123	-0.146	0.885	-0.035
Medical and physiological aspects						
New Body-Mass-Index	21.26 (2.26)	23.34 (3.34)	-2.084	-3.069	0.003	-0.728
Sport activity (hours/week) ^a	2.00 (2.50)	3.00 (3.25)	0.500	732	0.237	0.141
Smoking status ^b			1.246	-	0.999	-
Abstainers / Very light smokers (%)	88.6%	86.1%				
Light and moderate smokers (%)	11.4%	13.9%				
Heavy smokers (%)	0%	0%				
Alcohol consumption ^b			0.953	-	0.999	-
Abstainers / Light drinkers (%)	57.1%	58.3%				
Moderate drinkers (%)	42.9%	41.7%				
Heavy drinkers (%)	0%	0%				
Hormonal contraception (%) ^b	20.0%	16.7%	0.803	-	0.767	-
Controlled breathing (% some expertise) ^b	20.0%	22.2%	1.141	-	0.999	-
Sleep deprivation last night (hours)	-0.77 (1.42)	-1.16 (1.31)	0.391	1.206	0.232	0.286
Current fatigue (0-10) ^a	3.00 (3.75)	3.00 (1.25)	0.000	624	0.891	0.017
Fatigue interference (0-10) ^a	2.00 (4.00)	2.00 (4.00)	0.000	695.5	0.322	0.119
Current pain (0-10) ^a	0.00 (0.00)	0.00 (0.00)	0.000	576	0.560	0.071
Pain interference (0-10) ^a	0.00 (0.75)	0.00 (0.00)	0.000	529.5	0.167	0.166
Current feeling of sickness (0-10) ^a	0.00 (1.00)	0.00 (1.00)	0.000	604.6	0.920	0.013
Feeling of sickness interference (0-10) ^a	0.00 (0.75)	0.00 (0.00)	0.000	529.5	0.167	0.166

Table 2 – Task control measures

Note. Results of the linear mixed effect models per control variable are reported. Test scores in each group are described by estimated marginal means and their 95% confidence interval (in square brackets). The scale range are given in parentheses after each variable. Uncorrected p-values are reported. Only the main test effect on breathing difficulty was significant before and after FDR-adjustment ($p < .05$).

Variable	Estimated marginal means				Linear mixed effect model					
	Biofeedback group		Control group		Group	Test	Group:Test	p	η_p^2	
	T1	T2	T1	T2						
Attention _{Encoding} (0-10)	6.58 [5.85, 7.30]	6.82 [6.03, 7.61]	6.67 [5.97, 7.36]	6.25 [5.49, 7.01]	.587	.004	.768	.009	.266	.018
Attention _{Recognition} (0-10)	7.58 [6.94, 8.21]	7.58 [6.80, 8.35]	7.61 [7.00, 8.22]	6.83 [6.09, 7.58]	.387	.011	.170	.028	.170	.028
IPQ total score (0-6)	3.11 [2.77, 3.46]	2.96 [2.59, 3.34]	3.32 [2.99, 3.65]	3.10 [2.74, 3.46]	.460	.008	.055	.054	.712	.002
Fatigue after test (0-10)	5.62 [4.83, 6.41]	5.97 [5.16, 6.78]	5.97 [5.20, 6.74]	6.17 [5.38, 6.95]	.592	.004	.232	.021	.728	.002
Fatigue interference (0-10)	5.35 [4.44, 6.27]	5.35 [4.47, 6.24]	5.50 [4.61, 6.39]	5.61 [4.75, 6.47]	.724	.002	.830	<.001	.830	<.001
Breathing difficulty (0-10)	4.32 [3.57, 5.08]	5.44 [4.58, 6.30]	4.56 [3.82, 5.29]	5.22 [4.39, 6.06]	.989	<.001	.003*	.123	.437	.009
CSQ dizziness (0-11.28)	0.87 [0.45, 1.29]	1.06 [0.523, 1.60]	1.04 [0.637, 1.44]	1.40 [0.890, 1.92]	.390	.011	.075	.047	.568	.005

CSQ focus (0-8.49)	2.87 [2.22, 3.53]	2.55 [1.92, 3.18]	2.78 [2.15, 3.40]	2.91 [2.31, 3.51]	.744	.002	.643	.003	.260	.019
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Groups did not significantly differ for any of the demographic, medical, psychological, and lifestyle measures except for the level of the new Body Mass Index which was lower in the BG (Table 1). The new Body Mass Index was not associated with resting-state measures at T1 of RMSSD, $r = .12$, $p = .308$, or heart rate, $r = -.07$, $p = .542$. Also, none of the task control measures differed between groups at T1 or exhibited any main group or group x test interaction effects (Table 2). A moderate-to-large test effect was observable only on the breathing difficulty which increased from T1 to T2. Moreover, chi-square analysis showed that there was no group difference in critical lure awareness, $\chi^2(2) = 0.07$, $p = .956$ (supplementary results SR1).

3.2 Biofeedback effects

3.2.1 Baseline differences and manipulation check

At T1, there was no main group effect neither on respiration rate, $F(1,69) = 0.23$, $p = .633$, $\eta_p^2 = .003$, nor on respiration amplitude, $F(1,69) = 0.37$, $p = .544$, $\eta_p^2 = .005$ (Figure 3). However, there was a significant group effect on RMSSD, $F(1,69) = 6.22$, $p = .015$, $\eta_p^2 = .083$, and a trending effect on heart rate, $F(1,69) = 3.19$, $p = .078$, $\eta_p^2 = .044$. For none of the variables the group and phase factors interacted significantly. Post-hoc group comparison showed large group differences in RMSSD in all phases $d = [1.08, 1.76]$ as well as in heart rate in all phases, $d = [-1.84, -1.30]$.

A correct manipulation of RMSSD during the exercise phases (i.e., pre-encoding, pre-recognition) could be confirmed by a large group x test interaction effect $F(1,67) = 19.30$, $p < .001$, $\eta_p^2 = .224$. This effect was not significantly dependent on the phase, $F(1,67) = 3.18$, $p = .079$, $\eta_p^2 = .045$.

3.2.2 H2) vmHRV

For RMSSD during the memory processing phases (i.e., encoding, recognition), neither a group x test interaction effect, $F(1,67) = 0.44$, $p = .508$, $\eta_p^2 = .007$, nor a group x test x phase interaction effect, $F(1,67) = 0.86$, $p = .357$, $\eta_p^2 = .013$, was present. RMSSD increased between tests for the encoding phase in the BG, $p < .001$, $d = 1.030$, and in the CG, $p < .001$, $d = 1.053$. RMSSD increased also for the recognition phase in the BG, $p = .003$, $d = 0.771$, but not in the CG, $p = .080$, $d = 0.418$.

3.2.3 H3) Cognitive control over memory

There was no group x test interaction effect on any of the memory scores (Figure 4). Furthermore, no main group effects ($ps > .499$, $\eta_p^2 < 0.01$) were present. A main test effect was found only on $d'_{\text{distractor}}$, $F(1,67) = 5.29$, $p = .025$, $\eta_p^2 = .073$ such that it increased from the first to the second task, whereas d'_{critical} , $F(1,67) = 2.03$, $p = .159$, $\eta_p^2 = .029$, CC_{critical} , $F(1,67) = 0.58$, $p = .447$, $\eta_p^2 = .009$, and $CC_{\text{distractor}}$, $F(1,67) = 0.91$, $p = .343$, $\eta_p^2 = .013$, did not change between tests. A complete list of the effects and estimated marginal means for all memory variables is provided in the supplementary results SR2.

3.3 Psychophysiological results

3.3.1 H1) Executive functions and resting-state vmHRV

Resting-state RMSSD correlated neither with the digit span standard score ($r = -.064$, $p = .604$) nor with the Stroop global interference score ($r = .099$, $p = .411$).

1
2 554 **3.3.2 H4) Cognitive control over memory and vmHRV**

3
4 555 d'_{critical} and CC_{critical} did not correlate with RMSSD, neither during memory processing (encoding or
5 556 recognition) nor at baseline (Figure 5). Fatigue interference showed weak associations with memory
6 557 scores and was thus included as a covariate in the mediation model.

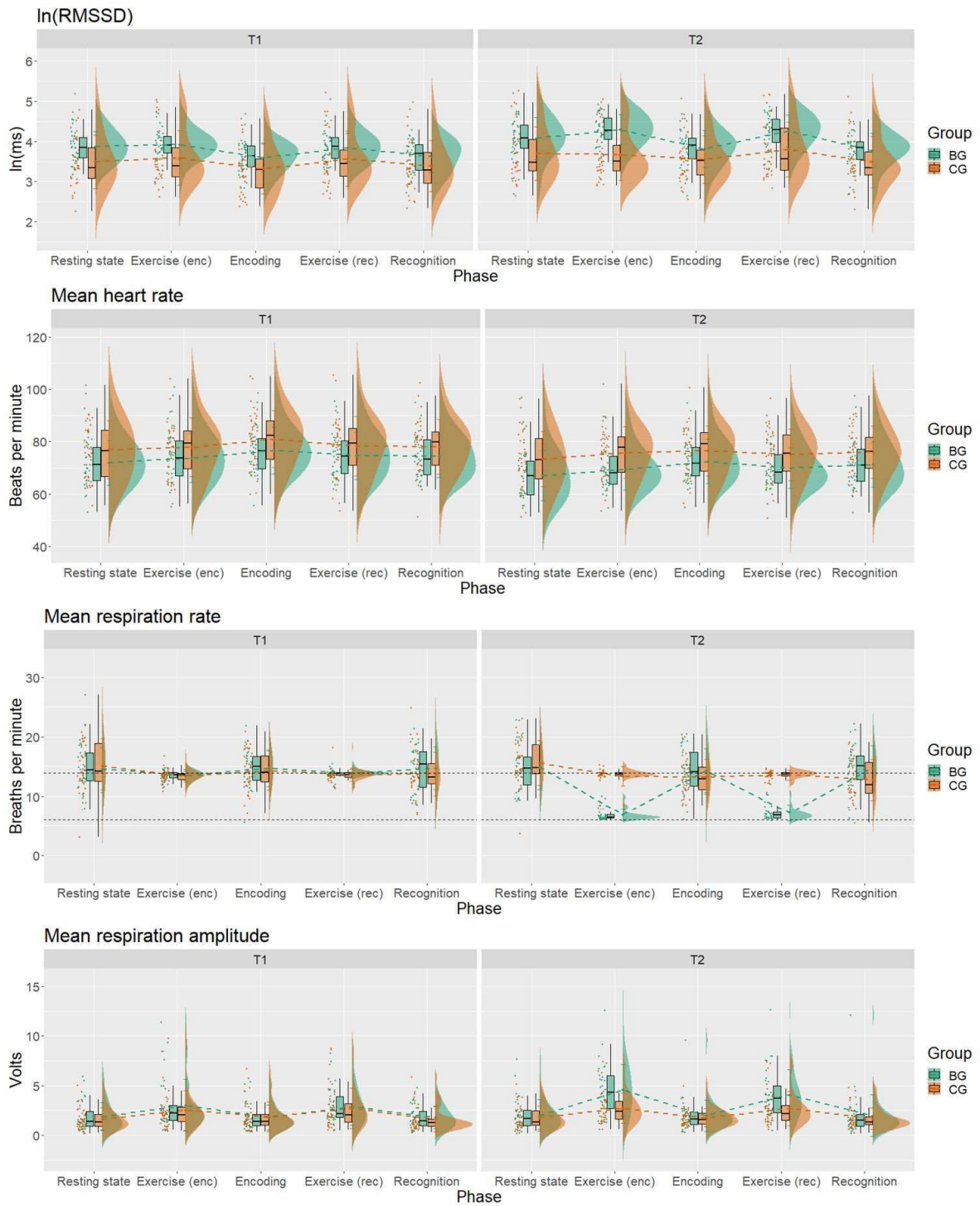
7
8 558 **3.3.3 H5) Mediation analysis**

9
10 559 The effect of test on d'_{critical} (A) or CC_{critical} (B) was not mediated via $RMSSD_{\text{encoding}}$ or
11 560 $RMSSD_{\text{recognition}}$. As Figure 6 illustrates, the regression coefficients between test and d'_{critical} or
12 561 CC_{critical} and the regression coefficients between $RMSSD_{\text{encoding}}$ or $RMSSD_{\text{recognition}}$ and memory
13 562 scores were not significant.
14
15
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46 **Figure 3 – Physiological responses**

47 *Note.* Cardiac and respiratory measures shortly before (i.e., resting-state) and during the memory
48 discrimination task per test are shown. Dashed colored lines represent mean values. During the exercise
49 phases in both tests both groups practiced variable breathing as a control exercise except the BG which
50 exercised HRV biofeedback during T2. HRV biofeedback compared to variable breathing increased RMSSD
51 during the exercise but did not affect RMSSD during subsequent encoding or retrieval. Moreover, large
52 groups differences in RMSSD and mean heart rate were already present at T1. The breathing rate and
53 breathing amplitude did not differ between groups at T1. Moreover, the measures confirmed that participants
54 followed the exercises correctly. Firstly, respiration rates were near the mean target values of 6 and 14 cycles
55 per minute (i.e., dashed black line) during HRV biofeedback and variable breathing, respectively. Secondly,
56 HRV biofeedback evoked stark increases in respiration amplitude.
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Autonomic and cognitive control in memory

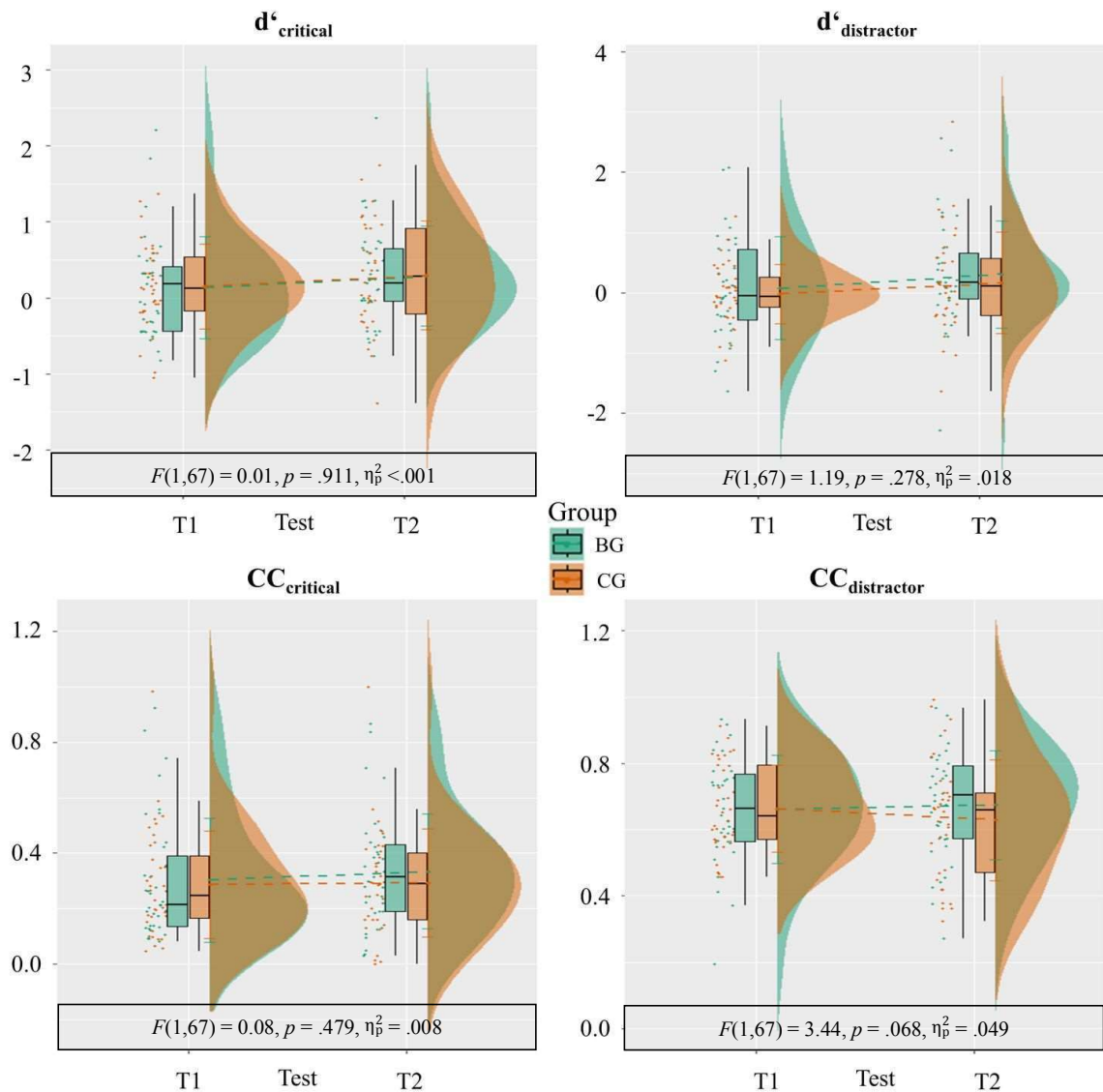


Figure 4 – Long-term memory results

Note. Memory performance was assessed as the capability to discriminate target items from semantically related critical lures (A) or from unrelated distractors (B) as well as the confidence in the correct choice towards critical lures (C) and distractors (D). Critical lures are likely to induce false memories and therefore required greater cognitive control over memory to be detected among target items. Results of the group-by-test interaction effect are depicted at the bottom of each graph. None of the interactions effects was significant before FDR-adjustment. Therefore, HRV biofeedback had no immediate effect on long-term memory performance, neither when a high nor when a lower level of cognitive control was required during memory processing.

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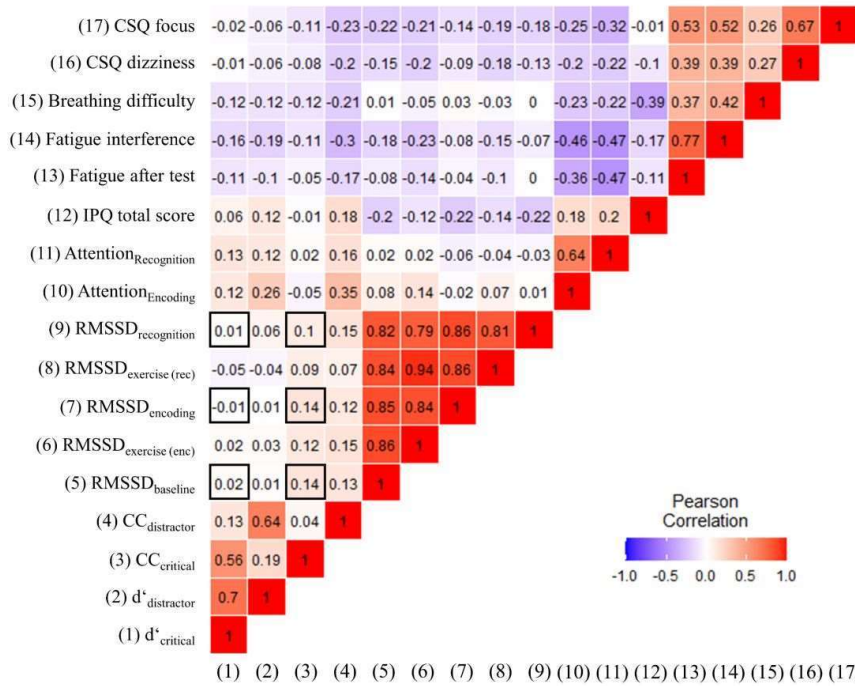


Figure 5 – Correlation Heatmap

A correlation matrix depicting Pearson correlation coefficients was generated including all memory scores, task control variables as well RMSSD measures of the different phases. Measures were pooled from both tests. Correlations were tested between measures of cognitive control over memory and RMSSD at baseline, encoding or recognition (highlighted values). None of these was significant before ($p \geq .096$) or after FDR-adjustment.

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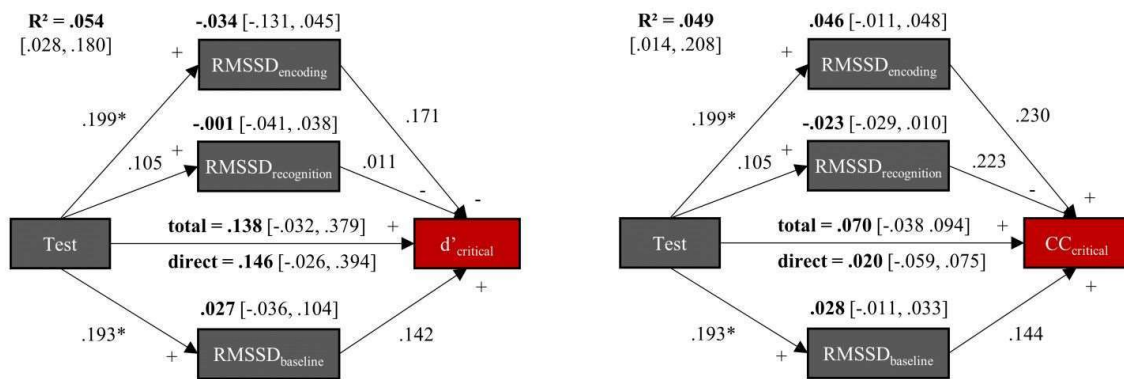


Figure 6 – Indirect test effect via vmHRV on cognitive control over memory

Note. The indirect test effect (in bold) on the memory scores $d^*_{critical}$ and $CC_{critical}$ via RMSSD at resting-state (baseline), encoding, and recognition was tested using separate structured equation models for the memory variables. Values depict standardized coefficients. 95% CI are given in squared brackets. RMSSD at none of the phases mediated the differences between the first and the second test on $d^*_{critical}$ or $CC_{critical}$. Model fit performance was good for both models, $df = 3$, $\chi^2 = 14.403^{**}$, RMSEA = 0.166, CFI = 0.963, SRMR = 0.069. $**p < .01$, $*p < .05$.

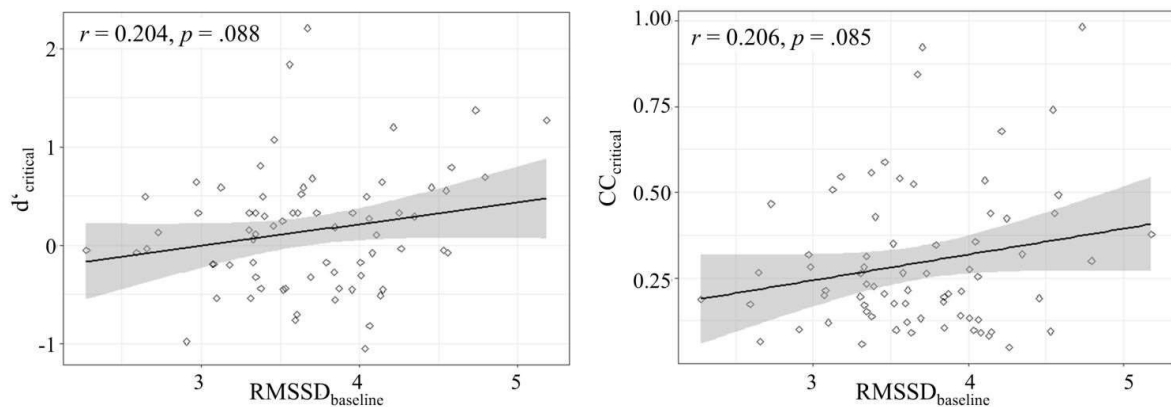
566 4 Exploratory Analysis

567 4.1 Overview

568 As levels of cardiac measures notably shifted from T1 to T2 across groups, the test effect on the
 569 psychophysiological relationship was checked. Moreover, as intended in the pre-registration, the
 570 relationship between cognitive control over memory and vmHRV reactivity was explored because
 571 reactivity values (i.e., change from baseline to a specific event such as memory encoding or retrieval)
 572 might provide crucial information beyond resting-state measures (Laborde et al., 2018; Magnon,
 573 Duthiel, et al., 2022; Porges, 2007). Finally, the joint association of vmHRV reactivity and heart rate
 574 reactivity with long-term memory performance was examined.

575 4.2 The psychophysiological relationship between tests

576 Contrary to our assumption, no correlation between cognitive control over memory and vmHRV
 577 could be confirmed. Because baseline cardiac activity changed over time and correlations were
 578 obtained from pooled data (T1 and T2) we assumed that the psychophysiological relationship
 579 between repeated measurements was not stable, which obscured previous results. Thus, correlations
 580 were determined for T1 and T2 separately (supplementary results SR3). It is notable that correlations
 581 between memory variables and $RMSSD_{baseline}$ changed in every instance from positive (T1) to
 582 negative (T2). Linear mixed effect regressions models confirmed a significant test effect on the
 583 relationship between $RMSSD_{baseline}$ and $d'_{critical}$, $F(1, 74.2) = 5.91, p = .017$, as well as between
 584 $RMSSD_{baseline}$ and $d'_{distractor}$ $F(1, 70.1) = 4.81, p = .032$. Similar results were found when including
 585 $RMSSD_{encoding}$ or $RMSSD_{recognition}$ ($ps = [.062, .102]$). No test effect was found for $CC_{distractor}$ or
 586 $CC_{critical}$ ($ps > .380$). Furthermore, temporal changes in correlations were not related to differences in
 587 the experimental condition, as there were no significant group-by-test interaction effects or main
 588 group effects that moderated the relationship between $RMSSD$ and memory variables. Trending
 589 correlations could be found at T1 when linking $RMSSD_{baseline}$ with $d'_{critical}$ and $CC_{critical}$ (Figure 7).
 590 Otherwise, none of the correlations between $RMSSD$ and memory variables was significant, neither
 591 at T1 ($ps > .150$) nor at T2 ($ps > .162$).



592 **Figure 7 – Correlations at the first test (T1)**

593 *Note.* Correlations between $RMSSD$ and measures of cognitive control over memory were determined for each
 594 test separately. Considering only results of the first test for the association between vmHRV and cognitive
 595 control provides best comparability with previous studies as these did not include repeated measures and
 596 correlations greatly changed here between measures. Trending correlations could be observed between
 597 $RMSSD_{baseline}$ and $d'_{critical}$ as well as between $RMSSD_{baseline}$ and $CC_{critical}$ when considering scores at the first test
 598 only.

1 2 592 **4.3 vmHRV reactivity** 3

4 593 Investigating the reactivity of cardiac vagal control has been proposed to provide valuable insights
5 594 into neurophysiological and behavioral self-regulation (Laborde et al., 2018). In this context, Laborde
6 595 et al. (2018) conceptualized the Vagal Tank Theory, a framework based on the polyvagal theory
7 596 (Porges, 2007) and neurovisceral integration model (Thayer et al., 2009), that proposes the change in
8 597 cardiac vagal control between a baseline and a specific event (i.e., reactivity) reveals self-regulatory
9 598 processes that cannot be observed by studying resting-states alone. The authors argue that the
10 599 reactivity reflects the effectiveness of the self-regulation mechanisms depending on the level of
11 600 physical activity and executive control required in response to the environment. It is predicted that in
12 601 situations with low activity and high executive demand that smaller vagal withdrawal (or increase) is
13 602 adaptive. It can be inferred that such smaller vagal withdrawal (or increase) would be linked to better
14 603 executive control when changes in energy demand are equal. Therefore, the investigation was
15 604 extended by an exploration of the relationship between vmHRV reactivity and cognitive control over
16 605 memory. Moreover, temporal baseline changes as well as large group differences at baseline for
17 606 scores of mean heart rate and RMSSD were found. Motivated by the reactivity approach and to
18 607 accommodate for within- and between-subjects variations in baseline vmHRV, baseline adjusted
19 608 reactivity were calculated for raw scores of RMSSD (RMSSD*). Resting-state measures before each
20 609 test were taken as the baseline for the respective test. RMSSD* was calculated per participant for the
21 610 encoding (RMSSD*_{encoding}) and recognition (RMSSD*_{recognition}) phases as the ratio of the encoding to
22 611 the baseline and recognition to the baseline, respectively. In this context, values below 1 indicate a
23 612 decrease (vagal withdrawal) and values above 1 an increase (vagal activation) in RMSSD relative to
24 613 the baseline. This approach provides the advantage that firstly it reduces effect due to variations in
25 614 baseline. Secondly, it eliminates the problem of different scales and differing measurement units
26 615 when including reactivity values of varying metrics in the same statistical model. It was hypothesized
27 616 that vmHRV reactivity would be positively associated to cognitive control over memory at encoding,
28 617 recognition or at both phases.

33 34 618 **4.4 Heart rate reactivity**

35 619 When interpreting measures of cardiac vagal control, the cardiac chronotropic state (i.e., mean heart
36 620 rate or heart period) has to be considered as it influences all conventional metrics of HRV (de Geus et
37 621 al., 2019; Shaffer & Ginsberg, 2017). Higher heart rates decrease vmHRV and lower heart rates
38 622 increase vmHRV; an effect that is known as the cycle length dependence. The presence of a strong
39 623 negative correlation between RMSSD and heart rate could also be seen in the data here
40 624 (supplementary results SR3). Though mean heart rate and vmHRV are directly related because both
41 625 underly the influence of the vagal nerve, they are no surrogate measures. Heart rate is also affected
42 626 by sympathetic activity and the presence of a non-vagal influence of the heart rate on vmHRV can
43 627 hitherto not be ruled out. Therefore, it was suggested to adjust the vmHRV for heart rate (de Geus et
44 628 al., 2019). In addition, heart rate values could provide further insight about sympatho-vagal balance.
45 629 Thus, scores of baseline adjusted heart rate reactivity (HR*) were calculated in the same manner as
46 630 RMSSD*. This transformation seemed not to have changed the relationship between vmHRV and
47 631 heart rate because similar large negative correlations between HR* and RMSSD* could be observed
48 632 at each phase (supplementary results SR3). Contrary, whereas T1 and T2 scores of vmHRV and heart
49 633 rate were highly correlated between tests, they were not for RMSSD* and HR*. This indicates that
50 634 reactivity values are much more sensitive to within-subjects variations in autonomic regulation than
51 635 state measures of RMSSD. Reactivity graphs are provided in the supplementary results SR4)

4.5 Biofeedback effect on cardiac reactivity

The biofeedback effect was tested on HR* and on RMSSD* controlling for HR* (adding as covariate) using linear mixed effect models including the group, test, and phase factors. All factors had a main effect on HR*: group, $F(1, 70) = 4.93, p = .030$; test, $F(1, 206) = 10.55, p = .001$; and phase, $F(1, 204) = 17.64, p < .001$. No interaction effect was present between group and test, $F(1, 70) = 0.62, p = .433, \eta_p^2 = .009$, or any other interaction except of the test-by-phase combination. Post hoc comparison showed that HR* increased among groups from T1 to T2 only for the recognition phase, $t(205) = 3.72, p < .001, d = 0.63$, but not for encoding phase, $t(205), p = .377, d = 0.15$.

After adjusting for HR* (adding as covariate), a significant group-by-test interaction effect on RMSSD* could be found, $F(1, 205) = 8.44, p = .004$. This interaction was not dependent on the phase, $F(1, 203) = 0.10, p = .754$. Contrasts between tests per group showed (phase levels collapsed) a significant increase in RMSSD* in BG $t(208) = 2.70, p = .008, d = 0.47 [0.11, 0.82]$ but not in CG $t(206) = -1.37, p = .173, d = -0.23 [-0.57, 0.11]$. No main test effect $F(1, 208) = 0.93, p = .336$ or main group effect, $F(1, 71) = 0.13, p = .719$ was present. However, there was a main phase effect showing that HR*-adjusted RMSSD* was lower during recognition than encoding, $t(209) = -2.67, p = .008, d = -0.33$. When adding fatigue interference as covariate to the models, neither did this directly affect HR* or RMSSD* nor did it notably change the above-described results.

4.6 Adjustment for heart rate reactivity

Analogous to the previous mediation analysis, structural equation models were fitted to predict memory outcomes using HR* and RMSSD* as sole or joint predictors (Table 3). When adjusting vmHRV reactivity for heart rate reactivity large model fit improvements could be observed for d'_{critical} and CC_{critical} at recognition only. $d'_{\text{distractor}}$ and $CC_{\text{distractor}}$ prediction improved at encoding only. Adding subjective attention did not notably reduce regression coefficients of HR* and RMSSD*. Detailed information on joint predictions for all memory variables are listed in the supplementary results SR5.

Table 3 - Effects of adjustment for heart rate reactivity adding it as a second predictor on the association between vmHRV reactivity and long-term memory

Note. The association between cardiac reactivity at encoding or retrieval and memory performance involving high (critical) or low (distractor) levels of cognitive control over memory was tested using separate structured equation models for the memory variables and phases (see Figure 8). Different models were built based on predictions by heart rate reactivity only and RMSSD reactivity only, as well as on their joint prediction. In addition, the effect of subjective attention to the task during the memory phases was controlled by adding it as a third mediator to the model. Memory performance based on the discrimination and metamemory of critical lures was best predicted by parallel effects of heart rate reactivity and RMSSD reactivity at recognition whereas memory performance based on distractors was best predicted by parallel effects at encoding. Though attention was significantly linked to distractor discrimination and metamemory, it did not influence the relationship between memory performance and cardiac reactivity. All models showed good performance (supplementary results SR5).

*** $p < .001$, ** $p < .01$, * $p < .05$.

Variable		Encoding ($n = 138$)			Recognition ($n = 138$)		
		Standardized coefficient	p	R^2	Standardized coefficient	p	R^2
d'_{critical}	Model 1: HR* sole predictor	$\beta_{\text{HR}^*} = 0.107$.195	.054	$\beta_{\text{HR}^*} = 0.199^*$.017	.074
	Model 2: RMSSD* sole predictor	$\beta_{\text{RMSSD}^*} = 0.005$.954	.046	$\beta_{\text{RMSSD}^*} = 0.060$.468	.054
	Model 3: Attention sole predictor	$\beta_{\text{Attention}^*} = 0.056$.501	.056	$\beta_{\text{Attention}^*} = 0.077$.361	.077

	Model 4: HR* & RMSSD* joint predictors	$\beta_{HR^*} = 0.178$ $\beta_{RMSSD^*} = 0.115$.091 .273	.065	$\beta_{HR^*} = 0.333^{**}$ $\beta_{RMSSD^*} = 0.238^*$.001 .014	.121
	Model 5: HR* & RMSSD* & Attention joint predictors	$\beta_{HR^*} = 0.173$ $\beta_{RMSSD^*} = 0.117$ $\beta_{Attention^*} = 0.042$.103 .268 .609	.062	$\beta_{HR^*} = 0.338^{**}$ $\beta_{RMSSD^*} = 0.247^{**}$ $\beta_{Attention^*} = 0.111$.001 .011 .167	.123
$d'_{distractor}$	Model 1: HR* sole predictor	$\beta_{HR^*} = 0.199^*$.016	.057	$\beta_{HR^*} = -0.028$.746	.025
	Model 2: RMSSD* sole predictor	$\beta_{RMSSD^*} = 0.039$.647	.027	$\beta_{RMSSD^*} = 0.146$.078	.054
	Model 3: Attention sole predictor	$\beta_{Attention^*} = 0.294^{***}$	<.001	.092	$\beta_{Attention^*} = 0.069$.415	.069
	Model 4: HR* & RMSSD* joint predictors	$\beta_{HR^*} = 0.358^{**}$ $\beta_{RMSSD^*} = 0.261^*$.001 .011	.104	$\beta_{HR^*} = 0.076$ $\beta_{RMSSD^*} = 0.187$.459 .063	.053
$CC_{critical}$	Model 5: HR* & RMSSD* & Attention joint predictors	$\beta_{HR^*} = 0.335^{**}$ $\beta_{RMSSD^*} = 0.261^{**}$ $\beta_{Attention^*} = 0.272^{**}$.001 .009 .001	.151	$\beta_{HR^*} = 0.098$ $\beta_{RMSSD^*} = 0.192$ $\beta_{Attention^*} = 0.078$.205 .056 .351	.049
	Model 1: HR* sole predictor	$\beta_{HR^*} = 0.029$.734	.017	$\beta_{HR^*} = 0.219^{**}$.009	.057
	Model 2: RMSSD* sole predictor	$\beta_{RMSSD^*} = 0.032$.707	.019	$\beta_{RMSSD^*} = 0.002$.909	.017
	Model 3: Attention sole predictor	$\beta_{Attention^*} = -0.125$.132	.050	$\beta_{Attention^*} = -0.032$.703	.022
$CC_{distractor}$	Model 4: HR* & RMSSD* joint predictors	$\beta_{HR^*} = 0.078$ $\beta_{RMSSD^*} = 0.080$.471 .458	.022	$\beta_{HR^*} = 0.323^{**}$ $\beta_{RMSSD^*} = 0.183$.001 .064	.083
	Model 5: HR* & RMSSD* & Attention joint predictors	$\beta_{HR^*} = 0.090$ $\beta_{RMSSD^*} = 0.081$ $\beta_{Attention^*} = -0.131$.396 .446 .114	.059	$\beta_{HR^*} = 0.315^{**}$ $\beta_{RMSSD^*} = 0.183$ $\beta_{Attention^*} = 0.000$.002 .064 .998	.081
	Model 1: HR* sole predictor	$\beta_{HR^*} = 0.228^{**}$.004	.132	$\beta_{HR^*} = 0.060$.464	.093
	Model 2: RMSSD* sole predictor	$\beta_{RMSSD^*} = 0.008$.924	.094	$\beta_{RMSSD^*} = 0.075$.354	.104
	Model 3: Attention sole predictor	$\beta_{Attention^*} = 0.271^{**}$.001	.111	$\beta_{Attention^*} = 0.016$.840	.092
	Model 4: HR* & RMSSD* joint predictors	$\beta_{HR^*} = 0.374^{***}$ $\beta_{RMSSD^*} = 0.240^*$	<.001 .015	.178	$\beta_{HR^*} = 0.146$ $\beta_{RMSSD^*} = 0.153$.141 .115	.116
	Model 5: HR* & RMSSD* & Attention joint predictors	$\beta_{HR^*} = 0.357^{***}$ $\beta_{RMSSD^*} = 0.246^{**}$ $\beta_{Attention^*} = 0.244^*$	<.001 .008 <.015	.181	$\beta_{HR^*} = 0.143$ $\beta_{RMSSD^*} = 0.155$ $\beta_{Attention^*} = 0.031$.149 .111 .704	.112

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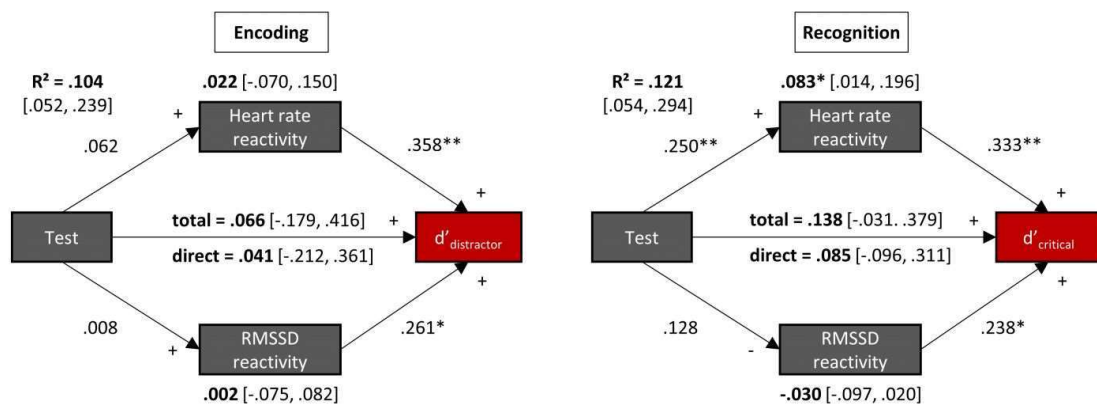


Figure 8 – Indirect test effect via cardiac reactivity on cognitive control over memory

Note. The indirect test effect (in bold) on the memory scores $d'_{critical}$ and $d'_{distractor}$ via cardiac reactivity (i.e., parallel effects of RMSSD reactivity and heart rate reactivity) at encoding and recognition, respectively, was tested using separate structured equation models for the memory variables. Values depict standardized coefficients. 95% CI are given in squared brackets. Heart rate reactivity and RMSSD reactivity were parallelly linked to both memory scores. However, only heart rate reactivity at recognition mediated the differences between the first and the second test on $d'_{critical}$. Model performance was good for both models.

$d'_{critical}$: $df = 2$, $\chi^2 = 3.025$, RMSEA = 0.062, CFI = 0.986, SRMR = 0.046.

$d'_{distractor}$: $df = 2$, $\chi^2 = 3.760$, RMSEA = 0.080, CFI = 0.977, SRMR = 0.051.

** $p < .01$, * $p < .05$.

676 5 Discussion

677 5.1 Overview

678 In this pre-registered study, we employed HRV biofeedback to investigate the psychophysiological
679 relationship between cardiac vagal control (i.e., vmHRV indexed as RMSSD) and cognitive control
680 during memory processing (i.e., encoding and retrieval). Cognitive control over memory was
681 assessed as true-to-false memory discrimination performance and metamemory of critical lures that
682 provoke false memories. Though the vmHRV manipulation during training was effective, HRV
683 biofeedback neither affected vmHRV during immediate memory processing nor did it improve
684 cognitive control over memory. Moreover, no robust association between vmHRV, neither at resting-
685 state nor during memory processing, and memory discrimination performance or metamemory could
686 be observed. An exploratory analysis revealed that the psychophysiological relationship changed
687 over repeated measures due to baseline changes in cardiac control (i.e., mean heart rate and vmHRV).
688 Reactivity values calculated as baseline change ratio percentages which accounted for baseline shifts
689 were considered. vmHRV reactivity and heart rate reactivity were found to concomitantly predict
690 cognitive control over memory. Furthermore, their joint prediction explained a much larger variance
691 than when considering vmHRV reactivity and heart rate reactivity as sole predictors. In this line,
692 vmHRV reactivity and heart rate reactivity when conditioned to each other, both positively correlated
693 with memory discrimination performance and correct confidence in non-target responses.
694 Specifically, cardiac reactivity at encoding was associated to the erroneous retrieval of distractors
695 whereas cardiac reactivity at recognition was associated to the erroneous retrieval of critical lures
696 (i.e., false memory). Critical lures opposed to the distractors were semantically related to the targets
697 and their correct identification required a higher degree of cognitive control. Therefore, cardiac
698 reactivity at encoding might have reflected attentional processes involved in learning whereas cardiac
699 reactivity at recognition might have reflected inhibitory and source monitoring processes.

700 5.2 vmHRV does not clearly correlate with cognitive control

701 Against our hypotheses no link between vmHRV and cognitive control could be confirmed. Firstly,
702 correlations between resting-state vmHRV and measures of working memory or inhibition could not
703 be replicated. We suspect the reason for this to be the timing of the resting-state measure. Resting-
704 state vmHRV is commonly assessed right before the cognitive evaluation, which was done in respect
705 to the main cognitive assessment (i.e., false memory paradigm). Consequently, the physiological
706 measure had to be performed after the working memory and Stroop task. Mental load induced by
707 these tests might have influenced resting-state vmHRV. Secondly, vmHRV was not linked to
708 cognitive control over memory. Contrary to this work, previous studies did not consider repeated
709 measures over the same experimental session and correlations changed here between tests. Therefore,
710 as part of an exploratory analysis, correlations at the first test were considered only. These reflected
711 the same positive relationship as found by Feeling et al. (2018) between resting-state vmHRV and
712 cognitive control over memory. However, in the present study correlations were smaller and no
713 statistical significance could be confirmed. We assume that differences in the experimental design
714 like the implementation of the respiration exercise, the higher number of stimuli, fatigue effects, and
715 the longer period between the resting-state and cognitive processing might have reduced the effect
716 size. It therefore remains questionable if resting-state vmHRV predicts cognitive control over
717 memory related to false memories.

718 5.3 The psychophysiological relationship is time-variant

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2 719 Contrasts between T1 and T2 showed significant intra-subject changes in the psychophysiological
3 720 relationship between cognitive control over memory and cardiac regulation (i.e., vmHRV and heart
4 721 rate) that influenced the outcomes. Correlations with vmHRV turned from positive to negative and
5 722 decreased for measures of heart rate at all measuring periods which explains why null results were
6 723 observed regarding the confirmatory analysis. We assume that these changes were due to relaxation
7 724 and fatigue effects induced by the tasks. In this context, a strong drop in resting-state heart rate and
8 725 increase in resting-state vmHRV could be observed between tests, a sign of mental fatigue induced
9 726 by increased parasympathetic activity (Gergelyfi et al., 2015; Matuz et al., 2021). Enhanced PNS
10 727 activity has been reported to predict increased sleepiness and mental fatigue during prolonged
11 728 activities involving cognitive loading while seated, such as car driving (Lu et al., 2022). This
12 729 assumption was corroborated by scores of self-reported fatigue which were higher after than before
13 730 the first task. Therefore, it is likely that participants were fatigued from the long periods of remaining
14 731 seated while being engaged in a lowly arousing task. Despite our efforts to reduce relaxation effects
15 732 by implementing a 5-min break before each task that required participants to stand or walk, this
16 733 resulted in baseline physiological shifts elicited by the parasympathetic branch. Moreover, no
17 734 evidence could be found that the biofeedback at T2 caused disassociation of the correlations between
18 735 test for the memory processing phases. In addition, psychobiological processes related to increased
19 736 basal vagal tone seemed not to have affected cognitive control over memory as cognitive
20 737 performance remained similar between tests. Conclusively, it can be problematic to perform repeated
21 738 measures in the same experimental session to assess the psychophysiological relationship between
22 739 vmHRV and cognitive control, as the physiological baseline shifts throughout the task. This is
23 740 especially true for long but also for shorter protocols of 30 min or below as strong physiological
24 741 effects could be observed already after 45 min (i.e., period between resting-state measures).
25 742 However, this finding also provides insight that the validity of vmHRV measures to predict cognitive
26 743 control is very time sensitive and depends on specific measurement settings. It seems that total or
27 744 log-transformed values of RMSSD, and likely also other correlated metrics of vmHRV, are no
28 745 appropriate parameters to explain the link between cardiac vagal control and cognitive mechanisms
29 746 during memory processing stages. Therefore, it seems more prudent to turn to other metrics of
30 747 vmHRV that account for physiological baseline shifts.

31 748 **5.4 vmHRV and heart rate reactivity are linked to cognitive control over memory**

32 749 When cardiac reactivity was assessed as the parallel effects of vmHRV reactivity and heart rate
33 750 reactivity on memory discrimination performance and metamemory, the data showed that both
34 751 measures were linked to long-term memory. Both, the chronotropic state and vmHRV are mostly
35 752 vagally driven at heart rates below 140 beats per minute (Gourine & Ackland, 2019) and have even
36 753 been advocated by some researchers as surrogate measures (Boyett, 2017; Boyett et al., 2017). Yet,
37 754 memory performance was much better modeled by the joint prediction of vmHRV reactivity and
38 755 heart rate reactivity than when only one predictor was included at a time. In addition, vmHRV
39 756 reactivity was only positively correlated to memory when conditioned to heart rate reactivity. This
40 757 suggest, in accordance with recent discussion (de Geus et al., 2019), that the heart rate exercised an
41 758 interference on the association between vmHRV and cognitive control over memory and that both
42 759 cardiac parameters provide distinct information about long-term memory. On the one hand, the mean
43 760 heart rate reflects mean efferent influences of the PNS and SNS. On the other hand, RMSSD as a
44 761 measure of vmHRV largely captures fast parasympathetic modulation of autonomic control that
45 762 reflect complex heart-brain interactions. The heart's intrinsic nervous system processes efferent as

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2 763 well as afferent information streams associated to different physiological systems such as autonomic
3 764 activity, baroreflex, and respiration which all influence beat-to-beat variations (Shaffer et al., 2014).
4 765 Therefore, it is possible that only by cancelling out the changes in mean parasympathetic and
5 766 sympathetic activity, as well as other non-vagal effects that the heart rate exerts on vmHRV, will one
6 767 unveil the information retained by dynamic cardiac vagal control that is associated with cognitive
7 768 processing.
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10 769 vmHRV was negatively associated to heart rate so that an increase in heart rate is accompanied by a
11 770 decrease in vmHRV. Yet, memory benefited from an increase in vmHRV relative to heart rate
12 771 increase. Thus, we theorize that enhanced memory performance was accompanied by a simultaneous
13 772 increase in tonic reciprocal SNS activity (i.e., mean increase in SNS and mean decrease in PNS
14 773 activity, respectively, that increases heart rate) and phasic (frequency) cardiac vagal control. A study
15 774 in canine models demonstrated such specific contribution of the PNS to vmHRV that is independent
16 775 from heart rate: strong reduction in cardiac vagal control decreased vmHRV even after heart rate
17 776 correction while baroreceptor reflex activation increased vmHRV after heart rate correction (Billman,
18 777 2013). Indeed, phasic cardiac vagal control deriving from baroreflex and cardiorespiratory coupling
19 778 affects only a small part of the net vagal influence on the heart (Craft & Schwartz, 1995; Eckberg,
20 779 2003). Thus, it is possible that mental stress induced by the cognitive task increased blood pressure
21 780 (Hjortskov et al., 2004) which in turn evoked parasympathetic activation via the baroreflex that was
22 781 captured by phasic cardiac vagal control. Hence, we posit the hypothesis that vmHRV reactivity
23 782 regressed on heart rate reactivity is indicative of phasic cardiac vagal control deriving from efferent
24 783 and afferent connections within a neural network which integrates autonomic and cognitive control.
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29 784 This view is consistent with our initial hypothesis and supports the notion of the neurovisceral
30 785 integration model. Moreover, model predictions indicate that the acceleration of the mean heart rate
31 786 plays an important role for cognitive control over memory. Moderate heart rate increases are known
32 787 to be linked to physiological and cognitive processes such as increased arousal and attention that
33 788 support goal-directed behavior (e.g., memory encoding). Sympathetic influence might have played a
34 789 role on attention networks whereas vagal withdrawal regulated energy expenditure in face of the task
35 790 (Duschek et al., 2009). Regarding the latter, PNS responsivity has been proposed as an indicator of
36 791 the ability to orient to and cope with challenging tasks (Porges, 2007; Thayer et al., 2012). Moreover,
37 792 higher heart rate is also linked to higher cardiac output and with such cerebral blood flow (Jefferson
38 793 et al., 2017). This in turn increases the nutrient supply to the brain and consequently improves
39 794 cognitive function (Ogoh et al., 2008).
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44 795 At first glance it seems that the findings do not align with the polyvagal theory (Porges, 2007) and
45 796 vagal tank theory (Laborde et al., 2018). The models state that a reduction or increase in vagal
46 797 withdrawal supports behavior depending on the level of executive control and metabolic demand
47 798 required by the task. Non-executive tasks involving high physical activity would benefit from greater
48 799 vagal withdrawal whereas reduced vagal withdrawal (or activation) would support cognitive
49 800 regulation. However, we extend the model by arguing that vagal modulation underlies two
50 801 differential mechanisms that support cognitive control: 1) a mean reduction in vagal tone that
51 802 increases metabolic output and cerebral blood flow, 2) enhanced phasic (frequency) cardiac vagal
52 803 control that links to better executive functioning. In this line, whether an increase or decrease in
53 804 cardiac vagal control as measured by vmHRV is noted in response to an executive task would mainly
54 805 depend on the change in metabolic requirements. In this context, the effect of heart rate reactivity
55 806 observed here might have been exaggerated by a state of low energetic state and PNS domination at
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2 807 baseline (long sitting session, little external stimulation). In this line of thought, effective memory
3 808 processing triggered mobilization of metabolic resources linked to reduced vagal tone. Previous
4 809 works emphasized that greater vagal withdrawal due low levels of SNS activity link to greater
5 810 working memory capacities (Giuliano et al., 2017) and attenuated cognitive decline (Knight et al.,
6 811 2020). Accordingly, because metabolic demands overweighted executive demands, unadjusted
7 812 vmHRV reactivity is obscured by heart rate changes and does not reflect executive functioning.
8 813 Therefore, it is critical to consider the unique contributions of vmHRV reactivity and heart rate
9 814 reactivity, as they may reveal distinguishable processes related to metabolic demands and cognitive
10 815 control.
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14 816 The observed heart rate interference might provide an explanation why meta-analyses revealed only
15 817 small correlations between vmHRV and cognitive control ($r = 0.09$, Holzman & Bridgett, 2017; Zahn
16 818 et al., 2016; $r = 0.15$). In addition, it might also explain why other studies found no robust link
17 819 between memory retrieval success and HRV measured during cognitive processing (Hilgarter et al.,
18 820 2021) or vmHRV reactivity at encoding (Paige et al., 2020). Moreover, an indirect effect of cardiac
19 821 reactivity via increased subjective attention could be excluded. Attention most notably played a role
20 822 during encoding that enhanced the identification of target items and discrimination of distractors,
21 823 probably due stronger encoding of target items (Blondé et al., 2022; Mulligan, 1998). However, the
22 824 link between memory and attention did not come at cost in predictive power of cardiac reactivity.
23 825 This suggest that an automatic neurophysiological integration and processing of information at a
24 826 memory linked to cardiac responses that may lay beyond consciousness.
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28 827 Independent of the true processes that distinguish vmHRV reactivity and heart rate reactivity, we
29 828 advocate that measuring vmHRV during memory processing or at resting-state alone is not sufficient
30 829 to describe the complex interaction between cardiac control and cognitive control over memory. The
31 830 findings support the idea that cardiac vagal control withdrawal is attenuated or even increased during
32 831 cognitive processing as function of metabolic needs and behavioral restraint to mental fatigue to
33 832 maintain task performance. The reason for this is thought to be the changes in net parasympathetic
34 833 and sympathetic effects that mask the phasic dynamics of cardiac vagal control associated with
35 834 cognitive control. Consequently, extending on the vagal tank theory and previous studies that found a
36 835 more robust psychophysiological connection when considering autonomic reactivity to a cognitive
37 836 task, rather than baseline autonomic activity (Knight et al., 2020; Magnon, Dutheil, et al., 2022), we
38 837 propose that PNS reactivity and heart rate reactivity should concomitantly be investigated.
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43 838 **5.5 Cardiac reactivity at encoding and recognition**
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45 839 Cardiac reactivity (i.e., concomitant and independent increase in heart rate and vmHRV compared to
46 840 baseline) at recognition but not at encoding positively predicted the capability to discriminate critical
47 841 lures from target items and metamemory of critical lures (i.e., higher confidence in correct and
48 842 reduced confidence in false response choice). Conversely, cardiac reactivity at encoding predicted
49 843 discrimination performance and metamemory for distractors. Unlike lures, distractors had only weak
50 844 to no semantic and associative similarity to the targets (i.e., shared conceptual and taxonomic features
51 845 or connections in associative networks). Moreover, the false memory task was designed to activate
52 846 memory for critical lures, because of their semantic association with targets, but not for distractors
53 847 during encoding and retrieval.
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2 848 Therefore, these results demonstrate that cardiac control during encoding is linked to the encoding
3 849 strength of learned items which supports true memory retrieval and correct rejection of unrelated
4 850 information. Presumably deeper encoding strengthened the gist representation (i.e., essential
5 851 meaning) of learned items and the memory of their origin (i.e., encoding phase). This in turn
6 852 facilitated during subsequent retrieval the source monitoring of the unrelated distractors (i.e.,
7 853 determining they were not learned during encoding) because targets' gist and verbatim traces
8 854 interfered with the distinct memory representation of the distractors. Contrary, cardiac control at
9 855 encoding did not seem to have affected cognitive control mechanisms that reduced the production
10 856 and strength of false memories (i.e., critical lures false recognition). In this context, we assume that
11 857 cardiac control in response to memorization does neither support gist reduction by suppressing the
12 858 activation of semantically related information, nor does it sufficiently enough strengthen verbatim
13 859 traces to interfere with gist traces of critical lures. Indeed, supplementary findings indicate that
14 860 cardiac reactivity was not linked to greater recall success or metamemory of learned words.

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19 861 However, findings suggest that cardiac reactivity at memory retrieval aids in suppressing the gist
20 862 trace of semantically related but false information. Along the Activation Monitoring Framework
21 863 (Gallo, 2010; Roediger et al., 2001; Roediger & McDermott, 2000), the DRM false memory task
22 864 triggered activation of memories related to the critical lure which need to be inhibited when recalling
23 865 learned information. As only correct confidence to critical lures but not to distractors was related to
24 866 cardiac reactivity at recognition, we assume that cardiac reactivity supported cognitive control
25 867 mechanism that inhibit previously activated information. This in turn lead to better source monitoring
26 868 of information with low distinctiveness to relevant information and thus a reduction in false memory
27 869 strength and production. In summary, the findings support the view that phasic (frequency) alongside
28 870 tonic components of cardiac vagal control are associated with cognitive control over memory. On the
29 871 one hand, the study provides evidence that phasic cardiac vagal control at memory retrieval is linked
30 872 to inhibitory processes which support the suppression of pre-activated information. On the other
31 873 hand, greater phasic cardiac vagal control at encoding is linked to better detection of unrelated and
32 874 irrelevant information that may be related attentional and cognitive control processes assisting
33 875 encoding (e.g., working memory, inhibition).

5.6 Biofeedback effect on cognitive control over memory

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40 877 Against our hypotheses HRV biofeedback compared to the control breathing exercise did not
41 878 increase vmHRV during subsequent memory processing. A likely explanation is that the high
42 879 baseline PNS activity that was observed throughout the experiment dampened vmHRV increases
43 880 evoked through HRV biofeedback. Moreover, high basal PNS activity promoted stronger vagal
44 881 withdrawal in response to the task. In this line of thought, individual differences in heart rate
45 882 acceleration during cognitive processing may have obscured initial results. Indeed, the exploratory
46 883 analysis indicated a small-to-moderate HRV biofeedback effect on vmHRV reactivity dependent on
47 884 heart rate reactivity. Consequently, in respect to the previous discussion, it seems that short HRV
48 885 biofeedback stimulates phasic cardiac vagal control during subsequent memory encoding and
49 886 retrieval. Therefore, the question arises why no HRV biofeedback effect on memory was found given
50 887 that phasic vagal and cognitive control were associated. The answer could be that given the
51 888 association was only small, the physiological stimulation was too weak to evoke cognitive changes.
52 889 For this reason, we do not rule out that HRV biofeedback in conditions with low vagal tone or
53 890 increased SNS such as high levels of stress or many major psychiatric disorders (Alvares et al., 2016;

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2 891 Gorman & Sloan, 2000) could evoke immediate effects on memory due to (phasic) vagal stimulation.
3 892 In the same sense longer training could have effects even in healthy and relaxed subjects. In fact,
4 893 supplementary analyses suggested a biofeedback effect on the confidence towards the correct
5 894 rejection of critical lures and false detection of distractors. However, these outcomes could be
6 895 spurious as they did not survive FDR correction. Finally, an immediate HRV biofeedback effect on
7 896 cardiac vagal control and long-term memory in dependence of autonomic baseline activity remains to
8 897 be verified.

11 898 **5.7 Limitations**

13 899 The most significant results from this study should be interpreted with care as they were derived from
14 900 exploratory analyses instead of the a priori analyses. Confirmatory analyses are required to
15 901 corroborate the relationship between cognitive control over memory and vmHRV reactivity.
16 902 Moreover, it remains unclear if cognitive functioning can be ascribed to cardiac control or if
17 903 perceptual processing influenced autonomic regulation. On the one hand, it is possible that cardiac
18 904 reactivity at recognition reflected physiological processes that are linked to better cognitive control.
19 905 On the other hand, the detection of critical lures might have entrained autonomic and baroreflex
20 906 mechanisms through the orienting response (Nieuwenhuis et al., 2011). In this regard, critical lure
21 907 items became salient and task-relevant stimuli that triggered the orienting response whenever they
22 908 were correctly detected because they stood out from other distractors due to their strong similarity to
23 909 the memorized items. In addition, non-arousing neutral words were used as stimuli to replicate
24 910 previous results (Feeling et al., 2021). However, emotional arousal and measurement context of true
25 911 and false memory (Abichou et al., 2021, 2022) may be important factors that need to be accounted
26 912 for when applying the results to the real world. Arousal not only affects memory but is also linked to
27 913 HRV since it plays a role in prefrontal inhibition of the amygdala (Sakaki et al., 2016). Thus, we
28 914 assume a stronger link between autonomic and cognitive control during memory processing for
29 915 emotionally-laden stimuli or real-life situations. Future research could provide important insights into
30 916 the link between autonomic and cognitive control in memory and clarify the dual role of tonic and
31 917 phasic cardiac vagal regulation for cognitive control by examining neuroimaging data and additional
32 918 markers of autonomic nervous system activity such as electrodermal activity, pre-ejection period, or
33 919 pupil dilation recorded in real-life relevant situations inducing varying levels of physiological
34 920 activation at varying levels of baseline autonomic activity.

41 921 **6 Conclusion**

42 922 This work followed two main objectives that were firstly to test the immediate effect of HRV
43 923 biofeedback on vmHRV during memory processing as well as on cognitive control over memory and
44 924 secondly to investigate their psychophysiological relationship. Regarding the latter, evidence is
45 925 provided that cognitive control over memory is not associated to state measures of cardiac control.
46 926 vmHRV neither at resting-state nor during memory processing was reliably linked to memory
47 927 discrimination performance or metamemory. One of the reasons was that baseline parasympathetic
48 928 activity increased over time, possibly due to relaxation effects, which influenced the relationship
49 929 between cognitive control and vmHRV. This time dependency poses an important problem for
50 930 psychophysiological research, because the time between the arrival of the participants in the
51 931 laboratory and the recording can vary greatly. Therefore, a state description (e.g., a single resting
52 932 state measurement) of cardiac vagal control appears to be an insensitive measure for assessing the
53 933 interaction between autonomic and cognitive control. In framework of an exploratory analysis,

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2 934 vmHRV reactivity (i.e., RMSSD baseline change ratio percentages) regressed on heart rate reactivity
3 935 was proposed as a measure of phasic cardiac vagal control that is linked to executive processing.
4 936 Unique contributions of both heart rate reactivity and vmHRV reactivity were both positively linked
5 937 to cognitive control over memory. It is theorized that cognitive control is supported by two parallel
6 938 mechanisms: 1) a mean vagal withdrawal to mobilize metabolic resources which supports cognitive
7 939 functioning and 2) the maintenance or increase in phasic (frequency) cardiac vagal control which is
8 940 associated to greater cortical-inhibitory-control. The findings indicate that this autonomic control at
9 941 retrieval was linked to inhibitory functions at a memory level. In this context, adaptive autonomic
10 942 regulation seems to increase true-to-false memory discrimination through enhanced source
11 943 monitoring and suppression of associated but irrelevant information. Autonomic control at encoding
12 944 on the other hand presumably strengthened gist traces of learned items which did not improve true
13 945 memory retrieval but reduced erroneous retrieval of unrelated distractors. Moreover, it was found that
14 946 HRV biofeedback neither influenced vmHRV nor cognitive control over memory in young healthy
15 947 adults. High baseline parasympathetic activity might have hindered the vmHRV stimulation through
16 948 HRV biofeedback. Consequently, due to the lack of physiological stimulation, there was also no
17 949 cognitive effect. In addition, the results underline that HRV biofeedback did not influence long-term
18 950 memory through increased attention. Exploratory results suggested that HRV biofeedback affected
19 951 changes in phasic cardiac vagal control in response to memory processing (i.e., encoding, retrieval)
20 952 but the effect was too small to affect cognition. Therefore, the outcomes do not confirm the utility of
21 953 HRV biofeedback to immediately stimulate autonomic and cognitive control but proved that vmHRV
22 954 and heart rate do have an effect on cognitive control over memory. Further investigations with longer
23 955 training periods and in settings with decreased baseline PNS activity (e.g., during a stressful period)
24 956 are required. Finally, the outcomes support previous psychophysiological models (Laborde et al.,
25 957 2018; Porges, 2007; Thayer et al., 2009; Thayer & Lane, 2000). Moreover, they highlight the interest
26 958 in investigating reactivity values of vmHRV and heart rate in parallel to assess the relationship
27 959 between autonomic and cardiac control, thus paving the way for a new direction in
28 960 psychophysiological research.

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1
2 1292 **Conflict of Interest**

3
4 1293 *The authors declare that the research was conducted in the absence of any commercial or financial*
5 1294 *relationships that could be construed as a potential conflict of interest.*

6
7 1295 **CRedit author statement**

8
9 1296 **Lukas Bögge:** Conceptualization, Methodology, Software, Validation, Formal analysis,
10 1297 Investigation, Resources, Data Curation, Writing- Original draft preparation, Writing- Reviewing and
11 1298 Editing, Visualization, Project administration. **Itsaso Colás-Blanco:** Writing- Reviewing and
12 1299 Editing. **Juliette Ferragu:** Investigation, Data Curation. **Alexandre Gaston-Bellegarde:**
13 1300 Programming. **Valentina La Corte:** Writing- Reviewing and Editing. **Pascale Piolino:**
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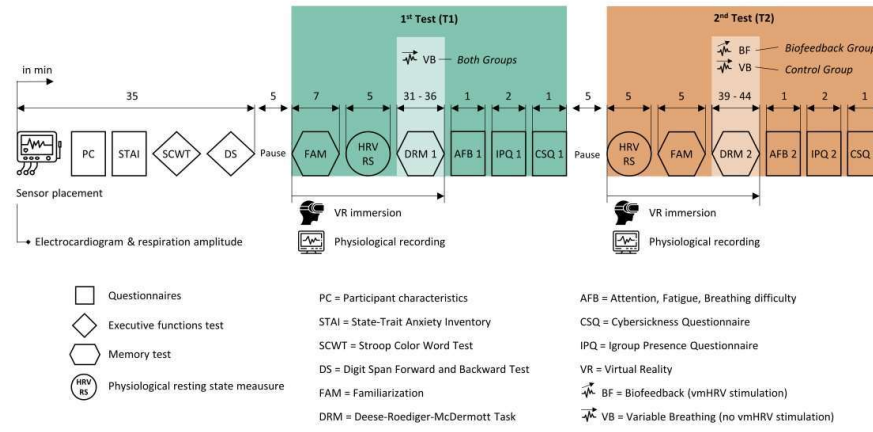
26
27 1309 **Acknowledgments**

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29
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32
33 1312 **Data Availability Statement**

34
35 1313 Anonymized original datasets, supplementary materials and results are publicly accessible under the
36 1314 terms of the Creative Commons Attribution 4.0 International license (CC BY-NC-SA 4.0, copyright
37 1315 holder: Lukas Bögge and Memory, Brain & Cognition Laboratory), where applicable, in the Open
38 1316 Science Framework: https://osf.io/593p6/?view_only=07d070654c12467cb8c509f6e175a029.
39 1317 (Private view link only. The OSF project including the complete data set will be made publicly
40 1318 available and the link replaced upon acceptance of the manuscript.)

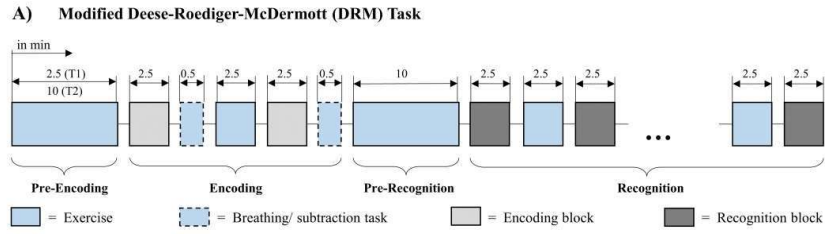
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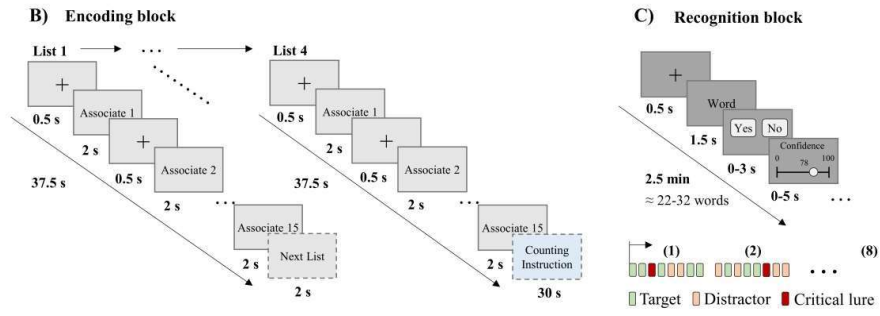
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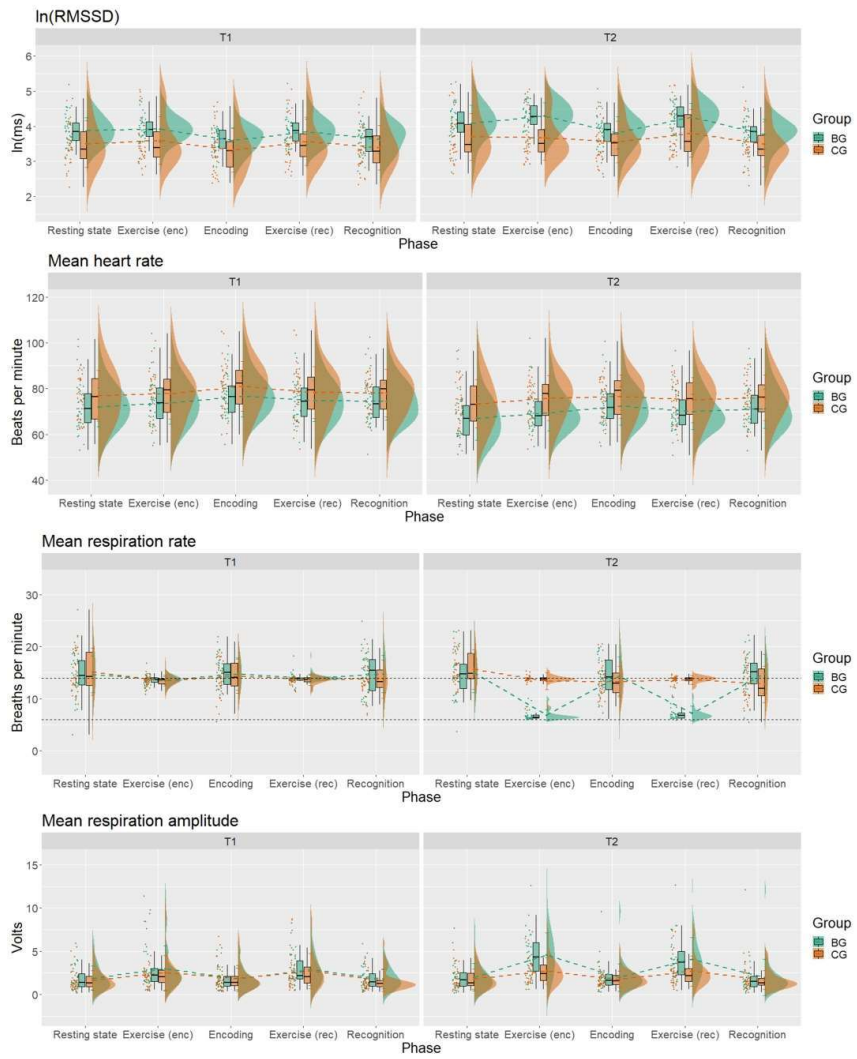
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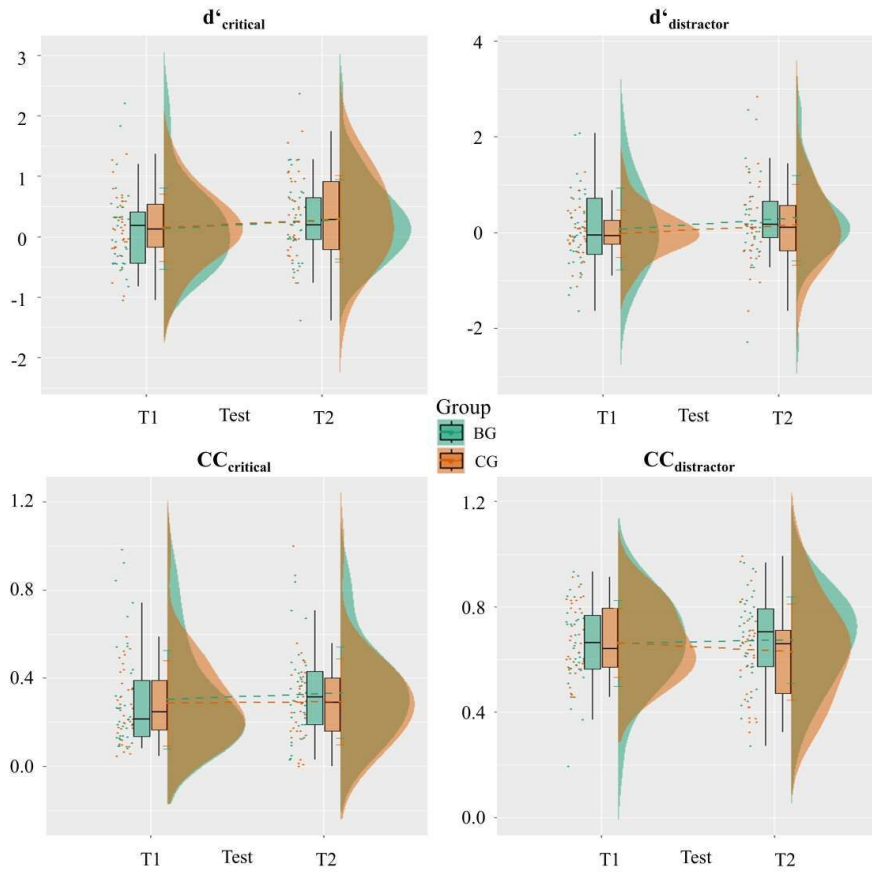
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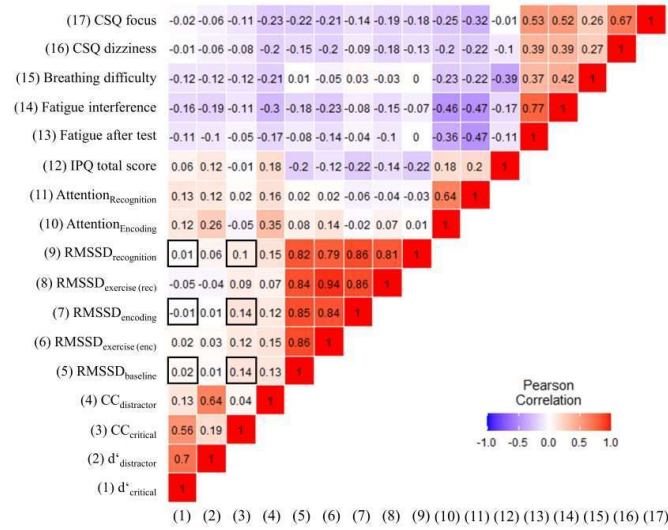
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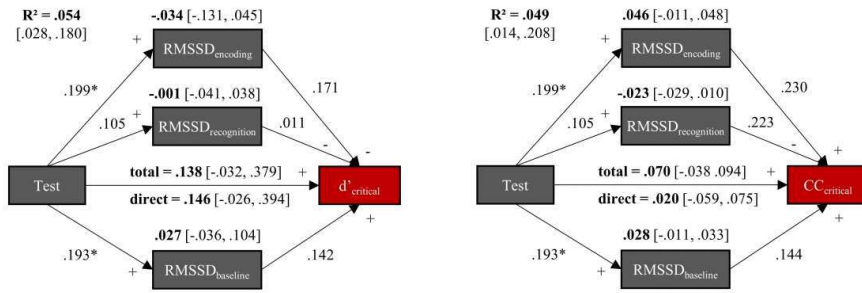
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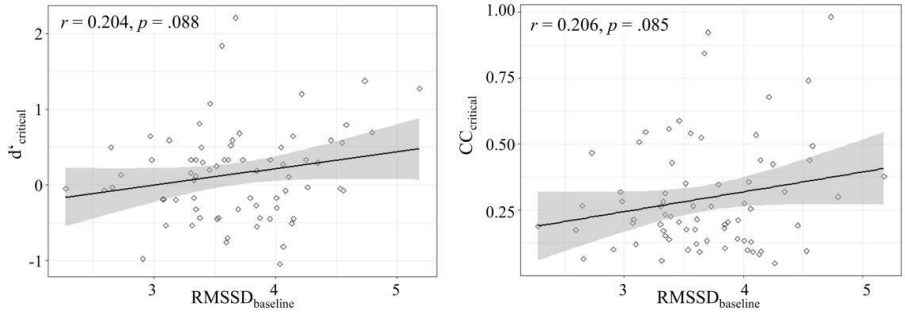
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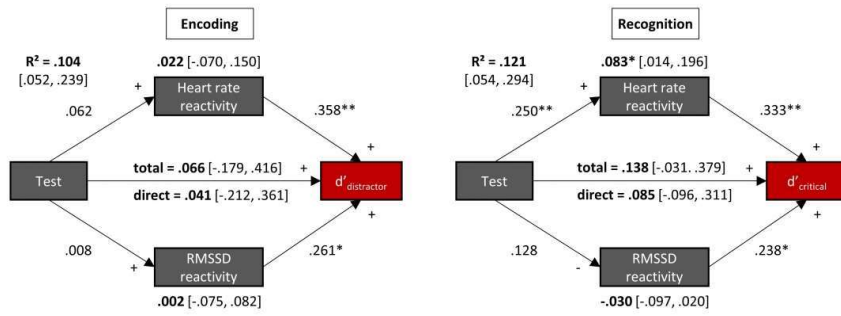
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10.3 Conclusion

The main results of the second study (BIOTRAC-2) can be summarized as follows:

- There was no robust association between cognitive control over memory and RMSSD, neither at resting-state nor during memory processing.
- Short HRV biofeedback directly before encoding and retrieval did not improve RMSSD during memory processing and cognitive control over memory.
- Exploratory results indicated that parallel effects of RMSSD and heart rate reactivity at memory retrieval predicted cognitive control over memory.

Contrary to the hypotheses, measures of cardiac vagal control were not associated with cognitive control over memory. Findings from Feeling et al. (2021) could not be replicated, probably partly due to methodological differences but mostly because the psychophysiological association was time-variant. An important finding of this study is that correlations of state measures of cardiac vagal control with cognitive outcomes drastically changed between repeated measures. It is assumed that a general decrease in heart rate and increase in vmHRV due to relaxation and/or fatigue effects were strong confounders. Moreover, HRV biofeedback neither affected vmHRV nor cognitive scores. Thus, the utility of HRV biofeedback to investigate the *in situ* psychophysiological relationship between cardiac vagal control and cognitive processes cannot be confirmed. A reason no positive results were found could be the absence of emotional processing as neutral stimuli were used only. The neurovisceral integration posits an interaction between emotional, executive, autonomic processing. Hence, it is possible that the identification and discrimination of false memories is dependent on emotional salience, which may moderate the association between cardiac vagal and cognitive control over memory.

In addition, the exploratory analysis provided an interesting outlook when phasic vmHRV is considered. vmHRV reactivity alone did not predict cognitive control over memory, but the parallel reactivity of vmHRV and heart rate did. It was assumed that heart rate indicated mean vagal withdrawal to mobilize metabolic resources and vmHRV phasic (frequency) cardiac vagal control linked to greater cortical-inhibitory-control, which in parallel supported executive control. Consequently, for the following experiment, we planned to consider emotional processes and parallel effects.

11 Chapter 11 – HRV Biofeedback Effect on Cognitive Control and Self-Referential Processes and its Association to Autonomic Regulation during Past and Future Thinking

This article is currently in preparation for submission to *Psychophysiology* (Journal ISSN: 1469-8986), which is almost completed. The research project, including the research data, all supplementary materials and results, as well as video material of VR environment, will be made publicly available upon article acceptance (OSF link: <https://osf.io/xgfdc/>)

11.1 Introduction

The third article in this thesis, termed BIOTRAC-3, targeted to investigate the HRV biofeedback and cardiac vagal control effects on executive control and self-relevant processes in relation to emotional processing in higher-level cognitive functions.

For the final study, processes during mental time travel, i.e., the recall of episodic autobiographical memory and episodic future thinking, were considered to examine the association of vmHRV reactivity with different thought processes relevant to daily-life behavior. Moreover, episodic future thinking is assumed to imply a higher degree of executive functions. Thus, comparing retro- and prospective mental time travel could help to corroborate the assumption that cardiac vagal control processes are related to cognitive control in higher cognition. An experimental design was considered to overcome the limitations of the previous studies. Participants were asked to recall or simulate in total 24 personal episodes two to five years in the past or future, each based on either a negative or positive trait-adjective. Right afterwards, they rated the phenomenological properties of the event's vividness, subjective valence, visual perspective, personal importance, probability of (re)occurrence, and temporal distance to the present. Additionally, the construction time of the event was recorded. These variables were selected as they seem to best capture cognitive control as well as self-referential processes in mental time travel (Jeunehomme & D'Argembeau, 2017). As in BIOTRAC-2, short HRV biofeedback was performed directly before the cognitive task and the complete procedure was automatized and implemented in VR. This paradigm allowed, in contrast to BIOTRAC-2, firstly to study the influence of emotional

processing on the relationship of cardiac vagal control with cognitive control and self-referential processing. Secondly, the experiment length, and thus possible confounding effects of relaxation, was reduced by administering the task only once. Simultaneously, basing the analysis on repeated events instead of summarized measures (e.g., recollection rate) increased statistical power, allowing the detection even of small correlations. Consequently, this study enabled us to study the interaction of emotional processing, cognitive demands with HRV biofeedback and its relationship to cardiac vagal control on self-relevant processing and cognitive control during mental time travel.

We hypothesized, in line with results of BIOTRAC-1 and 2, that higher vmHRV reactivity (lower cardiac vagal control attenuation/ higher stimulation) during mental time travel would predict thought properties related to better cognitive control, especially when cognitive demands are high (future thinking), and stronger self-referential processing in both time directions. Furthermore, it was expected that emotional processing moderates the psychophysiological relationship such that vmHRV reactivity is associated with self-positivity bias, i.e., engagement of self-referential processes (e.g., self-importance) and cognitive resources (executive functions) during positive mental time travel and disengagement during negative mental time travel.

11.2 Article in Preparation (Bögge et al., *IN PREP*)

Connecting heart and thoughts: Cardiac vagal control during mental time travel and resting thoughts and the influence of prior biofeedback

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10 **Keyword:** heart rate variability, biofeedback, cardiac vagal control, mental time travel, future
11 thinking, episodic autobiographical memory, emotional regulation, self-referential processing, virtual
12 reality.

13 In preparation for submission to *Psychophysiology* (Journal ISSN: 1469-8986).

14 Abstract

15 The heart and the brain are connected through a complex neurovisceral network that gives rise to both
16 cardiac control and thought. Underlying brain structures have been associated with cognitive vagal
17 control, emotion regulation, and self-referential processing, which play a crucial role in how thoughts
18 are shaped and our capacity to mentally travel back and forth in time, including episodic
19 autobiographical memory and future thinking. Measures of tonic resting heart rate variability (HRV)
20 provide the empirical basis for the connection between cardiac vagal control and cognitive processes
21 involved in self-regulation and adaptive thinking. However, little is known about how cardiac vagal
22 control during cognitive activity is related to properties of thought.

23 In this single-session experiment, 40 young, healthy adults were asked to anticipate future and recall
24 past personal events based on positive and negative cues in a controlled virtual reality environment
25 while HRV, as the root mean square successive difference (RMSSD) in heart period, was recorded.
26 Mental time travel phases were alternated with short exercises of either slow-paced breathing with
27 HRV biofeedback or natural-paced breathing to test whether HRV biofeedback evokes concomitant
28 changes in HRV and phenomenological properties of thought. Furthermore, the cardiac vagal control
29 and HRV biofeedback effect on thought properties during task-unspecific rest was explored.

30 Higher (phasic) RMSSD reactivity (relative baseline change) correlated with greater vividness during
31 positive future thinking ($\rho = +0.22$), while higher tonic RMSSD during negative episodic memory
32 recall predicted a lower personal importance of the event ($\rho = -0.25$). HRV biofeedback, compared to
33 the control breathing exercise, increased vividness and buffered a decrease in RMSSD reactivity for
34 positive cues when compared to negative cues.

35 The results suggest, in line with the Vagal Tank Theory, that cardiac vagal control responsivity
36 underlies goal-directed cognitive control, but only in the presence of high executive demands and/or
37 motivational bias (positive future thinking). Moreover, tonic cardiac vagal control seems to influence
38 memory selection and self-referential properties of negative memories that support implicit emotion
39 regulation. The findings have important clinical implications as they underline that cardiac vagal
40 control underpins adaptive thinking, contributing to mental well-being.

41 1 Introduction

42 1.1 Autonomic control

43 Cardiac vagal control is the regulatory input to the heart through the vagus nerve which underlies
44 physiological regulation, but also mental processes involved in adaptive thinking and mental time
45 travel. The heartbeat is regulated by efferent pathways arising from the brainstem, that integrates
46 afferent viscerosensory inputs and top-down commands coming from the higher brain structures
47 involved in behavior. Parasympathetically-induced beat-to-beat fluctuations in the heart period can be
48 analyzed by measuring vagally mediated heart rate variability (vmHRV), thus providing an index of
49 cardiac vagal control. The neurovisceral integration model (Thayer & Lane, 2000, 2009) proposes a
50 neuroanatomical framework which links cardiac vagal control to emotion regulation and cognitive
51 control. The interrelation between cortical and subcortical structures, most notably the ventromedial
52 prefrontal cortex and amygdala, form the anatomic basis (Benarroch, 1997) of autonomic as well as
53 cognitive regulation, giving rise to the psychophysiological relationship between cardiac vagal control
54 and adaptive behavior underlying self-regulation (Thayer et al., 2012). The authors propose that self-
55 regulation efficacy is rooted in the functioning of negative feedback loops that inhibit non-adaptive
56 behavior. Indeed, fMRI studies showed that a higher activity in executive brain regions (prefrontal and
57 anterior cingulate cortex) was related to higher resting vmHRV. Various studies have verified a link
58 between higher resting vmHRV and better regulatory capacities of the autonomous nervous system,
59 underlying healthy body functioning (Gevirtz, 2013; Lehrer et al., 2020), and adaptive cognitive
60 functions (see for review Forte et al., 2019). In line with neurovisceral integration model, vmHRV
61 seems mostly associated with functions associated with executive brain regions involved in inhibition
62 and working memory with important implications on adaptive thought processes such as the
63 suppression of negative or false memories (Feeling et al., 2021; Gillie et al., 2014), and intrusive
64 thoughts (Gillie et al., 2015). Lower levels of vmHRV have been demonstrated to reflect comprised
65 emotional regulation, lower stress vulnerability, and increased perseverative cognition that is the
66 repetitive or sustained activation of cognitive representations of stressors (e.g., negative thoughts)
67 (Mather & Thayer, 2018; Ottaviani et al., 2016; Williams et al., 2015, 2017). Thus vmHRV ties to
68 maladaptive thought patterns, even in healthy adults, that are manifested in autonomic rigidity,
69 inflexibility, i.e., low vmHRV, (Ottaviani et al., 2013, 2015, 2016) that predicts important health
70 outcomes (Carnevali et al., 2018).

71 Importantly, the neural network involved in autonomic control also includes core hubs of the default
72 mode network that is engaged during future-oriented cognition and self-referential thought. The link
73 between vmHRV and self-referential processing has not yet been systematically investigated, but the
74 pivotal role of the ventromedial prefrontal cortex, for both mental-self processing (Qin et al., 2020)
75 and autonomic control (Benarroch, 1997) and its ties to emotional regulation centers, supposes that
76 vmHRV predicts self-referential processes dependent of the emotional context.

77 Results have traditionally been derived from resting state measures linking cognitive outcomes to
78 autonomic trait characteristics. Little research has been dedicated to how cardiac vagal control during

79 cognitive activity relates to mental processes. In this line, tonic on-task vmHRV or phasic vmHRV
80 reactivity (i.e., change from baseline) can be measured. The Vagal Tank Theory (Laborde et al., 2017)
81 proposes that the reactivity in cardiac vagal control predicts how efficiently cognitive resources
82 underlying self-regulation are deployed. They predict that when the organism faces situations with low
83 physiological demands from physical activity and high executive demands, greater reactivity, i.e.,
84 attenuated cardiac vagal withdrawal or a vagal increase, reflects greater self-regulatory efficiency.
85 Consequently, assessing vmHRV reactivity (phasic) and tonic vmHRV during thinking could provide
86 additional insight on the relationship between cardiac vagal control and goal-directed thought
87 processes, such as future-oriented cognition and mental time travel.

88 1.2 Mental time travel

89 Mental time travel (MTT) refers to our capacity to think about the personal past and future, and it
90 concerns our ability to disengage from our physical environment to mentally place ourselves into
91 another “self-location” in time, either in the past or in the future (Arzy et al., 2008; Buckner & Carroll,
92 2007; Kurczek et al., 2015; Markowitsch & Staniloiu, 2011). In our daily live, we frequently engage
93 in MTT, as we remember specific events from our past (episodic autobiographical memory, EAM), or
94 imagine specific events that could happen to us in the future (episodic future thinking, EFT). These
95 two mental operations have been considered as parts of the same constructive simulation process
96 (Addis, 2018; Schacter & Addis, 2007), in which previous knowledge interacts with new perceptual
97 and experiential information to generate mental simulations of experience. Regardless of the time
98 direction of our thoughts, MTT involves self-referential processing, visual imagery (vividness; actor
99 or observer perspective), and episodic binding of temporo-spatial, perceptual, and emotional
100 information (Schacter et al., 2012). Both processes engage a core network including pre-frontal cortex
101 (PFC) structures such as the vmPFC, posterior cingulate cortex, parietal regions such as the precuneus,
102 and medial temporal areas such as the hippocampus, which are also involved in autonomic control
103 (Benarroch, 1997). There are, however, some differences between MTT to the past and to the future.
104 Past events, for instance, are usually more detailed and more vividly re-experienced than future events
105 (Colás-Blanco et al., 2022; D’Argembeau & Van der Linden, 2004). Future event simulation, on the
106 other side, tend to be more goal-oriented and is usually experienced in third-person rather than first-
107 person perspective (D’Argembeau et al., 2010; D’Argembeau & Van der Linden, 2006)

108 MTT is crucial to our cognitive functioning, as it gives a sense of continuity to the self, and it is linked
109 to adaptative behavior and well-being. In particular, the capacity to imagine specific and detailed future
110 events appears to favor planning, problem-solving, and goal-motivated behavior (Brown et al., 2012;
111 D’Argembeau & Mathy, 2011), as well as decision-making (Peters & Büchel, 2010), and emotion
112 regulation (Jing et al., 2016). MTT has demonstrated a positivity bias in healthy individuals, especially
113 during EFT (D’Argembeau & Van der Linden, 2006), which might serve to increase self-enhancement
114 (Salgado & Berntsen, 2020). The latter is a type of motivation that involves a preference for positive
115 over negative views, driving self-regulation. In clinical populations such as patients suffering from
116 depression, there is an incapacity to recall and anticipate positive experiences, which leads to in-
117 adaptive thinking about negative experiences (MacLeod & Salaminiou, 2001). Not only depression but

118 also brooding rumination (a negative past-oriented bias) in healthy subjects impairs vividness and self-
119 perspective and is linked to more past-thinking (Beatty et al., 2019; Lemogne et al., 2006).

120 Episodic as well as semantic memory processes seem to play a role in MTT (Irish & Piguet, 2013;
121 Schacter & Addis, 2007). In terms of cognitive resources, it has been proposed that EFT requires more
122 cognitive effort than EM, as it implies the flexible recombination of information into a novel, coherent,
123 and plausible scenario, as well as the inhibition of inappropriate information (Anderson et al., 2012),
124 which calls for executive functions. In fact, executive functioning deficits – such as the ones found in
125 depressed individuals – impact more importantly the future component of MTT, probably by affecting
126 the strategic retrieval of details from episodic memory necessary to simulate future events (Addis et
127 al., 2016).

128 To the best of our knowledge, no study has so far investigated the *in situ* link between cardiac vagal
129 control and specific properties of thought, including MTT. Given its neurovisceral basis underlying
130 both components and its implication for self-regulation, we assumed that greater tonic cardiac vagal
131 control and reactivity would be associated with more adaptive MTT.

132 1.3 vmHRV stimulation through biofeedback

133 Manipulating vmHRV during cognitive processing could shed light on the causal relationship between
134 autonomic and cognitive processes, overcoming the interpretation limitations of previous correlational
135 studies. One promising tool is HRV biofeedback, which is a self-regulation technique, typically based
136 on slow breathing, that increases vmHRV (Lehrer & Gevirtz, 2014). The training evokes physiological
137 coupling in the cardiovascular system due to resonance effects of the baroreflex system and respiratory
138 drive of cardiac vagal control, leading to high-amplitude cardiac oscillations. Those oscillations are
139 hypothesized to stimulate brain activity and connectivity underlying autonomic and emotion regulation
140 (Mather & Thayer, 2018).

141 Regular training showed to alleviate mental health problems, such as anxiety and depression (Goessl
142 et al., 2017; Pizzoli et al., 2021), and improve cognitive performance in the healthy population (Bögge
143 et al., 2022; Sutarto et al., 2013; Tinello et al., 2021). Moreover, HRV biofeedback has been shown to
144 concomitantly affect vmHRV and brain networks involved in cognitive processes crucial to our
145 thoughts, such as attention, thinking about oneself, emotional processing, and the capability to inhibit
146 unwanted impulses or distractors (Bachman et al., 2023; Cho et al., 2023; Nashiro et al., 2022a, 2022b;
147 Schumann et al., 2021). Also a single HRV biofeedback session can evoke increases in vmHRV that
148 carry over after (Bögge et al., 2022; Lehrer et al., 2003) and has shown to affect cognitive control
149 functions and mind wandering in the healthy, young adults (Blum et al., 2019; Prinsloo et al., 2011,
150 2013; Rockstroh et al., 2019).

151 Thinking about our past and future consumes a large part of our daily life and is crucial for our
152 wellbeing. For example, thinking about one's future is useful to make meaningful plans, whereas
153 constant rumination may lead to depressive symptoms. The possibility of affecting the cognitive
154 processes involved in thoughts about personal past and future also bears the potential to support

155 adaptive thinking. Consequently, it seems interesting to test the effect of HRV biofeedback on thought
156 processes like MTT and its psychophysiological underpinnings.

157 **1.4 Objectives and hypotheses**

158 A single session intervention study with alternating training and assessment phases was designed that
159 investigated the immediate effect of HRV biofeedback on the MTT properties compared to a paced-
160 breathing control exercise. Furthermore, the study aimed at testing the psychophysiological association
161 between cardiac vagal control reactivity and MTT by manipulating vmHRV through HRV
162 biofeedback. To overcome shortcomings of our previous protocol which showed no effects and
163 associations with cognitive control during non-emotional memory processing (low arousing and
164 neutral stimuli), (Bögge et al., 2023), MTT was cued by negative or positive personality trait-
165 adjectives.

166 It was assumed that higher cardiac vagal control reactivity and the biofeedback effect would be linked
167 to more adaptive MTT into the future (EFT) and past (EAM), and thus greater self-regulation. More
168 adaptive MTT was thought to be characterized by an increase in phenomenological experience of MTT
169 related to higher **self-referential processing, cognitive control, and self-enhancement** for positive
170 cues and decrease in phenomenological experience for negative cues. In this line it was hypothesized,
171 firstly, that greater vmHRV reactivity during positively-cued MTT is associated with greater personal
172 importance, self-perspective, vividness, outcome expectation, valence, and shorter event construction
173 time. Secondly, the relationship between vmHRV reactivity and MTT properties is inverted during the
174 during negatively-cued MTT. Thirdly, HRV biofeedback enhances adaptive MTT and cardiac vagal
175 control reactivity. MTT temporality (future, past), was assumed to moderate only the relationship
176 between vmHRV and cognitive control, with associations being strongest when executive demands are
177 high, i.e., during EFT. Additionally, we included tonic measures of vmHRV during MTT, for which
178 the same assumptions were made, with higher tonic vmHRV indicating more adaptive MTT. Finally,
179 an exploratory analysis tested the effects of cardiac vagal control and HRV biofeedback on thought
180 properties of resting-state mind wandering, assessed at experiment start and end.

181 **2 Materials and Methods**

182 **2.1 Participants**

183 **2.1.1 Power analysis**

184 Based on a priori conducted power analysis using G*Power 3.1.9.7, a minimum sample size of 40
185 participants was determined ($\alpha = 0.05$, $\beta = 0.80$, two-tailed). Two separate calculations were
186 performed: one for the group effect between repeated measures ($n = 6$) of the MTT task and one for
187 the correlations between repeated measures of vmHRV and MTT characteristics. Given the lack of
188 comparable studies, we estimated a sample size that would allow the detection of moderate effects
189 larger than a Cohen's f of 0.3. The repeated measures correlation coefficient was assumed not to be
190 larger than 0.30 due to the usually high variability between MTT probes (Colás-Blanco et al., 2022).
191 Previous literature found correlation coefficients of resting vmHRV with thought characteristics of

192 around $r = 0.30$ (Feeling et al., 2021; Gillie et al., 2014). Due to the variability in the repeated measures
193 data, a coefficient of $r = 0.2$ was estimated. The first and second calculation yielded a minimum sample
194 size of 40 and 33, respectively. Consequently, the target sample size was set to 40. Likewise, no study
195 has been so far conducted on the association between cardiac vagal control and resting thoughts. For
196 the exploratory analysis, this study was powered to detect an HRV biofeedback effect of $\eta_p^2 = 0.049$
197 and a correlation coefficient of $r = 0.306$.

198 **2.1.2 Recruitment**

199 To account for possible exclusions, 50 volunteers were recruited via an experiment dissemination
200 platform and a course platform accessible by psychology students of the Université Paris Cité. After
201 exclusions, 40 participants were kept for the final data analysis (see below). Participants were paid 30€
202 in gift-cheques or received course credits for agreeing to participate. The study was conducted in
203 compliance with the ethical standards according to national legislation (Jardé law) and with the 1964
204 Helsinki Declaration and its later amendments. Ethical approval to conduct the study was obtained
205 from the Université Paris Cité institutional review board (N° IRB: 00012022-130). All participants
206 provided their informed and written consent right before the experiment started. They were then
207 assigned to either a biofeedback group (BG) or an active control group (CG) using block randomization
208 (block size = 4) stratified by sex (male, female). Participants remained blind to the assignment, the
209 existence of another group, and the hypotheses throughout the experiment. The experimenters were
210 also blind to the group assignment during cognitive task instructions and familiarization (see
211 “Familiarization”).

212 **2.1.3 Inclusion criteria**

213 Participants were required to be healthy adults between 18 – 35 years old who are native French
214 speakers and have acquired university entrance qualification. Subjects were excluded from
215 participation if they reported to be concerned by at least one of the following conditions: history or
216 treatment for psychiatric, neurological, neurodevelopmental, cardiac, or severe respiratory disorders,
217 hypo- or hyperthyroidism, severe inflammation, type 2 diabetes, treatment with a cognitive impact,
218 frequent dizziness or nausea, vertigo, impaired but not corrected visual or auditive capabilities, reading
219 problems, substance abuse, and medication that affects the cardiac activity. Furthermore, high scores
220 of anxiety and depression and the subjective feeling of pain and being sick led to exclusion (see
221 following section). In addition, where physiological data indicated a potential arrhythmia, participants
222 were excluded (see section 2.3). Finally, participants were asked not to smoke or vaporize two hours
223 preceding the experiment, not to consume caffeinated substances or alcohol or any other stimulative
224 or sedative substances (e.g., medicaments, drugs) on the experiment day, and not to exercise intense
225 physical activity 24 hours preceding the experiment. Inclusion and exclusion criteria were checked at
226 the beginning of the experiment. Due to ethical reasons, all participants who registered via the course
227 platform to earn course credits were eligible to participate. Their data were excluded afterwards if
228 found to be ineligible for data analysis. In total 10 participants were excluded: four due to high scores
229 of anxiety and/or depression, three due to interruption of the experiment by the subject, two due to

230 medical conditions and medication intake, and one due to cigarette and caffeine consumption before
 231 the experiment.

232 **2.1.4 Participants characteristics**

233 Participants characteristics were assessed at the beginning of the experiment through digitalized
 234 questionnaires and visual analog scales presented on the computer screen using customized Python
 235 scripts and the Python package Neuropsychia (Makowski & Dutriaux, 2017). Variables of the first
 236 questionnaire are described in the supplementary material SM1 (<https://osf.io/xgfdc/>). In addition,
 237 levels of state and trait anxiety as well as depression were determined by means of the French
 238 translation of the State-Trait Anxiety Inventory (STAI; Schweitzer & Paulhan, 1990; Spielberger,
 239 1983) and Beck Depression Inventory (Beck & Beamesderfer, 1974; Collet & Cottraux, 1986),
 240 respectively. Participants were excluded if the tests indicated either a high or very high score (state or
 241 trait anxiety: >55, depression: >15) or if any of the pain or sickness scores were higher than 5.
 242 Furthermore, visual imagery capacities were assessed based on the imagery part of the Individual
 243 Differences Questionnaire (Paivio, 1971).

244 Participants characteristics did not statistically significant differ ($\alpha = 0.05$) between groups (Table 1),
 245 except for a moderate difference in weekly sports activity. The sample consisted to 72.5% of students
 246 from diverse fields (BG: 13, CG: 16). Only four participants reported to have had prior experience with
 247 biofeedback (BG: 3).

248 **Table 1 – Sample characteristics**

249 *Note.* Mean values and standard deviations are presented per group. Groups were compared using Student’s t-
 250 test if not indicated otherwise. If applicable, units or the scale range are given in parentheses after each
 251 variable. Uncorrected p-values are reported.

252 ^a The variable is not normally distributed. The median, inter-quartile-range (in parenthesis) and results of the
 253 Mann-Whitney U test are reported.

254 ^b Groups were compared using the Fisher’s Exact test.

255 ^c A smaller value indicates greater cognitive inhibition.

256

Variable	Mean values		Group comparison			
	Biofeedback Group (n = 22)	Active Control Group (n = 18)	Estimate	Statistic	p	Effect size
Demographics						
Age (years)	24.99 (5.48)	23.84 (4.22)	1.144	0.727	0.472	0.231
Sex (% female) ^b	68.2%	66.7%	1.070	-	0.999	-
Laterality (% right-handed) ^b	81.8%	72.3%	1.753	-	0.673	-
Higher education (years)	2.82 (2.34)	3.22 (1.70)	-0.404	-0.611	0.545	-0.194
Compensation (% course credits) ^b	13.6%	11.1%	1.256	-	0.999	-
Neuropsychological assessment						
State Anxiety – STAI-Y1 (20-80)	30.86 (7.03)	32.00 (7.86)	-1.136	-0.482	0.632	-0.153
Trait Anxiety – STAI-Y2 (20-80)	40.23 (9.80)	42.56 (11.13)	-2.328	-0.703	0.486	-0.224
Depression – BDI (0-39)	4.32 (3.98)	5.11 (4.03)	-0.793	-0.623	0.537	-0.198

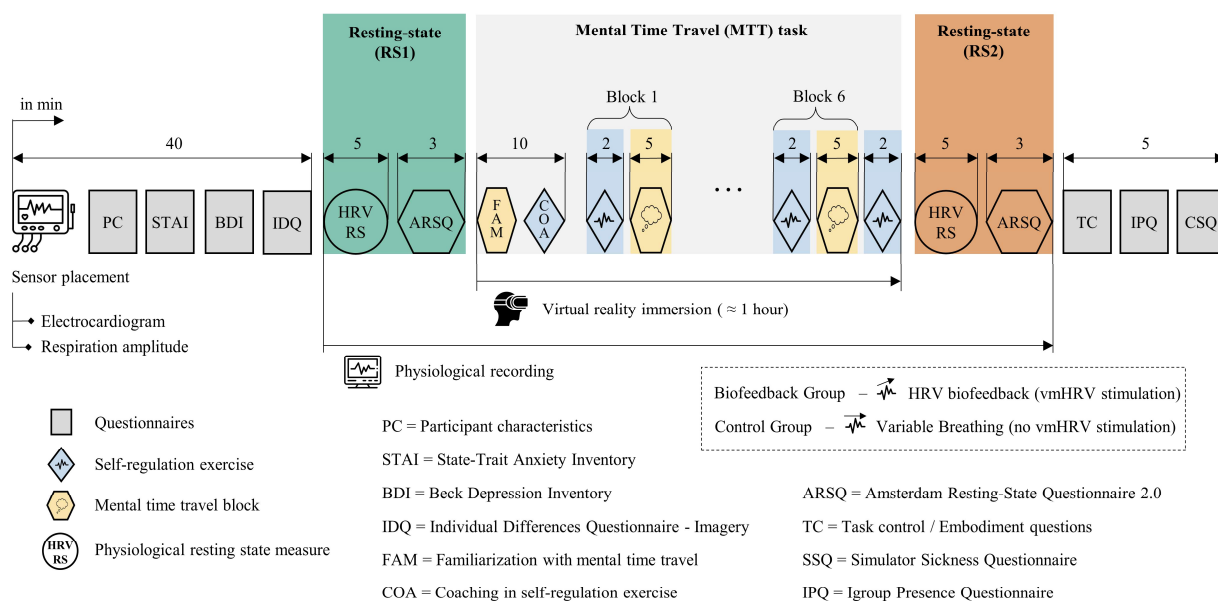
The role of cardiac vagal control in thoughts

Visual Imagery – IDQ (0-23)	18.45 (3.38)	17.78 (4.41)	0.677	0.550	0.586	0.175
Medical and physiological aspects						
New Body-Mass-Index ^a	22.63 (3.39)	20.90 (5.14)	1.952	127	0.055	0.305
Sport activity (hours/week) ^a	2.50 (1.88)	1.00 (0.75)	1.000	110.5	0.015	0.386
Smoking status ^b			0.342	-	0.258	-
Abstainers / Very light smokers (%)	72.7%	88.9%				
Light and moderate smokers (%)	27.3%	11.1%				
Heavy smokers (%)	0%	0%				
Alcohol consumption ^b			0.608	-	0.526	-
Abstainers / Light drinkers (%)	54.6%	66.7%				
Moderate drinkers (%)	45.4%	33.3%				
Heavy drinkers (%)	0%	0%				
Hormonal contraception (%) ^b	22.7%	16.7%	0.687	-	0.709	-
Controlled breathing (% some expertise) ^b						
Sleep deprivation last night (hours)	-0.83 (1.30)	-0.69 (1.05)	-0.134	-0.354	0.725	-0.113
Subjective perception						
Current fatigue (0-10)	3.50 (1.92)	3.61 (2.30)	-0.111	-0.166	0.869	-0.053
Fatigue interference (0-10)	2.18 (1.97)	2.44 (2.26)	-0.263	-0.393	0.696	-0.125
Current pain (0-10) ^a	0.00 (1.00)	0.00 (0.00)	0.000	167	0.304	0.165
Pain interference (0-10) ^a	0.00 (0.75)	0.00 (0.00)	0.000	163.5	0.185	0.213
Current feeling of sickness (0-10) ^a	0.00 (1.00)	0.00 (0.00)	0.000	173	0.409	0.133
Feeling of sickness interference (0-10) ^a	0.00 (0.00)	0.00 (0.00)	0.000	194	0.868	0.030
Current stress (0-10)	1.27 (1.16)	1.39 (1.50)	-0.116	-0.276	0.784	-0.087
Stress within last 12 hours (0-10)	2.59 (1.87)	2.61 (2.40)	-0.020	-0.030	0.976	-0.010

257 2.2 Procedure

258 2.2.1 Overview

259 All participants were assessed individually in an experimental room of our laboratory within a single
 260 session of around 2.5 hours (Figure 1). During the experiment, participants remained visually shielded
 261 from the experimenter, seated in front of a desk equipped with a monitor, keyboard, and a virtual reality
 262 (VR) setup. After completing the characteristics assessment, participants performed a MTT task in
 263 virtual reality to assess the phenomenological characteristics of retrospective and prospective episodic
 264 event simulation following a series of short self-regulation exercises. Depending on the group
 265 assignment, participants performed either HRV biofeedback (BG) or variable breathing as a control
 266 exercise (CG) that does not stimulate vmHRV. Resting-state thoughts were evaluated by means of the
 267 Amsterdam Resting State Questionnaire 2.0 (ARSQ; Diaz et al., 2014) following a 5-minute period of
 268 quiescence before (RS1) and after (RS2) the MTT task. Finally, at the experiment end, further control
 269 measures concerning the MTT task were taken. Physiological recordings of cardiac, respiratory, and
 270 electrodermal activity were derived during the MTT task and the resting-state periods.



271 **Figure 1 – General procedure**

272 *Note.* Participant characteristics were recorded at the beginning of the experiment. Resting-state thoughts were
 273 assessed (i.e., ARSQ) before and after the mental time travel (MTT) task. During MTT participants were asked
 274 to simulate and subsequently evaluate in total 24 episodic events in the future and in the past (12 each). The
 275 MTT task was divided into six blocks of four simulations, with each block preceded and followed by an exercise
 276 to manipulate vmHRV. The biofeedback group performed heart rate variability biofeedback based on slow-
 277 paced breathing to increase vmHRV and the control group a paced natural-breathing exercise that does not affect
 278 vmHRV. This figure has been designed using images from Flaticon.com.

279 **2.2.2 Technical setup**

280 Physiological data, including a 3-Lead electrocardiogram (ECG) and changes in thoracic-abdominal
 281 circumference (respiration amplitude) were collected with the MP150 data acquisition system
 282 (BIOPAC Systems, Inc., 2015) according to the manufacturer’s guideline (BIOPAC Systems, Inc.,
 283 n.d., 2016). ECG surface electrodes, following Einthoven’s triangle, were placed on the torso that
 284 collected data from Lead II. Signals were sampled at a rate of 1000 Hz. A heart rate waveform was
 285 calculated online based on beat-to-beat time intervals for monitoring and biofeedback purposes. During
 286 the recording, participants were instructed to sit upright, rest their arms in their laps, avoid moving and
 287 talking, and breath naturally unless instructed otherwise.

288 The VR system and integration of the physiological system were based on our previous studies (Bögge
 289 et al., 2022, 2023). Video material along with supplementary materials are available on a public
 290 repository (<https://osf.io/xgfdc/>) VR permits an embodied and contextualized immersion in realistic
 291 settings with a high self-presence, and thus ecological and controlled setups (Slater et al., 2022). A
 292 head-mounted display, including headphones, and two hand controllers (HTC Vive Pro) were used to
 293 for immersion. In the VR environment, participants were embodied by a human avatar of the same
 294 gender and age in the first-person perspective sitting on a lonely beach and gazing at the open sea. Sea
 295 sounds matching the scenery were played via the headphones. The headset and controllers established

296 visuomotor real-time synchronization between the physical body and the artificial avatar body for the
 297 head, arms, hands, and legs. For each time travel block, the environment was exchanged, except for
 298 the avatar, by a dark blue and empty space without any audio output to reduce perceptual bias during
 299 event simulation and potential eye strain. All instructions, cues, and response options were displayed
 300 as white text in the central view in front of the avatar. The right or left controller recorded the users'
 301 responses depending on their laterality. Cardiac signals (i.e., ECG, heart rate) were fed to the VR
 302 system allowing for their online display (i.e., biofeedback).

303 2.2.3 Training

304 The self-regulation procedure was largely based on our previous study (Bögge et al., 2023). During the
 305 MTT task, participants exercised either HRV biofeedback or a variable breathing exercise based on
 306 paced-breathing in virtual reality (Figure 2). HRV biofeedback followed principles of resonance
 307 frequency training (Lehrer et al., 2000, 2013) to enhance vmHRV through slow breathing around the
 308 resonance frequency of 6 cycles per minute (cpm). Variable breathing was implemented as an active

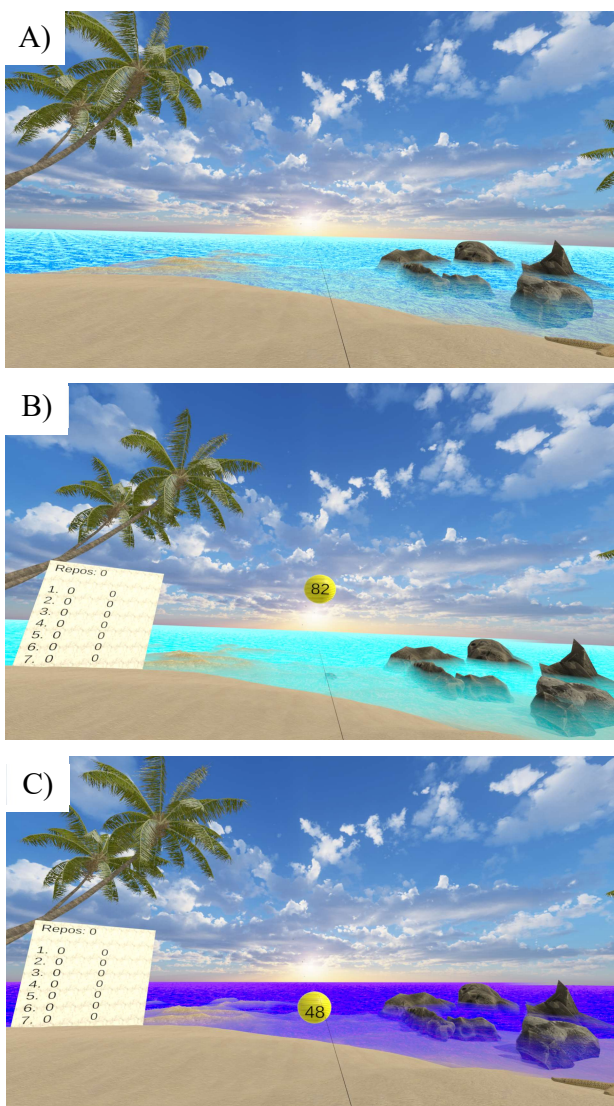


Figure 2 – Heart rate variability biofeedback in virtual reality

Note. **A)** Virtual reality (VR) environment without biofeedback. **B)** Biofeedback when heart rate is high (inspiration). **C)** Biofeedback when heart rate is low (expiration).

During heart rate variability (HRV) biofeedback participants followed vertically shuttling breathing pacer (yellow sphere) running at constant rhythm of 6 cycles per minute (0.1 Hz). The color of the sea displayed the current heart rate calculated from the beat-to-beat heart period of an electrocardiogram which was also numerically presented on the pacer. When heart rate was at the participants median level the sea had a natural color (A). It turned gradually blue during inspiration as heart rate rose (B) and violet during expiration as heart rate dropped (C). Participant could modulate breathing flow speed and volume to maximize heart rate amplitudes (i.e., maximal color change). They also had the option halt and resume the pacer to regulate the breathing rhythm on their own. Subjects in the control group followed pacer running at a variable rhythm between 12 and 16 cycles per minutes that mimicked natural breathing patterns. Feedback about their synchronicity with the pacer was numerically given on the pacer, but no heart rate biofeedback. Participants were asked to keep synchronicity levels high, but not to force deeper breathing. A marble stone on the left displayed feedback for each completed minute to either group (i.e., HRV calculated as RMSSD or mean synchronicity).

309 control exercise adapted from Leganes-Fonteneau et al. (2021) that mimics natural breathing patterns.
310 It also requires breathing self-regulation effort but does not increase vmHRV. Breathing was paced
311 during both exercises by a vertically shuttling sphere appearing in front of the avatar at a constant
312 rhythm of 6 cpm (HRV biofeedback) or a variable rhythm of 12 to 16 cpm (mean = 14 cpm), (variable
313 breathing). Participants could follow the pacer by breathing either through the mouth or nose, however,
314 nasal breathing was advised for the biofeedback group. During HRV biofeedback, the heart rate was
315 represented numerically on the sphere and by the color of the sea (i.e., sea turned gradually cyan/violet
316 when the heart rate increased/decreased). Besides following the pacer, participants were asked to adapt
317 their breathing (i.e., velocity, volume) to achieve high-amplitude fluctuations in the heart rate that were
318 synchronized with the breathing pattern. Contrary to the control condition, the breathing pacer during
319 HRV biofeedback served as guidance that participants could follow or not. The BG had the option to
320 freely halt and resume the pacer movement by point-clicking with one of the hand controllers.
321 Participants were advised to halt the pacer if they wished to adapt their breathing by purely focusing
322 on the colors of the sea and to resume the pacer if they struggled to increase vmHRV without its aid.
323 Furthermore, synchronous cardio-visual stimulation was performed by displaying heartbeat flashing in
324 the color intensity of the sea. This was done to help the subject with the interpretation of the
325 biofeedback. During variable breathing, instead of cardiac feedback, respiratory feedback was given
326 in form of the synchronicity level between the pacer and the actual respiration displayed numerically
327 on the pacer. Synchronicity was calculated for each paced ventilation cycle by determining the time
328 interval proportions of real to paced inspiration and expiration. In turn, inspiration and expiration time
329 intervals were determined from the maximal and minimal respiration amplitude within each paced
330 ventilation phase. Synchronicity ranged from -100 (inversely phased) to 100 (completely in-phase).
331 Participants in the CG were asked not to force deeper breathing and to maintain maximal synchronicity
332 during the whole exercise. If values dropped below 75 a beep was played to remind the participant to
333 focus on the task. In addition, a marble stone wall provided performance feedback during the exercise
334 for each completed minute (CG: mean synchronicity, BG: RMSSD).

335 2.2.4 Mental Time Travel Task

336 To investigate the immediate effect of HRV biofeedback on phenomenological characteristics of MTT,
337 an experimental task was designed to intermix MTT with the above-described exercise. After each
338 exercise phase, except for the last one, participants were asked to mentally travel in time (e.g., Colás-
339 Blanco et al., 2022) four times (Figure 3). For each block, they were asked to engage twice in EFT
340 (imagining a future event) and twice in EAM (recollection of a past event). At the beginning of each
341 trial, participants were informed about the targeted temporality of the event. Subsequently, the trial
342 was divided into 3 phases (Addis et al., 2007; Colás-Blanco et al., 2022): 1) event construction, 2)
343 event elaboration, and 3) thought probes. In the first phase, participants were presented for 3 seconds

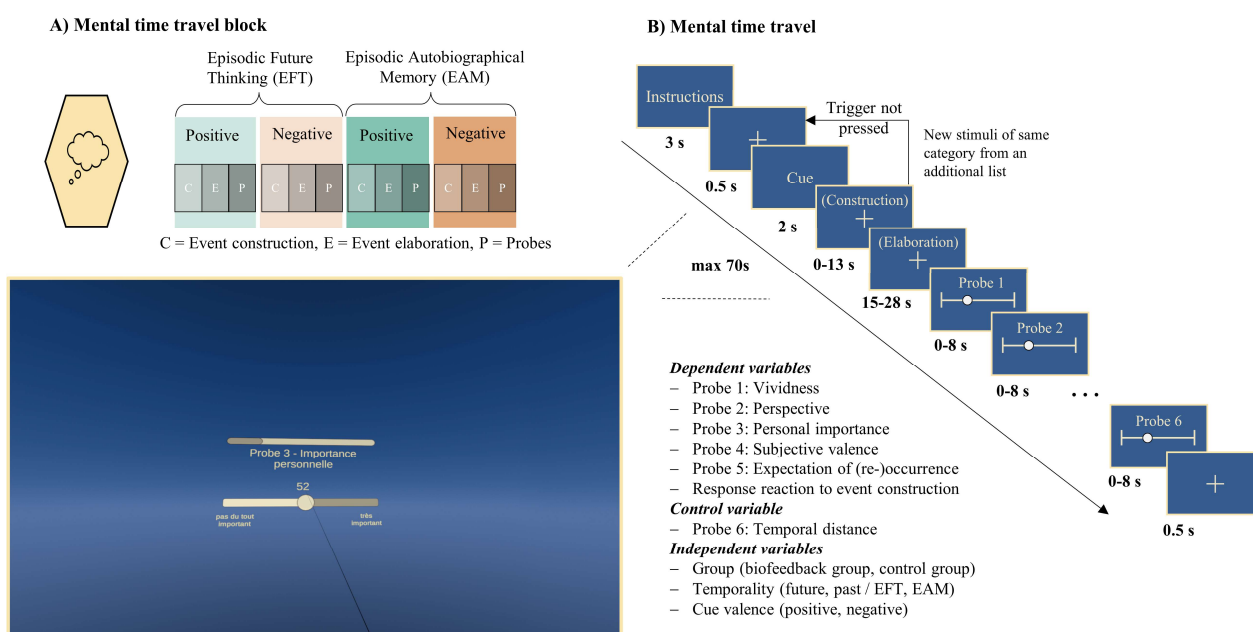


Figure 3 – Mental time travel in virtual reality

Note. A) Between self-regulation exercise phases, the virtual reality (VR) scene changed to an empty environment. Mental time travel blocks were divided into four episodic event simulations: two into the future (EFT) and two into the past (EAM). For both temporalities, mental time travel was cued by a negative or positive personality-trait adjective. Cue, temporality, and cue-valence order were counterbalanced. B) Participants were asked to evoke an event (construction) and press the VR controller trigger when one was found. They then had an additional 15 seconds to add details to the event (elaboration). If no event could be found within 15 seconds of stimuli onset the trial was repeated once with a backup cue. After the construction and elaboration (30 seconds) participants rated the phenomenological characteristics of their event on a continuous scale from 0 to 100 by using the VR controller.

344 with a cue-word describing a personality trait-adjective that was either positively valenced (e.g.,
 345 *enthusiastic, imaginative*) or negatively valenced (e.g., *selfish, lazy*), (one positive and one negative
 346 word for the future and past simulation, respectively; see <https://osf.io/xgfdc/>). Then, they had to
 347 mentally search and construct a specific personal event linked to this word, by either pre-experiencing
 348 an episode that might possibly happen in the future (EFT) or by re-experiencing an event of their
 349 personal past (EAM), (construction phase). Each personal event had to be unique, be specific in place
 350 and time and span a few minutes to some hours but not more than 24 hours and include at least the
 351 participants themselves, plus the person subject of the event, if it was not them. Furthermore, events
 352 should have occurred between two and five years ago or should possibly happen in two to five years.
 353 Participants confirmed successful event construction (i.e., event found) through button press of either
 354 of the VR controllers. Response reaction time from stimuli onset was recorded. In case they did not
 355 find any event within 15 seconds after stimuli onset, the trial was started again with a novel word of
 356 the same valence (positive or negative). If no event was found again, the trial was dropped, and the
 357 experiment proceeded to the next trial or phase. Upon successful event construction, participants were
 358 asked to mentally add details to the event, such as objects, persons, activities, feelings, or thoughts
 359 (elaboration phase), for which they were given additional 15 seconds. Finally, after 30 seconds have

360 elapsed since the stimulus onset, participants evaluated seven different properties of their simulation
361 (i.e., vividness, personal importance, perspective, valence, expectation of (re-)occurrence, temporal
362 distance; see osf.io/xgfdc/). Subjects rated thought probes on a visual analog scale from 0 to 100 that
363 appeared in front of their avatar by using the VR controller. Following each time travel block, the beach
364 environment was re-initiated, and participants had to continue immediately the exercise. Participants
365 were asked to refrain from performing rapid movements or talking or pronouncing their thoughts for
366 the whole duration of the task as this would disturb the physiological measurements. Scene changes to
367 and from the time travel environment were announced through a sound beep with a prior notice of 3
368 seconds. A total of six MTT blocks were completed, each containing every combination of the within-
369 group factors temporality (past, future) and item valence (negative, positive). For counterbalancing
370 purposes, stimuli were divided into sets of two containing one positive and one negative word. Any
371 block always contained the same two sets with fixed positions within the block (first and second set).
372 Block order was counterbalanced using a 6x6 balanced Latin square. The temporality order was
373 counterbalanced by doubling each of the six task versions and assigning the same temporality to either
374 the first set (first two stimuli) or the second set (last two stimuli). The order of the words within each
375 set, and thus the valence order, was randomized. Task versions were assigned based on dynamic
376 randomization stratified by group (see <https://osf.io/xgfdc/>).

377 **2.2.5 Task and training familiarization**

378 At the beginning of the immersion, participants were allowed one minute to freely look around to
379 discover the environment. Thereafter, participants were familiarized with the MTT task by completing
380 at least four simulations, first two into the past and then two into the future, based on neutral cue words
381 (e.g., “light-hearted”, “busy”). The procedure (i.e., construction, elaboration, probes) for each
382 simulation was the same as described above. All participants were trained on the same set of words
383 that did not occur elsewhere in the experiment. After travelling twice into the past, participants were
384 asked to describe one event of their choice. This was done to check if participants really recalled an
385 event that matches the pre-requisites (i.e., uniqueness, short duration, specific in place and time, etc.;
386 see <https://osf.io/xgfdc/> for the precise instructions). The same check was done after participants
387 completed the simulation into the future. Participants were informed about this check-up before
388 familiarization. During both checks, any remaining questions were clarified. If participants were unable
389 to successfully construct an event (i.e., it did not meet the specifications, or they did not want to talk
390 about their thoughts), the familiarization was repeated. The experimenters were unaware of the group
391 assignment during the familiarization or before. Group assignment was coded in the virtual reality
392 system and could a priori not be traced back. In this context, the VR system unblinded experimenters
393 only after the successful completion of the familiarization right before the coaching phase, when all
394 cognitive task instructions had already been given.

395 Participants were familiarized with the exercise directly before the MTT task. Individuals in the CG
396 were presented with the variable pacer and the synchrony feedback (see “Exercise”). As during the
397 exercise, they were asked to follow the pacer and keep the synchrony level above 75. Normal to shallow
398 breathing depth was advised to avoid hyperventilation and stimulation effects on HRV. Coaching was

399 completed when the synchrony of 5 consecutive cycles has been above 75. For participants in the BG,
400 at first only biofeedback was displayed and its meaning was explained (i.e., sea color turns blue: heart
401 rate increases; sea color turns violet: heart rate decreases). Participants were asked to breathe naturally
402 and to observe the fluctuations in the color of the sea for around 30 seconds. Subsequently, the goal of
403 the training, which is to increase heart rate fluctuations and cardiac-respiratory synchrony, was
404 explained. They were presented with the slow pacer which they were asked to follow while observing
405 the changes in the heart rate signal. Deeper and more prolonged inhalations than normal into the
406 abdomen were advised. We recommended participants who experienced difficulties in breathing at the
407 desired rhythm to reduce their normal breathing rate breath by breath until it matches the pacer's
408 rhythm. Furthermore, we asked participants to pay attention to and adjust their inhalation/exhalation
409 speed and volume (i.e., shallower/ deeper breathing), allowing them continuous and slow breathing.
410 Coaching of the BG was done as soon as they completed 5 breathing cycles following the pacer, where
411 significant heart rate changes were notable. After the familiarization, participants were asked whether
412 they experienced difficulties performing the task and the familiarization was repeated if necessary.
413 During the coaching period participants could freely ask questions or might be given additional
414 instructions by the experimenter.

415 **2.2.6 Resting-state measures**

416 Thoughts occurring during rest (i.e., mind wandering) were assessed right before (RS1) and after (RS2)
417 the MTT task using a computerized version of the ARSQ 2.0 (Diaz et al., 2014). ARSQ 2.0 is a
418 validated 38-items questionnaire (osf.io/xgfdc/) that assesses the properties of thoughts the participant
419 had during the 5-minute resting state period while sitting. We followed the original task instructions
420 by asking participants to rest the arms in the lap, refrain from moving, talking or sleeping, and to breath
421 naturally while keeping eyes closed until the experimenter signals the end of the resting phase.
422 Thereafter, participants filled out the questionnaire by using the same setup as for the control measures.
423 The ARSQ 2.0 assessed thoughts in 10 dimensions, each based on three probes: 1) Discontinuity of
424 Thoughts, 2) Theory of Mind, 3) Self, 4) Planning, 5) Sleepiness, 6) Comfort, 7) Somatic Awareness,
425 8) Health Concern, 9) Visual Thought, 10) Verbal Thought. The probe order was randomized except
426 for the last two validation items. The procedure between RS1 and RS2 was identical and both
427 questionnaires were unannounced. Furthermore, resting-state measures were used to derive baseline
428 physiological measures.

429 **2.2.7 Task control measures**

430 For both groups, task control variables were assessed at experiment end using a computerized visual
431 analogue scale of 0-10 for levels of currently perceived fatigue (0 being “no fatigue”, 10 being “extreme
432 fatigue”) and general attention to the exercise as well as to event simulation during the MTT task (0
433 being “not attentive at all”, 10 being “extremely attentive”). Furthermore, the level of presence in the
434 VR and VR-induced discomfort were assessed by the Igroup Presence Questionnaire (IQP; Schubert
435 et al., 2001) and Simulator Sickness Questionnaire (SSQ; Kennedy et al., 1993), respectively.

436 Task controls did not differ between groups for any of the variables (osf.io/xgfdc/). Linear mixed effect
437 models revealed a large main test effect on fatigue, $F(1,38) = 20.42$, $p < .001$, $\eta^2 = .349$, indicating
438 that participants were significantly more fatigued after than before experiment. Furthermore, Levene
439 test showed a difference in group variability for attention during MTT task (higher variability in BG),
440 $(1, 38) = 4.796$, $p = 0.035$, indicating that HRV biofeedback evoked higher variability in attentive
441 levels to the MTT.

442 2.3 Data processing

443 Physiological recordings were manually inspected, and artefacts removed using AcqKnowledge 5.0.4
444 Software (BIOPAC Systems, Inc., 2019). Recordings were then divided into segments corresponding
445 the phases of the overall and MTT task procedure: resting-state phases RS1 and RS2 (each 300
446 seconds), exercise (120 seconds), MTT per trial (construction and elaboration, 30 seconds). Segments
447 of the electrocardiogram and respiration amplitude were individually processed with the Python
448 package NeuroKit2 (Makowski et al., 2021) at default settings, unless otherwise specified.
449 Preprocessing included a Butterworth high pass filter at of 0.5 Hz as well as a notch filter at 50 Hz for
450 the electrocardiogram and a bandpass filter of 0.05 – 1 Hz for the respiration amplitude. Artefacts in
451 the heart period signal were detected and corrected as described by Lipponen & Tarvainen (2019). The
452 root mean square successive difference in the heart period series (RMSSD) was assessed as a measure
453 of vmHRV following guidelines of Shaffer & Ginsberg (2017) and the Task Force of the European
454 Society of Cardiology and the North American Society of Pacing and Electrophysiology (1996).
455 Furthermore, the mean heart rate as well as the mean rate and mean amplitude for the respiration (only
456 for resting state and exercise segments) were derived as control variables. Further information on the
457 processing can be found in the NeuroKit2 documentation (Makowski, 2023). The complete
458 physiological data set of a participant was excluded in the case of a potential arrhythmia (i.e.,
459 proportion of ectopic beats to total beats $>2\%$, average heart rate <40 bpm or >100 bpm at both resting-
460 state measures). Segments were excluded whenever R peaks could not be properly detected or
461 corrected (i.e., large and unexpected spikes in the heart rate signal). Furthermore, MTT trials in which
462 participants did not evoke an event were excluded. From a total of 1288 segments, 1266 were included
463 for the final analysis (three segments were excluded due to R peak correction failures, 19 because no
464 event was found). Finally, RMSSD as well as the event construction time values were transformed
465 with the natural logarithm due to violation of the normality assumption. Reactivity (phasic) values of
466 RMSSD were calculated for each segment as the baseline change ratio percentage by dividing the raw
467 RMSSD score by the raw RMSSD of the RS1 baseline phase and subtracting 1 from the results for a
468 more intuitive interpretation. Thus, positive phasic RMSSD values represent an increase in RMSSD
469 from baseline (vagal activation), and negative phasic RMSSD values a decrease (vagal withdrawal).
470 Phasic heart rate was computed in the same fashion.

471 2.4 Data analyses

472 The analysis was carried out with R 4.3.1 (R Core Team, 2023). Inference was based on the standard
473 $p < .05$ criteria. All tests were two-tailed, and uncorrected p-values are reported. The post-hoc

474 Benjamini-Hochberg false discovery rate (FDR)-controlling procedure at $\alpha = 0.05$ adjusted for multiple
475 comparisons (Benjamini et al., 2009; Benjamini & Hochberg, 1995). Statistical significance after
476 correction is reported in the text and tables. The analysis tested the correlations between phasic measure
477 RMSSD ratio representing vmHRV reactivity (see section above) and thought properties as well as the
478 effect of HRV biofeedback on RMSSD ratio and thought properties. MTT variables included the
479 phenomenological characteristics of MTT (i.e., vividness, personal importance, perspective, subjective
480 valence, expectation of (re-)occurrence, temporal distance) and the log-transformed event construction
481 response time.

482 **2.4.1 Psychophysiological association during mental time travel**

483 Correlations were performed between phasic RMSSD and MTT variables at every condition level
484 (positive future, negative future, positive past, negative past) across trials. Furthermore, to provide a
485 more global association score, correlations were performed for conditions pooled together. The
486 spearman correlation coefficient ρ was calculated since MTT variables were found to be non-normal
487 distributed across and at combined condition levels. Furthermore, for exploratory purposes, on-task
488 tonic RMSSD (e.g., RMSSD during MTT) associations with thought properties were considered,
489 following the same analysis, since we assumed that phasic and tonic RMSSD could reveal distinct
490 patterns. The analysis was accompanied by the investigation of correlations with heart rate ratio to
491 check for potential confounding effects and a more profound investigation of cardiac control. These
492 results are presented in the supplementary materials.

493 **2.4.2 Psychophysiological effect of HRV biofeedback during mental time travel**

494 After a physiological manipulation check, the effect of HRV biofeedback on the phasic measure
495 RMSSD ratio representing vmHRV reactivity (see section above) and thought properties was tested.
496 Variables were analyzed based on linear mixed effect regression (LMER) models using the *lmerTest*
497 3.1.3 package (Kuznetsova et al., 2020) and allowing for random coefficients across subjects to
498 enhance statistical power and Type-1 error control (Yang et al., 2014). Residuals were found across
499 tests to be normally distributed. Degrees of freedom were determined using the Satterthwaite approach
500 and restricted maximum likelihood model to further increase Type-1 error control (Luke, 2017).
501 Estimated marginal means (EMM) were contrasted using the *emmeans* 1.8.3 (Lenth et al., 2023)
502 package. Effect sizes derived from contrasts were based on the Cohen's d and interpreted as small,
503 medium, and large for scores of 0.2, 0.5, and 0.8 (Cohen, 1988). Reference conditions were RS1, CG,
504 negative items, and past stimulation for the test, group, item valence, and temporality factors,
505 respectively.

506 Correct manipulation by the HRV biofeedback system was controlled by checking physiological
507 measures across the main phases (RS1, exercise, MTT, RS2). Group differences at RS1 were checked
508 for all physiological parameters using independent t-tests. Group differences for RMSSD ratio and
509 heart rate ratio were tested by group main effects (LMER: \sim Group * Block) during the exercise phase
510 and by independent t-tests at RS2 to check whether vmHRV manipulation through biofeedback has

511 worked. Planned one sample t-tests verified whether ratio values were significantly different from 0
512 for groups combined or for each group separately, if a previous group difference was found.

513 RMSSD ratio during MTT as well as MTT variables were analyzed by separate LMER models which
514 included block and temporality order as random factors ($DV \sim \text{Group} * \text{Item Valence} * \text{Temporality} +$
515 $(1|\text{Participant}) + (1|\text{Block}) + (1|\text{Temporality Order})$). Where significant interaction effects involving the
516 group factor were found, pairwise comparison were performed. The same analysis performed on tonic
517 on-task RMSSD was added as a control to see if patterns of vmHRV reactivity were also reflected in
518 tonic measures. Since RMSSD (ratio) and heart rate (ratio) are moderately-to-strongly associated (e.g.,
519 Bögge et al., 2023; Shaffer & Ginsberg, 2017), heart rate ratio and heart rate were tested additionally
520 to check if changes in RMSSD derived purely from changes in heart rate. Models were retested with
521 heart rate (ratio) as a covariate to see if tests persisted after heart rate control.

522 2.4.3 Resting state thoughts

523 As part of an exploratory analysis of resting state thoughts, all ten factors as well as all the three non-
524 factor and five validation items were derived from the ARSQ 2.0. An overall score of thought activity
525 was calculated by taking the mean of all 10 factors excluding Sleepiness, Comfort, Somatic Awareness,
526 and Health Concern. Additionally, we added the item “I thought about the future” from the Planning
527 dimension (i.e., Future) as a complement to the non-factor items Past and Present. LMER tested the
528 Group x Test interaction effect for each of the 20 variables, tonic RMSSD and tonic heart rate at RS1
529 and RS2. Due to lower complexity of the models, they could be analyzed with the rstatix 0.7.1 package
530 that additionally provided partial eta square effect sizes. Finally, spearman correlations were computed
531 between ARSQ variables and tonic physiological measures as well as between changes in ARSQ scores
532 (RS1-to-RS2 differences) and changes in physiological resting state activity (phasic RMSSD and
533 phasic heart rate). Correlations between and across MTT and ARSQ variables are presented in the
534 supplementary materials (<https://osf.io/xgfdc/>).

535 3 Results

536 3.1 The relationship between vmHRV and mental time travel

537 Spearman correlations of RMSSD ratio with each MTT variables on every factor level of valence and
538 temporality are presented in Table 2. After FDR correction, only vividness was found to be positively
539 correlated with RMSSD ratio during positive EFT ($\rho = 0.22, p = 0.026$). A post hoc check based HRV
540 reactivity values commonly used in literature (task HRV – resting HRV) revealed the same results (ρ
541 $= 0.21$, FDR-corrected $p = 0.043$). Globally (conditions pooled), higher RMSSD ratio during MTT
542 was linked to higher vividness, $r = 0.08, p = 0.014$ and more observer perspective, $r = -0.09, p = 0.008$,
543 but not to construction time, $r = -0.01, p = 0.852$, personal importance, $r = -0.02, p = 0.553$, subjective
544 valence, $r = 0.01, p = 0.748$, expectation of (re-)occurrence, $r = -0.01, p = 0.798$, or temporal distance,
545 $r = 0.07, p = 0.055$.

546 **Table 2 – Associations between vmHRV reactivity and properties of mental time travel**

547 Spearman correlations between RMSSD ratio during mental time travel (MTT, construction and elaboration
 548 phase) and the MTT-associated thought properties across conditions (phenomenological properties as well as
 549 the response reaction time until an event was evoked) are presented. Uncorrected p-values are presented, and
 550 significant results before FDR correction are marked in bold. After correction, only vividness during positive
 551 future thinking was found to be associated with RMSSD ratio.

Variable	RMSSD ratio during mental time travel (Spearman correlations)							
	Future				Past			
	Positive		Negative		Positive		Negative	
	ρ	p	ρ	p	ρ	p	ρ	p
Construction time (ln)	-0.12	0.070	-0.02	0.747	0.02	0.723	0.08	0.216
Vividness	0.22*	<.001	0.05	0.441	-0.05	0.455	0.08	0.257
Perspective	-0.11	0.089	-0.09	0.163	-0.09	0.156	-0.04	0.588
Personal importance	0.12	0.065	0.00	0.955	-0.01	0.875	-0.14	0.040
Subjective Valence	0.07	0.312	0.03	0.675	0.02	0.710	0.06	0.38
Expectation of (re-)occurrence	-0.02	0.726	-0.03	0.668	0.00	0.946	0.06	0.348
Temporal distance	-0.06	0.368	0.10	0.150	0.16	0.018	0.06	0.425

552 * $p < 0.05$ after Benjamin-Hochberg FDR correction.

553

554 Spearman correlations of tonic RMSSD with each MTT variables on every factor level of valence and
 555 temporality are presented in Table 3. After FDR correction, only personal importance was found to be
 556 negatively correlated with RMSSD during negative EAM ($p = 0.005$). Globally (conditions pooled),
 557 higher tonic RMMSD during MTT was linked to lower expectation, $r = -0.140$, $p < 0.001$ and lower
 558 importance, $r = -0.110$, $p < 0.001$, but not to construction time, $r = 0.00$, $p = 0.929$, vividness, $r = 0.00$,
 559 $p = 0.851$, perspective, $r = 0.00$, $p = 0.936$, subjective valence, $r = 0.00$, $p = 0.993$, or temporal distance,
 560 $r = 0.01$, $p = 0.728$. Intra-subject variability was calculated as the summarized correlation coefficient
 561 between repeated measures (<https://osf.io/xgfdc/>). Generally, high variability could be observed across
 562 variables and conditions. Greatest stability (low variability) could be observed for vividness and
 563 personal importance responses during negatively-cued EAM.

564

565 **Table 3 – Associations between tonic on-task vmHRV and properties of mental time travel**

566 Spearman correlations between tonic RMSSD (raw values) during mental time travel (MTT, construction and
 567 elaboration phase) and the MTT-associated thought properties across conditions (phenomenological properties
 568 as well as the response reaction time until an event was evoked) are presented. Uncorrected p-values are
 569 presented, and significant results before FDR correction are marked in bold. After correction, only personal
 570 importance during negative past thinking was found to be associated with on-task RMSSD.

Variable	RMSSD Ratio during MTT (Spearman correlations)							
	Future				Past			
	Positive		Negative		Positive		Negative	
	ρ	p	ρ	p	ρ	p	ρ	p
Construction time (ln)	-0.11	0.081	-0.13	0.040	0.14	0.027	0.09	0.182
Vividness	0.14	0.035	0.09	0.185	-0.17	0.007	-0.08	0.231
Perspective	0.04	0.601	0.05	0.421	-0.08	0.199	0.03	0.689
Personal importance	0.07	0.278	-0.10	0.143	-0.11	0.097	-0.25*	<.001
Subjective Valence	0.02	0.808	0.04	0.574	0.02	0.710	0.07	0.316
Expectation of (re-)occurrence	-0.06	0.366	-0.09	0.198	-0.15	0.019	-0.17	0.009
Temporal distance	-0.08	0.253	0.026	0.703	0.04	0.563	-0.04	0.554

571 * $p < 0.05$ after Benjamin-Hochberg FDR correction.

572 Heart rate ratio had no global correlations with any of the thought properties. Global correlations of
 573 tonic heart rate partly reflected measures of tonic RMSSD but with less predictive power. For a more
 574 detailed account see the <https://osf.io/xgfdc/>.

575 FDR-corrected significant correlations could be found between RMSSD ratio during RS2 (i.e., change
 576 between resting-states) and expectation of (re-)occurrence during negative EAM as well as between
 577 heart ratio during RS2 and positive EFT. Participants that evaluated higher expectation of (re-
 578)occurrence of a negatively cued past episode, also exhibited greater RS2 RMSSD ratio (greater
 579 RMSSD increase between resting-states), $r = 0.26$, $p < 0.001$. Participants that took more time to
 580 construct a positively cued future event showed greater RS2 heart rate ratio (greater heart rate increase
 581 between resting-states), (<https://osf.io/xgfdc/>).

582 3.2 Manipulation check during resting and exercise phases

583 Physiological measures for each phase are listed in Table 4 and illustrated for RMSSD ratio and heart
 584 ratio in Figure 4. Respiratory rates during the exercise were close to the target values (BG: 6 cpm, CG:
 585 14 cpm), confirming that participants complied with the breathing instructions. Groups did not differ
 586 at the baseline level RS1 for any of the physiological measures including RMSSD ($p = 0.740$), heart
 587 rate ($p = 0.838$), respiration rate ($p = 0.172$), or respiration amplitude ($p = 0.106$). Group had a strong
 588 main effect on RMSSD ratio during the exercise phase, $F(1,38) = 6.50$, $p = 0.015$, $\eta^2 = 0.146$,
 589 confirming the successful vmHRV manipulation. One sample t-tests comparing RMSSD ratio in each
 590 group to the mean of 0 showed a large positive difference in BG, $M = 0.528$, $SD = 0.461$, $t(153) =$

591 14.20, $p = <0.001$, $d = 1.144$, but also a moderate difference in CG, $M = 0.207$, $SD = 0.384$, $t(125) =$
 592 6.042 , $p = <0.001$, $d = 0.538$. Heart rate ratio did not differ between groups during the exercise, $F(1,38)$
 593 $= 0.15$, $p = 0.701$, $\eta^2 = 0.004$. One sample tests including both groups revealed a moderate decrease
 594 in heart rate ratio, $M = -0.022$, $SD = 0.056$, $t(279) = -6.667$, $p < 0.001$, $d = -0.398$. Independent t-tests
 595 for measures at RS2 indicated no group differences in RMSSD ratio $t(38) = -0.511$, $p = 0.613$, $d = -$
 596 0.162 , or heart rate ratio, $t(38) = -0.565$, $p = 0.575$, $d = -0.180$. Post-hoc one sample t-tests demonstrated
 597 that RMSSD ratio was a little larger than 0, $M = 0.113$, $SD = 0.281$, $t(39) = 2.546$, $p = 0.015$, $d = 0.403$,
 598 and heart ratio moderately smaller than 0, $M = -0.034$, $SD = 0.054$, $t(39) = -3.958$, $p < 0.001$, $d = -$
 599 0.626 , across groups.

600 **Table 4 – Physiological measures across phases and groups**

601 Means and standard deviations of tonic and phasic (ratio) of heart rate variability (HRV), heart rate and
 602 respiratory function are presented across groups and experimental phases. Recordings were taken during the
 603 mental time travel (MTT) for each trial (30s), including the construction and elaboration phases, the self-
 604 regulation exercises before and after each MTT block (120s), and the 5-min resting-state periods before (RS1)
 605 and after (RS2) the MTT task (500s). For illustration purposes, the non-transformed values of root-mean square
 606 successive differences in the heart period (RMSSD) are presented, however, due to violation of the normality
 607 assumption log-transformed values were used in the analysis. Ratio values represent reactivity as a relative
 608 change to RS1, with positive and negative values indicating a respective increase and decrease. High-frequency
 609 (HF) HRV ratio and peak-to-trough respiratory sinus arrhythmia (P2T-RSA) ratio were added as controls for
 610 RMSSD ratio. P2T-RSA RSA confirms a respiratory-related cardiac vagal control increase evoked during HRV
 611 biofeedback seen in RMSSD. RMSSD probably increased as well during the control exercise due to a drop in
 612 heart rate.

Variable	Biofeedback Group ($n = 22$)				Active Control Group ($n = 18$)			
	RS1 ($n = 22$)	Exercise ($n = 154$)	MTT ($n = 513$)	RS2 ($n = 22$)	RS1 ($n = 18$)	Exercise ($n = 126$)	MTT ($n = 425$)	RS2 ($n = 18$)
RMSSD [ms] (no normality)	35.9 (24.2)	54.3 (30.8)	31.1 (28.0)	36.9 (26.6)	36.5 (23.1)	38.7 (30.0)	30.0 (17.0)	34.8 (17.0)
Heart rate [cpm]	78.0 (11.70)	75.6 (11.62)	78.0 (11.64)	75.6 (11.34)	77.3 (9.86)	75.8 (9.54)	77.4 (9.97)	74.2 (9.05)
RMSSD ratio [n.u.]	0.000 (0.000)	0.528 (0.461)	-0.054 (0.299)	0.134 (0.259)	0.000 (0.000)	0.207 (0.384)	-0.038 (0.434)	0.088 (0.311)
P2T-RSA ratio [n.u.]	0.000 (0.000)	2.075 (1.618)	-	0.257 (0.394)	0.000 (0.000)	0.116 (0.673)	-	0.006 (0.396)
Heart rate ratio [n.u.]	0.000 (0.000)	-0.025 (0.056)	0.001 (0.064)	-0.029 (0.064)	0.000 (0.000)	-0.019 (0.055)	0.002 (0.055)	-0.039 (0.039)
Respiration rate [cpm]	14.10 (3.23)	7.69 (2.58)	-	12.73 (3.21)	12.18 (4.44)	14.01 (0.48)	-	12.31 (3.37)
Respiration amplitude [V]	1.63 (1.36)	3.81 (2.97)	-	1.98 (2.00)	2.44 (1.79)	3.04 (2.05)	-	2.76 (2.14)

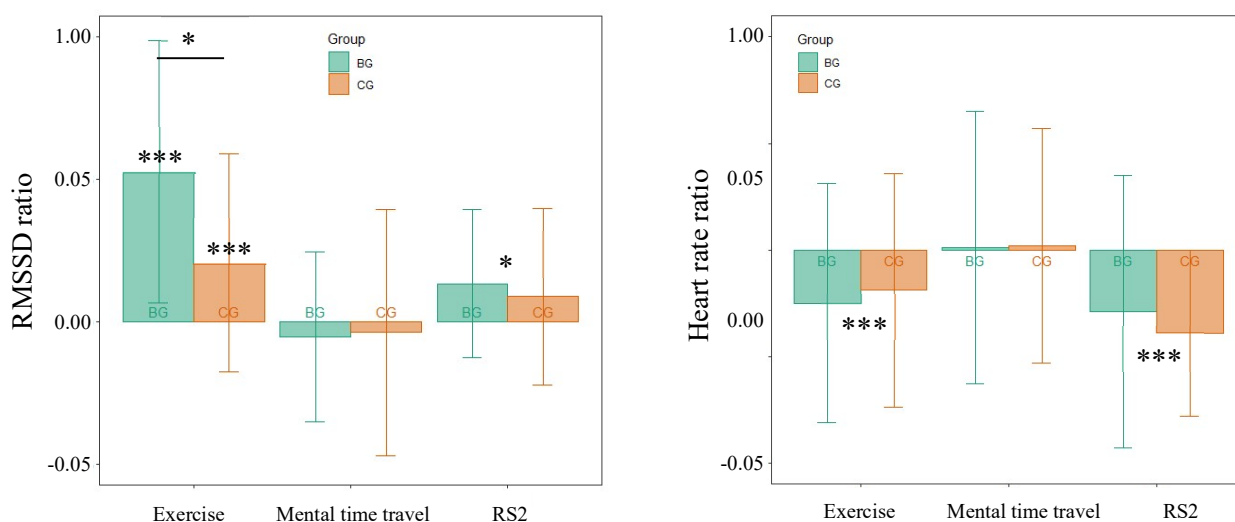


Figure 4 – RMSSD ratio and heart rate ratio across phases

Note. Measures of vmHRV reactivity (left) and heart rate reactivity (right) are presented across groups (BG = biofeedback group, CG = control group) and phases. Means and standard deviations are depicted. Reactivity indexed the relative change from baseline measured during the 5-min resting-state period before the mental time travel task. Positive values indicate an increase from baseline (vagal increase) and negative values a decrease (vagal withdrawal). Physiological signals were recorded during the self-regulation exercise (BG: HRV biofeedback, CG: paced-natural-breathing), mental time travel (event construction and elaboration), and a 5-min resting period after the mental time travel task. vmHRV reactivity differed between groups only in during the exercise, verifying the HRV manipulation. Asterisks signify a significant deviation from 0. * $p < 0.05$, *** $p < 0.001$.

613

614 3.3 Biofeedback effect on HRV reactivity during mental time travel

615 Linear mixed effect model revealed a significant group x item valence interaction effect on RMSSD
 616 ratio, $F(1, 892) = 3.98, p = 0.046$. Contrasts by item valence showed no group differences, but contrasts
 617 by group demonstrated that in CG positive items (EMM = -0.075, 95% CI = [-0.197 0.047]) were
 618 linked to lower RMSSD ratio than negative items (EMM = -0.008, 95% CI = [-0.130, 0.114]), $t(892)$
 619 = -2.479, $p = 0.013, d = -0.241$, whereas in the BG there was no difference between positive (EMM =
 620 -0.057, 95% CI = [-0.168, 0.052]), and negative items (EMM = -0.051, 95% CI = -0.161, 0.059), $t(892)$
 621 = 0.241, $p = 0.809, d = 0.022$. The valence difference in CG remained significant after FDR correction.
 622 No significant main effects of item valence, $F(1, 892) = 2.79, p = 0.095$, temporality, $F(1, 892) = 3.67,$
 623 $p = 0.056$, or any other group interactions ($p \geq 0.476$) were present. Contrasts confirmed that
 624 differences in RMSSD ratio from negative to positive items, $t(892) = -1.670, p = 0.095, d = -0.110,$
 625 and past to future simulations, $t(892) = -1.916, p = 0.056, d = -0.126$ were of negligible effect size. The
 626 overall RMSSD ratio averaged over condition was EMM = -0.048, 95% CI = [-0.128, 0.032].
 627 Considering the confidence intervals, RMSSD ratio was found not to be significantly different from 0
 628 at any condition level during MTT. Weekly sports activity (see section 2.1.4), when added as a
 629 covariate to the LMER model, was neither associated with RMSSD ratio nor did it change the model
 630 outcomes.

631 Heart rate ratio was added as a control variable to test if group effects on RMSSD ratio persisted
632 after controlling for heart rate ratio. As expected, RMSSD ratio and heart rate ratio moderately to
633 strongly correlated during RS1, MTT, and RS2 (supplementary materials). Heart rate ratio exhibited
634 a temporality main effect, $F(1,887) = 6.06$, with heart rate ratio being higher for future simulations,
635 $t(887) = 2.462$, $p = 0.014$, $d = 0.162$. Otherwise there were no main or interaction effects ($p \geq 0.207$).
636 When adding heart rate ratio as a covariate to the model predicting RMSSD ratio, the group x valence
637 interaction effect was reduced but was still trending, $F(1,887) = 2.66$, $p = 0.099$. Moreover, the valence
638 contrast in the CG remained significant, contrast: $t(886) = -1.992$, $p = 0.047$, $d = -0.194$.

639 We additionally checked whether the group x item valence effect was also reflected in tonic on-task
640 measures of RMSSD. Applying the same model on RMSSD revealed a similar trend, $F(1, 887) = 3.68$
641 $p = 0.055$, but no other group effect ($p > 0.155$). Parallel to RMSSD ratio, pairwise contrast showed
642 that RMSSD was lower for positive than negative items, $t(887) = -2.328$, $p = 0.020$, $d = -0.226$, but no
643 other differences ($ps > 0.155$).

644 When controlling for RS1 RMSSD by including it as an interaction term, a trending interaction between
645 group and RS1 RMSSD on RMSSD ratio occurred, $F(1, 35) = 4.10$, $p = 0.051$. This effect was not
646 moderated by item valence or temporality. Supplementary correlations analyses (ref) underline, that
647 higher RS1 RMSSD had a reducing effect on RMSSD ratio in the CG but not in BG.

648 3.4 Temporality and cue valence effect on thought properties during mental time travel

649 Main item valence and temporality effects were present for almost all MTT variables. Only the control
650 measures temporal distance was not affected by any factor. The overall projection period was around
651 3.5 years (overall EMM = 42.2, 95% CI = [39.6, 44.9] in months). Simulations were rated much more
652 positive when based on positive items compared to negative items, $d = 1.86$, $p < 0.001$, confirming the
653 valence manipulation. Therefore, from now on we will refer to positively-cued events as positive
654 events, and to negatively-cued events as negative events. In addition, positive items in contrast to
655 negative items were associated with shorter construction time, $d = -0.224$, $p < 0.001$, and greater levels
656 of vividness, $d = 0.143$, $p = 0.029$, personal importance, $d = 0.421$, $p < 0.001$, expectation of (re-
657)occurrence, $d = 0.404$, $p < 0.001$, and a stronger actor perspective, $d = 0.400$, $p < 0.001$. Future
658 simulations contrasted with past remembering linked to lower vividness, $d = -0.567$, $p < 0.001$, higher
659 personal importance, $d = 0.137$, $p = 0.036$, greater positive valence, $d = 0.261$, $p < 0.001$, and a higher
660 expectation of (re-)occurrence, $d = 0.260$, $p < 0.001$.

661 3.5 Biofeedback effect on thought properties during mental time travel

662 The group x valence interaction had a significant effect on vividness, $F(1,904) = 3.99$, $p = 0.046^*$.
663 Otherwise, there were no significant group or group interaction effects on any MTT variable, except
664 for a trending but not significant effect on construction time (see <https://osf.io/xgfdc/> for the full table).
665 Pairwise contrast showed that vividness did not differ between groups but within groups. Positive items
666 (EMM = 62.7, 95% CI = [57.0, 68.4]) were linked to greater **vividness** than negative items (EMM =
667 56.5, 95% CI = [50.7, 62.2]) in the BG, $t(904) = 3.128$, $p = 0.002$, $d = 0.273$, but there was no difference

668 between positive (EMM = 63.4, 95% CI = [57.0, 69.7]) and negative (EMM = 63.1, 95% CI = [56.8,
669 69.5]) items in the CG, $t(904) = 0.126$, $p = 0.899$, $d = 0.012$. Since construction time also exhibited a
670 trending group x item valence interaction effect, $F(1, 909) = 3.22$, $p = 0.073$, pairwise contrasts were
671 checked as well. Since construction time closely relates to vividness (reliance on executive functions),
672 it was hypothesized *ad hoc* it will reveal the same pattern (shorter construction time for positive cues
673 in BG only). Indeed, there were no group differences in construction time, but was found to be shorter
674 for positive items (EMM = 8.29, 95% CI = [7.85, 8.74]) than negative ones (EMM = 8.49, 95% CI =
675 [8.04, 8.94]) in the BG, $t(909) = -3.800$, $p < 0.001$, $d = -0.331$, but not in CG, $t(909) = -1.020$, $p =$
676 0.308 , $d = -0.098$, (positive: EMM = 8.51, 95% CI = [8.08, 8.93], negative: EMM = 8.57, 95% CI =
677 [8.14, 8.99]). The valence difference in BG remained significant for both vividness and construction
678 time after FDR correction.

679 3.6 Resting-state thoughts

680 3.6.1 Biofeedback effect on resting state thoughts

681 A group x test interaction effect was present on ARSQ scores only for Theory of Mind (Figure 5). Post-
682 hoc comparison showed that Theory of Mind increased in BG, $p = 0.022$, but not in the CG, $p = 0.578$.
683 Across groups, scores decreased between RS1 and RS2 for measures of Comfort, $p = 0.008$, $d = -0.71$
684 and Health Concern $p = 0.018$, $d = -0.55$ and increased for Sleepiness, $p < 0.001$, $d = 1.04$, and
685 Difficulty Rating Feelings, $p = 0.008$, $d = 0.97$. Moderate-to-large differences could be denoted
686 between groups at RS1 before the MTT for several measures. Independent sample tests suggests that
687 BG reported lower scores of Theory of Mind, Comfort, Capability Making Statements*, Somatic
688 Awareness, Motivation*, and higher score of Sleepiness (all $p < 0.055$, effect sizes at least moderate).

The role of cardiac vagal control in thoughts

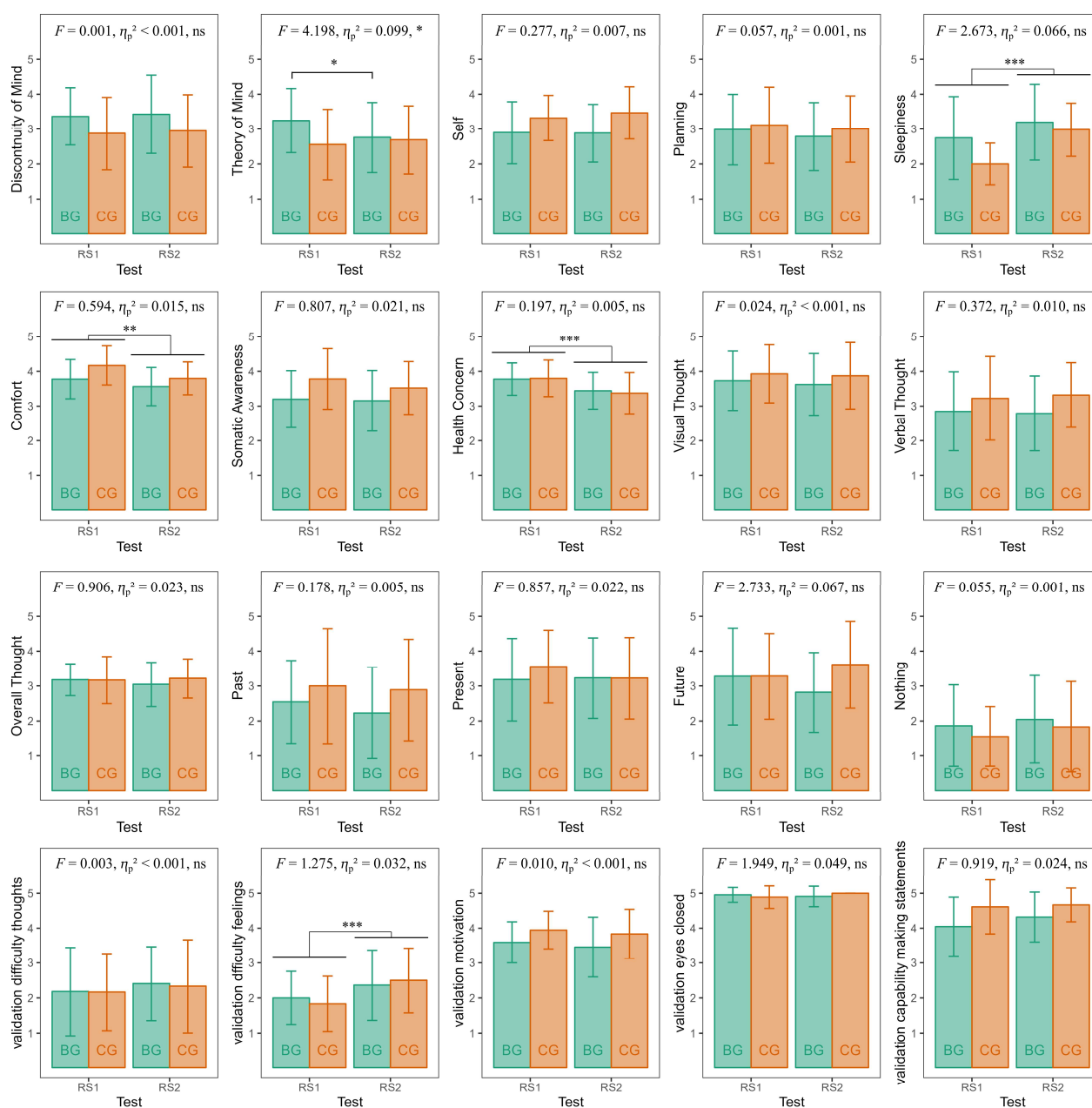


Figure 5 – HRV biofeedback effect on resting-state thought properties

Note. Thought properties during two 5-min resting-state periods before (RS1) and after (RS2) the mental time travel task were assessed using the Amsterdam Resting-State Questionnaire 2.0. Statistics of the group-by-test interaction effect derived from linear mixed effect models are reported in top of each graph. According to Cohen's interpretation, the effect of HRV biofeedback compared to natural-paced-breathing was negligible or small for all properties except of Theory of Mind (i.e., thinking of others), Sleepiness, and Future thinking. Across groups Comfort and Health Concern significantly decreased and while Sleepiness increased.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (uncorrected p-values)

690 **3.6.2 Association between Resting-state thoughts and vmHRV**

691 Spearman correlations between ARSQ scores with resting RMSSD and heart rate (RS1 and RS2
 692 pooled) revealed that Visual Thought and Verbal Thought were both correlated with RMSSD and heart
 693 rate (Table 5, see for the complete data set supplementary materials). Higher resting RMSSD predicted
 694 greater Verbal Thought and lower Visual Thought, whereas higher resting heart rate predicted lower
 695 Verbal Thought, and greater Visual Thought. It is to note that Pearson correlations showed strong
 696 correlation between resting RMSSD and resting heart rate, $r = -0.67$, $p < 0.001$ and between RS2
 697 RMSSD ratio and RS2 heart rate ratio, $r = -0.56$, $p < 0.001$. Thus, an overlap between RMSSD and
 698 heart rate associations might stem from the same physiological origin. Due to the intriguing
 699 relationship of RS1 RMSSD with Visual Thought, its association with the IDQ visual imagery score
 700 was tested. Spearman correlations verified that higher resting RMSSD associated with lower visual
 701 imagery capacities, $\rho = -0.31$, $p = 0.0494$. RS1 correlated by trend with IDQ visual imagery, $\rho = 0.28$,
 702 $p = 0.08$.

703 Furthermore, greater heart rate correlated with lower Past thinking and Discontinuity of Mind. This
 704 pattern was also reflected in the association between test changes in ARSQ scores and test changes in
 705 heart rate. Greater RS2 heart rate ratio (i.e., relative change from RS1) predicted a greater reduction in
 706 Discontinuity of Mind and Past thinking. RS2 RMSSD ratio predicted changes in none of the scores,
 707 except the thinking of Nothing score which was positively associated.

Variable	Pearson / spearman correlations				Spearman correlations			
	RS1 and RS2				RS1-to-RS2 differences in ARSQ			
	Resting RMSSD		Resting heart rate		RS2 RMSSD ratio		RS2 Heart rate ratio	
	ρ	p	ρ	p	ρ	p	ρ	p
Discontinuity_of_Mind ^a	0.10	0.380	-0.24*	0.035	0.04	0.825	-0.33*	0.040
Visual_Thought	-0.32**	0.004	0.23*	0.036	-0.23	0.146	-0.04	0.794
Verbal_Thought ^a	0.33**	0.003	-0.41**	<0.001	-0.07	0.654	-0.06	0.733
Past	0.13	0.236	-0.28*	0.011	-0.03	0.848	-0.41**	0.008
Nothing	0.09	0.405	-0.11	0.314	0.40*	0.011	-0.06	0.696

708 **Table 5 – Correlations between resting thought probes and vmHRV**

709 Resting state thought properties were assessed using the Amsterdam Resting-State Questionnaire (ARSQ), and
 710 RMSSD and heart rate recorded during the first resting-state (RS1) and second resting-state (RS2) phase before
 711 and after the mental time travel task. ARSQ scores were correlated with resting RMSSD and heart rate across
 712 the across RS1 and RS2 (left table side). Changes in ARSQ scores from RS1 to RS2 were correlated with the
 713 relative change from RS1 to RS2 for measures of resting RMSSD and resting heart rate (right table side). The
 714 spearman approach was applied, however, where scores were normally distributed (marked with “a”, left table
 715 side only) the Pearson approach was used.

716 From the table 2 it can be observed that notable differences were present in the psychophysiological
717 association between positive future and negative past thinking. In face of the previous results that are
718 centered on valence differences, as part of an unplanned analysis, differences in correlation
719 coefficients, linking RMSSD ratio with MTT variables, were tested between the positive EFT and
720 negative EAM condition using the R cocor function (Diedenhofen, 2022). It deploys various testing
721 methods which all revealed a significant difference between positive EFT and negative EAM
722 correlations for measures of construction time ($ps < 0.005$) and personal importance ($ps < 0.004$) but
723 not the other variables. Moreover, we further explored the global correlation and perspective.
724 Perspective was found to most strongly related to positive stimuli, $\rho = -0.10$, $p = 0.024$, and future
725 simulations, $\rho = -0.11$, $p = 0.019$.

726 3.6.3 Associations between mental time travel and resting thought properties

727 Pearson correlations between MTT probes (summarized over conditions per participant) and ARSQ
728 probes (RS1 and RS2 pooled together) are presented in the supplementary materials. Generally,
729 participants with higher scores in overall thought, future thought, and theory of mind constructed events
730 faster and experienced greater vividness during MTT ($|rs| = [0.21, 0.40]$, $ps < 0.05$). A greater
731 propensity towards planning was also linked to faster event construction. On the one hand, greater
732 visual thought at rest associated with greater vividness, event importance, but also more negative
733 valence. On the other hand, higher verbal thought is also positively linked to vividness, but its
734 relationship to subjective valence depended on the item valence. Subjects with greater verbal thought
735 tentatively rated events based on positive items as more positive and negative item events as more
736 negative. In the same fashion, higher somatic awareness relates to more positive evaluation of positive
737 item events and vice versa for negative items. Item valence also moderated the relationship of past
738 thinking with vividness, perspective, and probability. Past thinking positively correlated with a more
739 actor perspective, higher vividness, and higher probability during negative MTT. Contrary, more past
740 thinking tentatively linked to a more observer perspective and not at all to vividness or probability for
741 positive items. Finally, thinking of nothing associated with lower probability and a more observer
742 perspective.

743 **4 Discussion**

744 This study investigated the changes in vmHRV reactivity and thought properties during MTT following
 745 a short HRV biofeedback induction as well as the *in situ* psychophysiological relationship between
 746 vmHRV reactivity and MTT. Control checks verified that HRV biofeedback enhanced vmHRV during
 747 the exercise compared to paced-natural-breathing control group. Furthermore, the MTT task elicited
 748 the phenomenal event properties classically reported in previous studies: lower vividness and greater
 749 positivity for the future as compared with the past; greater vividness and actor perspective for positive
 750 as compared with negative events. It was found that the degree of vmHRV reactivity was positively
 751 correlated with vividness during positively-cued EFT (greater vividness of the events was associated
 752 with vagal increase or with a greater attenuation of vagal withdrawal). Moreover, HRV biofeedback
 753 compared to a paced-breathing control exercise influenced vmHRV reactivity and subjective ratings
 754 of vividness during MTT dependent on the emotional valence of the cue. Participants in the control
 755 group exhibited lower reactivity (greater vagal withdrawal) during positive MTT compared to negative
 756 MTT, whereas there was no difference in the HRV biofeedback group. Vividness was higher for
 757 positive MTT than negative MTT after HRV biofeedback only.

758 **4.1 Cardiac vagal control reactivity predicts cognitive control over thought**

759 In line with the hypotheses, the results demonstrate that the attenuation of vagal withdrawal or its
 760 increase during positive EFT supports cognitive control involved in the construction of the as scene,
 761 evidenced as an increased experience of vividness. This result is supported by a substantial, although
 762 not statistically significant, correlation predicting shorter event construction time for higher vmHRV
 763 reactivity during positive EFT. We expected the psychophysiological relationship to be more
 764 pronounced when the task demands higher cognitive effort, i.e., during EFT, however it is to note that,
 765 against our hypotheses, cardiac vagal control reactivity was not found to be related to cognitive control
 766 involved in negative EFT or EAM, or to self-referential processing, outcome expectation, or
 767 experienced valence during any MTT condition. A plausible explanation could be that the
 768 psychophysiological relationship will only be revealed during strong presence of cardiac vagal control.
 769 Indeed, large variability was observed in both behavioral and physiological (vagal increase and
 770 decrease) responses across conditions. MTT evoked only a numerical, but not significant, decrease in
 771 cardiac vagal control, which seemed largest for positive EFT. Since young, healthy adults were studied,
 772 it is likely that positive EFT evoked largest deployment of cognitive resources due to motivational bias
 773 (c.f., Anderson et al., 2012; D'Argembeau & Van der Linden, 2006; Salgado & Berntsen, 2020). Thus,
 774 we see support in our results for the Vagal Tank Theory (Laborde et al., 2017), which underline that,
 775 only if executive demands for directed attention are high, cardiac vagal control preservation or increase
 776 predicts self-regulatory efficacy underlying executive control. Furthermore, this effect seems to be
 777 moderated or mediated by motivational bias that might serve to increase self-enhancement to support
 778 adaptive self-regulation. Previous literature identified an increase vmHRV during the experience of
 779 positive emotions (dos Santos et al., 2022; McCraty et al., 1995, 2009). However, it can be excluded
 780 that the subjective experience of “positiveness” due to more vivid visual imagery of positive events

781 alone led to increased parasympathetic reactivity. Firstly, no association was found during even more
782 vivid positive EAM. Secondly, subjective valence ratings were unrelated across conditions.

783 HRV biofeedback had a valence-dependent effect on vmHRV reactivity and vividness, which supports
784 the previous notion of cognitive control and self-regulation. By preserving cardiac vagal control and
785 increasing vividness during positive MTT (or decreasing vividness during negative MTT,
786 respectively), HRV biofeedback shows to manipulate cardiac vagal control reactivity underlying self-
787 regulatory capacities. Importantly, it emphasizes a direct relationship between parasympathetic
788 regulation and cognitive control over thought as previous results suggest (Feeling et al., 2021; Gillie et
789 al., 2014, 2015). However, the directionality of the effect remains unclarified: Does a change in cardiac
790 vagal control reactivity affect mental processes, or is it purely an indicator of altered cognition? HRV
791 biofeedback might have stimulated cardiac vagal control reactivity mediating an increase in vividness.
792 But it is also entirely possible that motivational factors involved in biofeedback (Gaume et al., 2016)
793 mediated a positivity-biased cognitive engagement in EFT. Anyway, the findings make a case for the
794 existence of regulatory mechanisms that underly the regulation of both autonomic and thought
795 processes, corroborating the neurovisceral integration model (Thayer & Lane, 2000, 2009) and
796 previous research on perseverative cognition (Ottaviani et al., 2013, 2015, 2016).

797 **4.2 Tonic cardiac vagal control predicts emotional regulation of self-referential processing**

798 Additional results on tonic on-task vmHRV revealed that higher tonic vmHRV during negative EAM
799 predicted lower ratings of personal importance of the event. In fact, both phasic and tonic vmHRV
800 mirrored associations of vmHRV with vividness during positive EFT, and personal importance during
801 negative EAM, with more pronounced effects of phasic vmHRV on vividness, and tonic vmHRV on
802 importance, respectively. This underlines that information encoded in tonic and phasic vmHRV share
803 substantial overlap, but also reveal distinct patterns. Tonic measures very likely reflected resting or
804 trait states of cardiac vagal control, since they highly correlated with resting vmHRV and did not
805 change very much during MTT (relative change = -4.8%, 95% CI = [-12.8%, 3.2%]) in comparison to
806 the large inter-subject variability. This suggests, on the one hand, that vmHRV reactivity is a better
807 indicator of cognitive control than trait scores. Resting vmHRV is known to be correlated with
808 executive functions involved in scene construction, but meta-analyses stated correlations, as found in
809 this study, to be small ($r = 0.09$, Holzman & Bridgett, 2017; Zahn et al., 2016; $r = 0.15$). vmHRV
810 reactivity, however, is theorized to reflect dynamics in cognitive resource deployment, that might better
811 capture the psychophysiological association between cardiac vagal control and cognitive control
812 (Laborde et al., 2017), which was confirmed by this data set. On the other hand, it seems that trait
813 vmHRV (reflected in tonic on-task measures) is a better predictor of implicit (unconscious) emotion
814 regulation (Gyurak et al., 2011) involved in down-regulating the personal importance of negative
815 memories. In fact, we also observed some evidence of higher tonic vmHRV associated with lower
816 expectation of reoccurrence of both negative and positive EAM, and a global trend of future events
817 being more quickly evoked and vividly experienced and past events being less quickly evoked and
818 vividly experienced when tonic vmHRV was higher. As discussed earlier, a propensity towards
819 negative past thinking, anticipating negative future outcomes, and difficulties imaging the positive

820 future are hallmarks of rumination, depression, and anxiety (Kellogg et al., 2020) that are reflected in
821 autonomic rigidity (Ottaviani et al., 2015). Indeed, personal importance for negative EAM was found
822 to be the most stable phenomenological property within subjects (the same participant accredited all
823 the time high/low importance to the negative memory). It thus seems that in line with perseverative
824 cognition hypothesis (Brosschot et al., 2006; Ottaviani et al., 2013) cardiac vagal control plays a role
825 in thought control that directs memory search or manipulates memory properties towards reduced
826 relevance for the self and future. Remarkably, these effects were found in healthy adults, emphasizing
827 a protective function of cardiac vagal control for adaptive thought and mental health. Neuroimaging
828 data supports the presented findings. HRV biofeedback evoked heart rate oscillations, reflected in
829 vmHRV, have been found to modulate brain connectivity, especially between the ventromedial
830 prefrontal cortex and amygdala, involved in emotional regulation and self-referential processing
831 (Nashiro et al., 2023; Schumann et al., 2021). For example, Cho et al. (2023) found that this functional
832 connectivity mediated the effects HRV biofeedback-induced vmHRV on positive emotional memory
833 bias. Consequently, we assume that tonic vmHRV might have been indicative of autonomic and brain
834 functioning underlying emotion regulation and adaptive self-referential processing.

835 4.3 Resting state thoughts and future perspectives

836 A potential concern of our study was that we evaluated deliberately evoked thought processes, but in
837 reality thoughts often arise spontaneously which underly different cognitive processes (Christoff et al.,
838 2016). Therefore, an exploratory analysis on subjective reports of resting state thoughts (mind
839 wandering) before and after the MTT task was conducted.

840 Probably the most remarking findings were that higher resting vmHRV was correlated with lower
841 visual thought and higher verbal thought across resting-state phases. A negative correlation of resting
842 vmHRV with the IDQ visual imagery score confirmed the link between vmHRV and visual thinking
843 style. Lower visual thought, in turn was related to overall lower vividness, lower personal importance,
844 and more positive valence, while higher verbal thought also predicted lower vividness and a valence
845 buffering effect (i.e., reduced negative and positive valence). Moreover, changes in resting vmHRV
846 predicted an increase in thinking of “nothing”, which in turn was related to a more observer perspective
847 and less importance during MTT. These results suggest that higher cardiac vagal control might underly
848 a thinking mode close to contemplative or mindful thinking. In this line, resting vmHRV could be
849 related to calm, reflective, and introspective thinking style. In view of our previous results,
850 contemplative thinking might be associated with better emotional regulation of self-referential
851 processes due to a shared neurovisceral basis. Indeed, meditation has been shown to increase emotion
852 regulation related to an increase in the ventromedial PFC/ anterior cingulate cortex (Tang et al., 2016),
853 two core regions of both autonomic control and self-referential processing. Future studies need to
854 verify role of the parasympathetic nervous system in the automatic manipulation of self-referential
855 processing in spontaneous and deliberate thought.

856 In regard to the HRV biofeedback, it has to be noted that, despite significant group x valence interaction
857 effects on MTT and cardiac vagal control, effect sizes were small. Moreover, the HRV biofeedback

858 manipulation showed no substantial effect on resting-state thoughts. A plausible explanation might be
859 that exercise phases were too short, and participants were already relaxed (higher vagal activity due to
860 sitting for around 40 minutes) before the experiment. Phase durations were limited due prevailing
861 effects of fatigue/ relaxation on the psychophysiological relationship observed in our previous study
862 (Bögge et al., 2023), but still the experiment significantly fatigued the participants. In addition, we
863 made the interesting observation that HRV biofeedback increased variability in attentive levels during
864 MTT. It seems that while HRV biofeedback was very motivating for some, it was demotivating for
865 others. Thus, a current challenge in this literature is to come up with experimental designs that can
866 explore the causal relationship while controlling for fatigue, motivation bias, and general vagal
867 activation, for example by implementing cognitive stressors.

868 **5 Conclusion**

869 This experimental study examined the association of different thought characteristics with cardiac
870 vagal control and its reactivity during mental time travel into the past and future in young, healthy
871 adults. Furthermore, psychophysiological effects of HRV biofeedback compared to a control breathing
872 exercise shortly prior to mental time travel were investigated. The results suggest that higher cardiac
873 vagal control reactivity to mental time travel reflects neurovisceral processes that underly the scene
874 construction of imagined positive future events. This relationship was corroborated by the finding that
875 HRV biofeedback concomitantly altered vividness and cardiac vagal control reactivity for positive
876 compared to negative cues. Moreover, tonic measures of vmHRV show that higher cardiac vagal
877 control was related to lower personal importance during negative EAM retrieval. In line with previous
878 literature, the combined outcomes demonstrate that cardiac vagal control reactivity is involved in goal-
879 oriented cognitive control, while tonic cardiac vagal control during cognitive activity underpins
880 implicit emotion regulation. Thus, this work supports the notion that cardiac vagal control plays an
881 important role in self-regulation and extends its implication to cognitive control and self-referential
882 processing in an emotional context. It seems thus possible that cardiac vagal control in healthy adults
883 indexes the mind-body's operational mode towards self-enhancement and reduced self-negativity bias
884 which guide adaptive thought. The additional exploration of mind wandering properties revealed that
885 higher resting cardiac vagal control was associated with a stronger verbal and less visual thinking mode
886 which were associated with thought properties of contemplative thinking. Future research is warranted
887 to investigate the psychophysiological association of parasympathetic regulation with characteristics
888 of spontaneous thought.

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- 1199

1200 **Conflict of Interest**

1201 *The authors declare that the research was conducted in the absence of any commercial or financial*
1202 *relationships that could be construed as a potential conflict of interest.*

1203 **CRedit author statement**

1204 **Lukas Bögge:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation,
1205 Resources, Data Curation, Writing- Original draft preparation, Writing- Reviewing and Editing,
1206 Visualization, Project administration. **Itsaso Colás-Blanco:** Writing- Reviewing and Editing.
1207 **Pascale Piolino:** Conceptualization, Methodology, Resources, Writing- Reviewing and Editing,
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1218 data processing.

1219 **Data Availability Statement**

1220 Anonymized original datasets, supplementary materials and results are publicly accessible under the
1221 terms of the Creative Commons Attribution 4.0 International license (CC BY-NC-SA 4.0, copyright
1222 holder: Lukas Bögge and Memory, Brain & Cognition Laboratory), where applicable, on a public
1223 online repository (link: <https://osf.io/xgfdc/>).

1224 **Supplementary Materials**

1225 All supplementary materials as well as the research data and video material of the VR system can be
 1226 found on the Open Science Framework online repository (link: <https://osf.io/xgfdc/>).

1227

1228 **Table A1 – Spearman correlations of tonic as well as phasic heart rate during mental time**
 1229 **travel (MTT) with phenomenological characteristics of MTT**

Variable	Heart rate ratio during MTT				Tonic heart rate during MTT			
	Future		Past		Future		Past	
	Positive	Negative	Positive	Negative	Positive	Negative	Positive	Negative
Construction time (ln)	0.17*	0.04	0.04	-0.08	0.06	0.13	0.01	-0.05
Vividness	-0.07	0.04	-0.05	0.01	-0.01	-0.10	0.11	0.09
Perspective	0.06	-0.05	-0.01	0.02	0.006	0.02	0.00	-0.17*
Personal importance	-0.20**	-0.01	-0.01	-0.02	0.05	0.10	0.03	0.07
Subjective Valence	-0.17*	0.02	0.09	-0.03	0.02	0.03	-0.02	-0.02
Expectation of (re-)occurrence	-0.05	0.06	0.05	-0.04	0.04	0.06	0.10	0.14*
Temporal distance	-0.01	-0.07	-0.07	0.018	0.10	0.07	0.01	0.03

1230 ** $p < 0.01$, * $p < 0.05$

1231

1232

1233 **Table A2 – Spearman correlations of resting-state physiological measure with**
 1234 **phenomenological characteristics of mental time travel**

Variable	Tonic lnRMSSD during RS1				Tonic Heart rate during RS1			
	Future		Past		Future		Past	
	Positive	Negative	Positive	Negative	Positive	Negative	Positive	Negative
Construction time (ln)	-0.17	-0.28	0.08	-0.14	0.05	0.23	0.04	0.03
Vividness	-0.06	0.15	-0.17	-0.16	0.03	-0.21	0.16	0.17
Perspective	0.11	0.25	-0.04	0.26	0.00	0.07	0.03	-0.36*
Personal importance	-0.10	-0.03	-0.28	-0.15	0.22	0.24	0.11	0.14
Subjective Valence	-0.06	0.073	0.02	0.10	0.12	-0.03	-0.02	0.07
Expectation of (re-)occurrence	-0.11	-0.08	-0.18	-0.20	0.13	0.09	0.13	0.18
Temporal distance	-0.05	-0.07	-0.04	-0.15	0.10	0.16	0.11	0.12

1235 * $p < 0.05$

1236 **Table A3 – Spearman correlations of phasic physiological measures with phenomenological**
 1237 **characteristics of mental time travel**

Variable	RMSSD ratio during RS2				Heart rate ratio during RS2			
	Future		Past		Future		Past	
	Positive	Negative	Positive	Negative	Positive	Negative	Positive	Negative
Construction time (ln)	-0.14*	-0.07	-0.14*	-0.06	0.24***	0.16*	0.17*	0.07
Vividness	0.01	-0.06	0.12	0.14*	-0.09	-0.04	-0.20**	-0.14*
Perspective	-0.12	-0.11	-0.03	0.06	0.09	0.05	0.11	0.09
Personal importance	0.05	-0.06	0.12	0.09	-0.15*	0.06	-0.02	-0.02
Subjective Valence	0.04	-0.04	-0.01	-0.07	-0.15*	0.05	0.04	0.04
Expectation of (re-)occurrence	-0.03	0.07	0.12	0.26***	-0.02	-0.04	-0.17**	-0.12
Temporal distance	-0.17*	0.02	0.03	0.11	0.01	-0.14*	-0.07	-0.02

1238 *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

1239

1240 **Table A4 – Pearson correlations between phenomenological characteristics of spontaneous**
 1241 **thought assessed by the Amsterdam Resting-State Questionnaire 2.0**

Thought probe

	(20)	(19)	(18)	(17)	(16)	(15)	(14)	(13)	(12)	(11)	
(1) Discontinuity of Mind	1	0.13	0.064	0.029	-0.036	-0.28*	0.23*	-0.24*	0.25*	0.082	(20)
(2) Theory of Mind	0.2+	1	0.032	-0.065	-0.028	-0.037	0.087	-0.12	-0.14	-0.03	(19)
(3) Self	0.1	0.0013	1	0.35**	0.06	-0.17	0.19+	0.11	-0.014	0.24*	(18)
(4) Planning	0.29**	0.27*	0.25*	1	0.48***	0.17	-0.035	0.037	0.041	0.15	(17)
(5) Sleepiness	0.28*	-0.088	-0.028	-0.15	1	0.39***	-0.077	0.21	0.12	0.16	(16)
(6) Comfort	-0.24*	-0.0093	0.12	0.047	-0.14	1	-0.18	0.3**	-0.12	-0.23*	(15)
(7) Somatic Awareness	-0.095	-0.048	0.32**	-0.13	0.0036	0.044	1	-0.14	0.18	0.53***	(14)
(8) Health Concern	-0.11	-0.025	-0.16	0.11	-0.22*	0.39***	-0.088	1	-0.053	0.031	(13)
(9) Visual Thought	0.16	0.42***	0.16	0.34**	0.042	0.11	0.11	-0.010	1	0.38***	(12)
(10) Verbal Thought	0.15	0.26*	0.36***	0.3**	-0.012	0.042	0.12	0.065	0.063	1	(11)
(11) Overall Thought	0.55***	0.61***	0.5***	0.69***	0.017	0.01	0.062	-0.026	0.57***	0.63***	(11)
(12) Past	0.2	0.2	0.4***	0.17	0.051	0.07	-0.026	0.042	0.26*	0.17	(12)
(13) Present	-0.12	-0.046	0.26*	-0.0054	-0.043	0.014	0.29**	-0.14	-0.066	0.11	(13)
(14) Future	0.14	0.28*	0.18	0.78***	-0.2	0.078	-0.074	0.12	0.3**	0.19	(14)
(15) Nothing	-0.051	-0.21	0.042	-0.18	0.16	-0.23*	-0.039	-0.19+	-0.41***	-0.031	(15)
(16) validation difficulty thoughts	0.43***	-0.017	0.087	-0.0027	0.35**	-0.22	0.073	-0.1	0.037	0.015	(16)
(17) validation difficulty feelings	0.45***	-0.14	0.16	0.007	0.37***	-0.032	0.026	-0.0087	-0.019	0.056	(17)
(18) validation motivation	0.18	-0.059	0.2	0.15	-0.049	0.3**	0.14	0.15	0.21	0.18	(18)
(19) validation eyes closed	-0.091	-0.027	0.057	-0.044	-0.045	0.16	-0.12	0.12	-0.026	0.036	(19)
(20) validation capability making statements	0.042	-0.023	0.19	0.12	-0.1	0.19	0.039	0.037	0.2	-0.17	(20)
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	

1242 **Table A5 – Correlations between phenomenological characteristics of mental time travel**

Spearman correlations			(1)	(2)	(3)	(4)	(5)	(6)	(7)
(1) Event construction time	future	positive	1						
		negative	1						
	past	positive	1						
		negative	1						
(2) Vividness	future	positive	-0.18**	1					
		negative	-0.2**	1					
	past	positive	-0.16*	1					
		negative	-0.24***	1					
(4) Perspective	future	positive	0.0021	0.2**	1				
		negative	-0.12	0.2**	1				
	past	positive	-0.077	0.19**	1				
		negative	-0.14*	0.15*	1				
(4) Personal importance	future	positive	-0.16*	0.34***	0.16*	1			
		negative	-0.043	0.27***	0.086	1			
	past	positive	-0.13*	0.22***	0.16*	1			
		negative	-0.19**	0.39***	0.19**	1			
(5) Subjective valence	future	positive	-0.2**	0.33***	0.082	0.49***	1		
		negative	-0.0016	-0.065	0.07	-0.26***	1		
	past	positive	-0.041	0.13*	0.11	0.18**	1		
		negative	-0.036	-0.19**	-0.036	-0.26***	1		
(6) Expectancy	future	positive	-0.04	0.068	0.13*	0.21**	0.19**	1	
		negative	-0.099	0.13*	-0.0018	0.12	0.11	1	
	past	positive	-0.14*	0.022	-0.079	0.047	0.029	1	
		negative	-0.15*	0.11	-0.064	0.15*	0.12	1	
(7) Temporal distance	future	positive	-0.056	-0.068	0.076	0.062	0.25***	0.0085	1
		negative	0.0053	0.072	0.072	0.031	-0.0083	0.059	1
	past	positive	-0.058	0.13*	0.0015	-0.051	-0.048	-0.13*	1
		negative	-0.062	-0.028	0.17*	0.054	-0.042	-0.08	1

1243 *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Conclusion

The main results of the third study (BIOTRAC-3) can be summarized as follows:

- RMSSD reactivity during positive episodic future thinking positively correlated with the subjective experience of vividness.
- RMSSD (tonic) during negative episodic autobiographical memory retrieval correlated negatively with the personal importance of the event.
- HRV biofeedback compared to a control breathing exercise increased vividness and reduced the decrease in RMSSD reactivity (attenuated vagal withdrawal) for positive compared to negative mental time travel regardless of time direction.
- An exploratory analysis revealed that RMSSD during resting-state mind wandering is positively related to verbal and negatively to visual thought.

Like in BIOTRAC-2, neither phasic nor tonic measures of cardiac vagal control were associated with cognitive control over memory (speed of episodic memory access, vividness/ detail of the event). Higher tonic RMSSD seemed to hamper memory scene construction while facilitating future scene construction. Indeed, a clear relationship between cognitive and cardiac vagal control appeared only in RMSSD reactivity to positive future thinking. It, therefore, seems that the psychophysiological relationship between cardiac vagal control and goal-oriented cognitive control over thought is driven by the amount of cognitive resources required and an adaptive motivation bias. Episodic future thinking is cognitively more taxing than episodic autobiographical memory, and participants appeared to engage most resources towards positive simulations. Future projections underly a positivity bias that subserves self-enhancement. Therefore, the results suggest in congruence with the existing literature that cardiac vagal control reactivity reflects adaptive self-regulatory behavior that recruits executive functions to facilitate mental imagery of the positive future. The HRV biofeedback manipulation, which concomitantly affected RMSSD reactivity and vividness, substantiated this assumption. Furthermore, the role of cardiac vagal control in adaptive self-regulation was underlined by the finding related to tonic RMSSD. These findings suggest that cardiac vagal control underlies an inhibitory function of self-representation (personal importance) and future projection (future expectation) within consciously recollected negative memories. In line with previous psychological and neuroimaging data, we posit that cardiac vagal control indexes implicit emotion regulation capacities that do not manipulate the experienced valence but self-referential

properties of negative thought to reduce its harmful impact on the organism. Furthermore, exploratory investigation of mind wandering properties demonstrated that a rise in resting RMSSD from experiment beginning to experiment end was related to reduced mental activity (i.e., thinking of nothing). Changes in cardiac vagal control might have thus also underpinned increased inhibition of overall spontaneous thought activity.

In addition, young, healthy adults with higher vmHRV were found to be more verbal than visual thinkers during mind wandering independent of the group. This may explain why participants with higher tonic vmHRV more problems had retrieving and visualizing episodic memories. Nonetheless, these individuals also exhibited greater mental imagery for the future. Supplementary data exposed another surprising pattern. An increase in resting RMSSD before to after the experiment was positively correlated with vividness and especially personal importance during negative past thinking. It could be assumed that a general rise in RMSSD over the experiment was linked to mood worsening due to increased fatigue which escalated negative remembering. But sleepiness scores were not linked to RMSSD changes. This suggests that a propensity for negative, highly self-referential memories stressed the organism and led to a vagal recovery mode. Moreover, if this were to be true, it would challenge the Vagal Tank Theory's view that faster cognitive stressor recovery predicts better self-regulation.

In summary, this study highlights that cardiac vagal control is subject to physiological processes that manipulate cognitive control and self-referential processing as a function of emotional context to promote adaptive thinking. Many questions remain unanswered, such as how cardiac vagal control associated with the complex interaction between thought patterns. Future research is required to disentangle the relationship between autonomic regulation and spontaneous thoughts and should assess thoughts under more realistic conditions.

12 Chapter 12 – General Discussion and Perspectives

The scope of this thesis was to investigate the mind-body interaction between cardiac vagal control, indexed by HRV, and thought processes, including episodic (autobiographical) memory and future thinking. Specifically, the psychophysiological association with cognitive control, self-referential processing, and emotional processing were investigated. HRV biofeedback was used as a cognitive-physiological stimulation tool to test how cognitive and autonomic changes relate. One-week persistent and instantaneous effects of HRV biofeedback were tested and associated with the magnitude of change in cardiac vagal control during training and cognitive activity, respectively. *In situ* investigations included state (tonic) and reactivity (phasic) measures of vmHRV during memory and future thinking processes to dissect their respective relevance for the study of neurovisceral integration. The experimental design included the development of a new VR-HRV biofeedback system to improve training success and facilitate the combination of cognitive assessment and HRV biofeedback in a controlled environment. The results were expected to make a significant contribution to psychophysiological research as well as the study and care of mental wellbeing by confirming findings based on the neurovisceral integration model and extending them to the thought processes of young, healthy adults.

12.1 Summary of Results

Three experimental studies were conducted of which the first (BIOTRAC-1) was of longitudinal nature to explore persistent effects of HRV biofeedback in VR on diverse psychological functions, including cognitive control and emotion-dependent self-referential episodic memory. The following single-session experiments, study 2 (BIOTRAC-2) and study 3 (BIOTRAC-3), focused on instantaneous effects of HRV biofeedback on on-task processes of cardiac vagal control, memory, and future thinking. All experiments used very similar VR setups and included active control groups. However, for study 2 and 3 standard cognitive assessments were redesigned in VR for a seamless cognitive-physiological assessment and better experimental control. Moreover, advancements were made on the control group by including a paced breathing protocol that does not target HRV stimulation. All materials, including video recordings of the VR setup, supplementary results, and the research data are publicly accessible on project-specific online repositories:

BIOTRAC-1 Persistent effects <https://osf.io/u4t7p/> (OSF link)

BIOTRAC-2 False memory <https://osf.io/593p6/> (OSF link)

Preregistration: <https://osf.io/edhpc/> (OSF link)

BIOTRAC-3 Mental time travel <https://osf.io/xgfdc/> (OSF link)

Note. Materials are uploaded on the Open Science Framework (OSF).

The main results of all three works are summarized in [Table 4](#). Psychophysiological relationships were established for measures of P2T-RSA in BIOTRAC-1 because it better captures cardiac oscillations and cardiac vagal control during HRV biofeedback. On the contrary, RMSSD, used in BIOTRAC-2 and -3, is the more robust measure for short recordings during cognitive tasks when respiration patterns may strongly vary. Phasic measures reflected relative changes from baseline that accounted for some of the inter-subject variability in reactivity due to baseline differences and provided statistically more robust results than the usually used state difference scores.

The first study revealed that six sessions of HRV biofeedback over 3 weeks produced, compared with mindfulness-based self-regulation, 1-week persistent improvements in short-term memory, sustained attention, and positive self-referential memory. Effects on executive functions were in line with previous results reporting strong effects on short-term memory and sustained attention but none on cognitive interference assessed by the Stroop effect. In fact, improvements in cognitive control were found to be specific to reduced identification errors of similar stimuli in a visual discrimination task. Furthermore, HRV biofeedback improved positive self-referential episodic memory by enhancing the self-positivity bias during memory processing. Notably, vmHRV during training correlated only with measures that were significantly affected by HRV biofeedback and memory discrimination of self-referentially encoded items. In line with our assumption, these results suggest that high cardiac vagal control elicited brain changes related to executive, emotional, and self-referential-processing. Moreover, they

vmHRV measure	Behavioral HRV biofeedback effect (Group-by-Test interaction η_p^2)	Psychophysiological associations (Pearson's r , Spearman's ρ)
Bögge et al. (2022) <i>BIOTRAC-1</i>	Baseline-adjusted RMSSD and peak-to- trough RSA during training 1-week persistent improvements in: - Attention/Error rate, $\eta_p^2 = 0.17$ - short-term memory, $\eta_p^2 = 0.23$ - positive self-referential episodic memory recollection, $\eta_p^2 = 0.23$	Significant correlations with RSA: - Attention/Error rate, $\rho = 0.52$ - short-term memory, $\rho = 0.48$ - positive self-referential episodic memory recollection, $\rho = 0.43$ - Memory discrimination, $\rho = 0.48$
Bögge et al. (2023) <i>BIOTRAC-2</i>	State and reactivity (<i>exploratory</i>) RMSSD during memory encoding and retrieval No immediate improvements in: - False memory discrimination $\eta_p^2 < 0.001$ - Metamemory of critical items $\eta_p^2 = 0.008$	No significant correlations at rest, encoding, recognition (state/reactivity) - False memory discrimination $ r < 0.02$ / $ r < 0.02$ - Metamemory $ r < 0.14$ / $ r < 0.04$
Bögge et al. (in prep) <i>BIOTRAC-3</i>	State and reactivity RMSSD during mental time travel and during mind-wandering (<i>exploratory</i>) Group-by-Cue Valence interaction: Vividness was higher for positive than negative cues only in the biofeedback group, $d = 0.273$. Phasic RMSSD was lower for negative cues only in controls, $d = 0.241$.	Significant correlations of RMSSD: - Reactivity with vividness during positive future thinking $\rho = 0.22$ - State with personal importance during negative episodic memory $\rho = -0.25$

Table 4 – Results Summary of the Thesis Studies on the HRV Biofeedback and Cardio-Vascular Effects on Cognitive Control and Self-Referential Processing in Memory and Future Thinking

support the previously formulated hypothesis, that high amplitude physiological (cardiac) oscillations are the underlying cause of altered brain connectivity involved in emotion regulation (Mather & Thayer, 2018). Importantly, the involved networks also include self-referential processing hubs, most notably the ventromedial PFC. Thus, the results substantiated the idea that cardiac vagal control is linked to self-referential processing at higher mental levels, possibly through an interaction of brain circuits involved in self-referential, autonomic, executive, and emotional processing.

Building on the results and resulting assumptions of the first study and constrained by COVID restrictions, BIOTRAC-2 and BIOTRAC-3 were designed to investigate the involvement of cardiac vagal control in the cognitive and emotional regulation during memory and thought processes. For the first time, the simultaneous impact of short HRV biofeedback inductions on cardiac vagal control and cognitive processes was evaluated. The capability to discriminate true from false memories, was chosen as a cognitive parameter for the second study, because the previous findings pointed out a specificity of cardiac vagal control versus cognitive control involved in cognitive discrimination and response accuracy. In addition, an earlier study demonstrated a correlation between resting HRV and true-to-false memory discrimination performance (Feeling et al., 2021). The pre-registered investigation revealed all but negative results: Neither HRV biofeedback affected tonic HRV during subsequent memory processing (encoding and retrieval) and cognitive control over memory, nor were both parameters associated. Since we were unsure whether to investigate tonic or phasic HRV during the experiment planning, the pre-registration featured also a planned exploratory analysis of HRV reactivity. The following results revealed the same pattern, however, when controlling for heart rate reactivity, HRV reactivity during memory retrieval was associated with true-to-false memory discrimination performance. It was assumed that the repeated measures design and experiment lengths had a fatiguing effect (2 hours of low cognitive load while sitting before performing HRV biofeedback) that buffered the HRV biofeedback effect and moderated psychophysiological correlations. Indeed, supplementary data (supplementary materials A1) demonstrated a moderating effect of fatigue. Moreover, lowly-arousing neutral words that were used might be less sensitive to capture cardiac vagal control effects than emotionally-laden items.

Subject of the third study was to replicate findings from BIOTRAC-1 by showing that cardiac vagal control is related to self-referential processing dependent on emotional valence and cognitive control during mental time travel (episodic memory and future

thinking). To overcome previous limitations, BIOTRAC-3 was based on single-event-based analysis instead of deriving cognitive outcomes from averaged scores (such as memory recollection). Thus, experimentation time could be decreased and statistically power increased. The outcomes demonstrated robust associations of HRV with the degree of vividness/ detail during imagined positive future events and with the personal importance accredited to negative re-experienced episodic memories. Higher phasic HRV (reduced vagal withdrawal/vagal activation) predicted higher vividness, while higher tonic HRV predicted lower importance. HRV biofeedback had a valence-dependent effect on vividness and phasic HRV. It increased vividness and reduced vagal withdrawal, which was observed in the control group, during positive compared to negative simulations. The results underline that cardiac vagal control reactivity underpins goal-directed cognitive control to support adaptive thought, while tonic cardiac vagal control is more related to the manipulation of self-referential processes that subserves emotion regulation.

With regard to the results found in our three studies, this thesis highlights the following points:

- Only six HRV biofeedback sessions can largely improve cognitive control and positive self-referential memory, presumably through large-amplitude oscillations.
- HRV biofeedback had no instantaneous effect on memory control and cardiac vagal control during memory processing.
- Neither tonic nor phasic on-task HRV were related to false memory suppression.
- Phasic HRV predicts cognitive control over positive scene construction while tonic HRV was associated with personal importance of negative memories.

12.2 Stimulating Body and Mind with HRV biofeedback

12.2.1 Physiological effects of HRV Biofeedback

Enhanced vmHRV is the manifestation of higher cardiac vagal activity that reflects efferent output to the heart but is assumed also to index increased vagal afferent activity affecting brain functioning involved in the regulation of mind and body. One aim of the thesis was to see if stimulating HRV mediates neurophysiological changes affecting the organism's psychological and autonomic regulatory systems implicated in cognition and whether autonomic and behavioral responses are linked. HRV biofeedback was chosen as a self-regulation technique because it can stimulate quickly,

non-invasively, and with great effect, the cardio-vascular system of young healthy adults. Based on principles of the Resonance Frequency Training (Lehrer et al., 2000), slow breathing was the main approach to increase cardiac vagal control assessed as RSA and RMSSD. Biofeedback was implemented for its motivation component with the main intent to achieve maximal heart rate amplitudes. In each experiment, results were compared to an active control group to control for self-regulation effort and placebo effects on cognitive scores. Checks of vagal stimulation during training, which was a prerequisite for parasympathetically-mediated cognitive changes, were performed during each experiment. However, it was unclear whether HRV biofeedback would have carry-over effects on cardiac vagal control during cognitive processing. It was supposed that HRV would be higher or decrease less from baseline during the cognitive task when HRV was stimulated shortly before. This was an important point to test whether HRV biofeedback can manipulate phasic HRV, allowing a deeper investigation of the relationship between cardiac vagal control and cognition by comparing time congruent physiological and psychological changes.

Standardized effect sizes of physiological effects on HRV across experiments and groups are summarized in [Table 5](#). Effects sizes, similar to Cohen's *d* were all derived through contrasts of log-transformed RMSSD and peak-to-trough RSA with the first baseline (resting-state) measure based on linear mixed effect models that accounted for random subject variability. It is to note that in the BIOTRAC-2 study, the HRV biofeedback group (BG) had a significantly higher baseline RMSSD level than the control group (CG), which seemed to have affected effect sizes (i.e., reduced increase during HRV biofeedback and stronger decrease during memory processing in the BG). All studies demonstrated that HRV biofeedback largely increased HRV during training due to slowing of breathing near the resonance frequency (i.e., ~0.1 Hz) and an increase in respiration amplitude. These increases remained large when comparing HRV to the active control and can thus not be explained by the VR immersion or other relaxation effects that can increase HRV or by the fact that participants were engaging in meditation-like self-regulation exercise (i.e., focusing and regulating the breath). Mean breathing frequencies during HRV biofeedback were near the target value of 6 cpm (6.42 – 7.69 cpm), and its mediating effect on HRV was confirmed in study 1 by supplementary analyses. Thus, the HRV manipulation during training can be confirmed for all experiments. However, it was found that HRV also increased during exercise in the control group in study 1. This was of no surprise, since the active control group was also asked to self-regulate HRV through non-paced slow breathing but without

biofeedback. On the contrary, in study 2 and 3, controls performed paced breathing with a variable pacer (mean = 14 cpm). Close adherence to the task and non-significant effects on HRV could be confirmed, proving the effectiveness of the control condition. However, also in experiments 2 and 3 control subjects showed an upwards trend in RMSSD during and after training, sometimes with a moderate effect size. Main reason for this was found to be a fall in heart rate across groups indicative of increased vagal outflow alongside increased relaxation and fatigue. This became very apparent in the second experiment, as HRV strongly increased, and heart rates dropped after the first VR-task that included only control breathing (45 min). In contrast, in the third experiment, there was also a global increase in HRV from before to after the experiment, but the effect was less pronounced, although the task was longer (1 hour). It is thus very likely that the long periods paced-breathing exercise, independent if biofeedback was present or not, in combination with the VR immersion fatigued the participants. Additional investigations in study 2 revealed that psychophysiological relationships were time-variant due to baseline changes in cardiac vagal control. Furthermore, they highlighted a moderating effect of subjectively perceived fatigue interference with the task (supplementary materials A1). Consequently, one must bear in mind that both studies investigating instantaneous effects were marked by a continuous increase in vagal outflow that can influence psychophysiological investigations in general. While in the third study these did not affect the results (time differences were small and models statistically controlled for random block differences) it had a major impact on the second experiment (group differences were assessed in the second task after two hours of experiment). Many experiments do not account for this issue and even single time point resting-state need to address. The implications for experimental design are discussed in more detail in Chapter 12.4.1.

Standardized effect size of change in tonic HRV compared to baseline (Similar to Cohen d, derived from EMM contrasts of linear mixed effect models)									
HRV Variable	During HRV biofeedback		During cognitive task			After HRV			
	Biofeedback group (BG)	Control group (CG)	BG	CG	BG	CG			
Bögge et al. (2022)									
RMSSD	1.14**	1.06*	–	–	0.81**	0.46			
<i>BIOTRAC-1</i>									
RSA	2.94***	1.78***	–	–	0.92*	0.48			
Bögge et al. (2023)									
			Second test only		Second test only		After first test only		
			Encoding	Recognition	Encoding	Recognition	Encoding	Recognition	
			BG	CG	BG	CG	BG	CG	CG
<i>BIOTRAC-2</i>									
RMSSD	0.96***	-0.22	0.80**	0.37	-1.12***	-0.75**	-1.33***	-1.03***	0.96***
RSA	3.13***	0.54*	2.90***	0.77*	–	–	–	–	0.38
Bögge et al. (<i>in prep</i>)									
RMSSD	1.31***	0.47	-0.37	-0.46	0.55	0.27			
<i>BIOTRAC-3</i>									
RSA	3.91***	-0.31	–	–	0.73*	-0.27			

Table 5 – Results Summary of the Thesis Studies on Effect Sizes of HRV Biofeedback and Control Training on HRV

Contrary to the other studies, in the longitudinal experiment 1, where training was performed in individual sessions for 25 min without interruptions, HRV biofeedback was found to affect both HRV and heart rate during and after the training compared to the control group. Although the controls actively practiced increasing HRV, the HRV biofeedback evoked greater cardiac vagal control after training mediated by greater mean vagal outflow and lower respiratory rates. This is in line with previous results that showed that near resonance breathing increases RMSSD (Laborde, Allen, Borges, Dosseville, et al., 2022), baroreflex gain, LF power, and decreases heart and respiratory rates (Lehrer et al., 2003) right after training. Together, these findings have two important implications. Firstly, they underline that a rather short 25-min training of HRV biofeedback in our VR system can lead to lasting vagal stimulation and thus might contribute to shifting the physiological baseline reference (McCraty & Zayas, 2014; Thayer & Lane, 2000) and neurophysiological changes related to the autonomic and central nervous systems. Secondly, they show that blending a cognitive task with HRV biofeedback diminishes these carry-overs effects during resting-state.

HRV biofeedback was, against our assumption, found to have no general effect on cardiac vagal control during cognitive processing, including memory encoding and retrieval as well as episodic event construction, immediately after training. Together with the previous findings, this suggests that the demands of thought processes to cardio-vascular regulation outweigh the instantaneous HRV biofeedback effect. Study 3, however, highlights that the HRV biofeedback effect on cardiac vagal control may be dependent on emotional processing. HRV reactivity during positive and negative event construction was unaffected by HRV biofeedback, but in the control group vagal withdrawal was stronger for positive compared to negative stimulations. It thus seems that HRV biofeedback buffers vagal withdrawal in reaction towards the processing of positive past- and future-oriented oriented episodic thoughts. Contrary, no effect was found in study 2 where only neutral, abstract, and lowly arousing stimuli were used. Regarding the Vagal Tank Theory, this further suggests that HRV biofeedback promotes self-regulation efficacy and a more efficient use of executive resources specifically during positive thinking (Chapter 5.2.5)

It is furthermore to note that carry-over effects during cognitive processing might be greater with repeated HRV biofeedback training. For instance, no carry-over effect on resting-state RMSSD was present following a single session of 15-min slow-paced breathing (You et al., 2022). Also, Lehrer et al. (2003) observed that baroreflex and

LF power did not change after the first 30-min HRV biofeedback session, but this effect developed over the course of the intervention. It, therefore, seems that the HRV biofeedback effect on cardiac vagal control during thought processing depends not only on emotional factors but also on training lengths, continuity, and repetition. In this line of thought, repeated training might produce and enhance a vagal effect during the thought processing of emotionally-laden and neutral stimuli. Future investigations may examine this effect on HRV reactivity and its relationship to cognitive processing.

With regard to physiological results found in our three studies, this thesis highlights the following points. VR-HRV biofeedback:

- stimulated as intended cardiac vagal control during training.
- greatly enhanced vagal outflow shortly after training but only when not interrupted by cognitive processing phases.
- had no instantaneous effect on cardiac vagal control during memory processing of neutral stimuli but retained vagal activity during positive episodic past and future thinking (indicative of better resource management).
- might produce an effect on cardiac vagal control reactivity during thought processes when training is repeated.

12.2.2 Instantaneous cognitive effects of HRV biofeedback

For the first time the instantaneous effects of a short HRV biofeedback session on memory and specific thought properties were tested in young healthy adults. HRV biofeedback was found to have no substantial effect for any of the variables measured. Effects on vividness during mental time travel in parallel to cardiac vagal control reactivity were observed, but given the very small effect size, a single short HRV biofeedback session seems to have no practical relevance to influence memory and thought. Indeed, as we assumed that physiological and behavioral changes would occur simultaneously, it comes as no surprise no cognitive effect was observed. On the hand, this demonstrates that a short HRV biofeedback induction does not affect the neurovisceral basis underlying autonomic and thought control. Analogous to the previous discussion, the experimental design might not have allowed for measuring any effect because of the alteration between cognitive task and exercise phases, mental fatigue, and insufficiently long training sessions. Therefore, we do not exclude the possibility that a longer and uninterrupted single session of HRV biofeedback would affect memory and thought, as it has been shown for other cognitive functions. In

addition, clinical trials or studies with older adults are still pending to investigate the usefulness of brief HRV biofeedback on thought control. On the other hand, it also demonstrates that a single-session of HRV biofeedback exercises no relevant placebo effect or motivation bias within samples. Indeed, mean attentional levels during the tasks and subject-expectancy effects were not found to differ between groups in any experiment. However, it was also noted that HRV biofeedback increases variability in attention. While on average, HRV biofeedback does not affect motivation and attention at a mean level, it does at an individual level. Therefore, individual affinity for biofeedback seems to be an important factor for basic and clinical applications. Finally, in the line of thought of the previous section, the evolution of memory and thought processes during long-term HRV biofeedback intervention should be considered. Investigations of congruent changes in HRV reactivity and thought processes along multiple sessions might provide crucial insights into the neurovisceral basis of autonomic and thought regulation.

12.2.3 Long-term cognitive effects of HRV biofeedback

One striking result of this dissertation was that only six sessions of HRV biofeedback greatly improved cognitive functions related to cognitive control and valence-dependent self-referential processing and that these improvements were strongly correlated with the baseline-adjusted level of HRV (P2T-RSA) during training. We are well aware of the high number of variables in this study 1 that might have increased Type 1 error likelihood, but it should be noted that statistically conservative adjustments were chosen and only parameters considered where both a group-interaction effect and a significant correlation were present. Remarkably, P2T-RSA, with one exception, only correlated where groups significantly differ. Moreover, it is very intriguing that the demonstrated findings closely mirrored the ones recently found in the cohort studies led by Mara Mather (Bachman et al., 2023; Nashiro et al., 2022; Nashiro, Min, et al., 2023; Nashiro, Yoo, et al., 2023; Yoo, Nashiro, Min, et al., 2023).

12.2.3.1 Effects on cognitive control are sensitive to accuracy in interference resolution and short-term memory

For instance, Nashiro, Yoo, et al., (2023) came to the same conclusion as BIOTRAC-1: HRV biofeedback did not increase cognitive control, including measures of cognitive interference, working memory, processing speed, but HRV oscillation amplitude was related to changes in visual attention and inhibition (flanker score). The study applied the flanker test, where participants had to indicate the direction of the central arrow

that was either congruent or incongruent with the direction of arrows on the left and right. As in BIOTRAC-1, the scoring of the significant parameter was based on the accuracy of visual discrimination. Consequently, both studies support that the HRV biofeedback effect on executive functions is specific to accuracy (but not speed) in interference resolution by inhibiting lowly distinctive and task-irrelevant visual cues. Such cognitive control has been shown to involve a cluster of autonomic control-related brain regions including the ACC, striatum, medial PFC, and right insula (Deng et al., 2018). Mather & Thayer (2018) posited that high physiological (heart rate) oscillations strengthen connectivity in medial prefrontal regulatory regions including the ventromedial PFC and ACC and its connections to the amygdala. Thus, it is possible that HRV biofeedback-induced physiological oscillations strengthened feedback loops in brain regions involved in the inhibition success of unwanted information. This point was underlined by supplementary analysis assessing HRV markers that are sensitive (LF-HRV) and insensitive (RMSSD) to slow heart rate oscillations. While LF-HRV reflected the correlations found in P2T-RSA, RMSSD did not predict cognitive change for any dependent variable (<https://osf.io/u4t7p/>).

Also, Laborde, Allen, Borges, Hosang, et al., (2022) demonstrated improvements in cognitive control immediately after 15 minutes of slow-paced breathing (without biofeedback) that matched exactly the results presented here. Training improved interference control (Stroop task) based on accuracy, but no processing speed, as well as short-term memory. In their study, Laborde, Allen, Borges, Hosang, et al., (2022) assessed working/ short-term memory using the operation span task (Turner & Engle, 1989) that as the digit span forward task used in BIOTRAC-1 asks to reproduce a series of memorized digits in the same order. The major difference is that an arithmetic task has to be completed between encoding and recall. Thus, with respect to working memory, the maintenance of information and protection from interference, but not for active manipulation of its content, appear to be most sensitive to HRV biofeedback interventions. This observation seems to be related to enhanced PFC functioning rather than hippocampal functioning, because no improvements in long-term memory recall and recollection could be observed.

12.2.3.2 Self-referential processing and emotion regulation

Also, results on the emotional processing found in this work were recently reproduced in a large 5-week intervention study in younger and older healthy adults (C. Cho et al., 2023). The first experiment highlighted that HRV biofeedback affects the

interaction between emotional and self-referential processing by showing that the intervention enhanced the positivity bias in the self-reference effect on memory. Cho et al. (2023) could reproduce this positivity bias in memory, but moreover showed that this effect was mediated by medial PFC -amygdala connectivity. As discussed earlier, the medial PFC is involved in self-referential processes and, in concert with the amygdala, coordinates memory encoding. Moreover, in a meta-analysis comprising nearly 400 neuroimaging studies, the ventromedial PFC emerged as the sole brain region exhibiting heightened activity during positive affect compared to negative affect (Thayer et al., 2012). Thus, in parallel to the discussion on cognitive control, it seems possible that only six VR-HRV biofeedback training sessions had similar effects on the brain than daily 5-week training. A crucial difference between studies is that Cho et al. (2023) findings are based on other-referential encoding (memorizing affective photographs of unknown persons), while BIOTRAC-1 used self-referential encoding material. Since medial PFC-amygdala connectivity played a mediating role, it seems likely that HRV biofeedback evokes an overall positivity bias during memory processing, which specifically affects self-referential processes.

The interaction between self-referential and emotional processing was further corroborated by the findings of BIOTRAC-3. Negative memories of individuals with higher tonic HRV were less self-relevant (personal importance). Together, the results support the idea of an integrated network system, as part of the neurovisceral integration model, which is tasked besides with emotional and autonomic regulation with self-referential processes to modify emotionally labeled properties of thought. Implications for the neurovisceral integration model are discussed below.

showed that large oscillations in heart rate strengthen feedback loops in brain regions that can regulate brain activity associated with emotional and self-referential processes.

12.2.4 The role of the vagal nerve

It is often assumed that HRV biofeedback improves cognition through vagal activation. Despite the provided evidence, study 1 lets us only presume that increased vagal afferent activity mediated neurocognitive changes since other pathways exist (see Chapter 6.1). An important question that would arise from such an assumption is: If vagal activity mediates the HRV biofeedback effect on neurophysiological rewiring, would this also be reflected in the change of the autonomic regulation (i.e., changes in

tonic or phasic HRV)? Psychophysiological models supposed so due to readjustment of homeostasis and allostatic processes (i.e., the shift of inner baseline). In light of the small number of sessions conducted compared to the usual daily training for several weeks, the VR-HRV biofeedback probably did not evoke autonomic readjustments. The absence of a positive evolution in resting HRV confirmed this (supplementary materials A2 [Figure A21](#)). Nonetheless, physiological oscillation-related improvements were present one week after training, replicating previous findings. Also, Laborde, Allen, Borges, Hosang, et al., (2022) demonstrated improvements in cognitive control immediately after 15 minutes of slow-paced breathing (without biofeedback) that matched exactly the results presented here. Training improved interference control (Stroop task) based on accuracy, but no processing speed, and short-term memory. Moreover, the authors noted that RMSSD measured during or after training did not mediate cognitive control changes. Again, RMSSD, in contrast to RSA, poorly reflects PNS reactivity and cardiovascular oscillatory activity during slow-paced breathing (Ali et al., 2023). Thus, the results do not exclude the possibility that physiological oscillations mediated cognitive changes.

In summary, it is possible that physiological coupling during HRV biofeedback evokes immediate brain changes that last when training is repeated. However, these neurophysiological changes related to improved cognitive control might not necessarily be reflected in cardiac vagal control at rest.

The above-discussed results, however, still leaves the neurophysiological origin of the HRV biofeedback effect unspecified. One might assume a motivation bias or subject-expectancy instead. However, these seem unlikely since the experiments here as well as Nashiro, Yoo, et al. (2023) study, precisely controlled for placebo effects, and no group differences in self-reports could be observed. Nonetheless, non-vagal pathways might have been the underlying cause. Previous studies observed changes in EEG signature related to attention (Prinsloo et al., 2011) and error monitoring involved in conflict resolution (S. Hoffmann et al., 2019) following slow-paced breathing but failed to relate changes to HRV. Possible non-vagal pathways might be a change in respiratory rate typically observed after HRV biofeedback interventions or recruitment of frontal networks by volitional respiratory control (Herrero et al., 2018). Since the second experiment found neither physiological nor behavioral effects, it does not lend support to the clarification of cardiac vagal control activation during training-mediated behavioral and potentially neurophysiological changes. Therefore, it can be only

speculated if modulating cardiac vagal afferent improves inhibitory functions. However, evidence of this work points towards two main assumptions: Firstly, high amplitude cardiac oscillations and physiological coupling during slow breathing mediate persistent improvement in cognitive control, potentially through changes fronto-striatal-insula-cingulate circuitry of the salience and autonomic control networks. Most sensitive functions are accurate response inhibition and short-term memory. Secondly, behavioral changes might not be reflected in measures of HRV.

12.2.4.1 HRV biofeedback does not affect the same cognitive function that correlate with HRV

Another striking observation is that it is not the same cognitive control functions that correlate with HRV and are affected by HRV biofeedback. For example, working memory or cognitive interference scores that remained unchanged in this and previous studies, are generally correlated with HRV (Forte et al., 2021). Also, our post hoc analysis showed that the Stroop interference score was correlated with average resting HRV but did not change in either group. The neurovisceral integration model proposes that vmHRV and inhibitory control functions are linked to due to a common neural basis. However, these results suggest that the neurovisceral integration model alone cannot explain the mechanisms responsible for the improvements in cognitive control associated with HRV biofeedback and slow breathing.

12.3 Contribution to Existing Psychophysiological Models

12.3.1 Neurovisceral Integration Model

The neurovisceral integration model (Smith et al., 2017; Thayer & Lane, 2000, 2009) posits that cardiac vagal control is associated with overall better self-regulation of the organism, and specifically better cognitive control, emotion regulation, and better health. It is based on the CAN (Benarroch, 1993) that links heart and brain, and thus mind and body, and is shown to have major implications for research and health applications. However, it does not make predictions about how influences on cardiac vagal control, for example, through HRV biofeedback, will affect behavioral outcomes. Nor does it predict how cardiac vagal control is associated with self-referential processes. Mather & Thayer (2018) outlined in their seminal paper how physiological oscillations evoked by HRV biofeedback can affect the brain, involving structures that are implicated in emotion regulation and self-referential processing. While theories have focused on emotion regulation, they discarded the associations of emotions with the

processing of self-related information processing, which crucially determines how we experience the world. In the following, implications of the results on the neurovisceral model are discussed.

This work demonstrated, in line with very recent neuroimaging, peripheral-physiological, and behavioral data, that HRV biofeedback modifies, and that cardiac vagal control indexes, self-referential processing. Moreover, this process connects to emotion regulation since self-referential processes seem to modify behavior depending on the emotional context of thought. HRV biofeedback enhanced the positivity bias during self-referential memory encoding in as a function of cardio-respiratory oscillation amplitudes. It is not entirely certain how the effect came about, but it may be surmised that even a few HRV biofeedback sessions in VR are enough to rewire the brain, most notably the connection between the (ventro)medial PFC and amygdala. Thus, we predict that HRV biofeedback impacts emotion regulation via changes in components of self-referential processing. If HRV biofeedback enhances memory retrieval of positive self-related information, it seems possible that there is also an overarching effect on other thought processes. For example, positively-valued information may be more readily accessible or spontaneously brought to consciousness (positive mind-wandering). In the long term, this would have important consequences on mood, self-representation (e.g., self-enhancement), and future-oriented cognition such as prospective memory (remember and perform a planned action) and positive future thinking (e.g., simulating and planning). However, future research needs to confirm the results and check whether an increased positivity bias leads to adaptive behavior. Importantly, cognitive changes underlying the reset of neurophysiological architecture are not necessarily indexable by a change in resting cardiac vagal control. A probable reason is that cardiac oscillations affect feedback loops involved in emotional-self-referential processing but not in autonomic control. Potentially, changes in the cardiovascular system follow suite as the HRV biofeedback intervention progresses and might even be partially mediated through cognitive changes (i.e., less perseverative and more positive thinking that affect mental wellbeing and thus autonomic flexibility).

As well in line with previous research, HRV biofeedback was found to improve cognitive control specific to the accuracy in interference control and short-term memory. Analogous to the previous discussion, it assumed that neural activity was modulated by physiological oscillations, but the changes in neurophysiological underpinnings are not reflected in resting HRV. For the future elaboration of the neurovisceral integration

model, this means that executive functions relevant to self-regulation can develop independently of the basic cardiovascular functioning during training that targets a temporary increase in cardiac vagal control. Nonetheless, this leaves the prediction of HRV as a self-regulatory index untouched. In fact, an exploratory analysis confirmed once more that cognitive inhibition of the, measured as the Stroop effect, is associated with resting HRV. However, the data also shows that HRV as a marker of cognitive control over memory has its limitations. Neither resting, tonic on-task or phasic HRV during memory encoding and retrieval predicted inhibition of false memories. A major reason was task-induced fatigue and an accompanying drop in heart rate during experimentation, which need to be accounted for in future studies. Even when “more reliable” measures at task begin were considered, previous findings on false memories could not fully be replicated, potentially because the predictive power of HRV is smaller than previously assumed. In addition, memory control in the form of access speed and reconstruction detail during voluntary memory retrieval was not positively associated with HRV.

The neurovisceral integration model outlines the paramount significance of inhibitory control and neural feedback loops that guide adaptive behavior. This work argues that a pivotal role of neural networks tasked with cardiac vagal and thought control is the inhibitory regulation of self-referential processes. A clear relationship could be established between the perceived personal importance of negative memories and the level of RMSSD during the re-experience of negative memories ($\rho = -0.25^{***}$ [based cue-valence, as in study 2] or $\rho = -0.32^{***}$ [based on subjective-valence ratings]). Thus, we advocate that HRV indexes the organism’s capacity to down-regulate self-related value representations of negative thought. It is highly probable that this interrelation derives from a functional connectivity between the ventromedial PFC, amygdala, and other executive prefrontal regions that regulate emotional value representation, self-referential processing, but also cardiac vagal control. As discussed in Chapter 5.3.2.1, the ventromedial PFC is involved in self-referential processing, goal representations, positive affect, and inhibition of negative emotional responses. Furthermore, an important point to mark is that HRV was not associated with the subjective perception of the valence, i.e., higher HRV is associated with an experience of reduced importance but not with the negativity of negative memory. Together, this implies that within the neurovisceral integration model, a substantial part of emotion regulation is mediated through the modulation of self-referential processes. There are three main explications for this phenomenon: Firstly, self-referential properties of the memory were modified

during recollection, probably by the inhibition of the ventromedial PFC. Secondly, executive control associated with HRV suppresses the recall of memories that have a strong negative impact on the organism. Thirdly, feedback loops underpinning HRV reduced self-importance to negative events during memory processing before retrieval (i.e., encoding, consolidation). In either case, the results support the neurovisceral integration model implications in thought regulation to reduce negativity bias. Furthermore, the results support the preservative cognition hypothesis (Brosschot et al., 2006). In this respect, individuals who attach greater personal importance to negative autobiographical memories also exhibit compromised autonomic flexibility (low HRV).

In conclusion, HRV biofeedback and cardiac vagal control show to have an important impact on the interplay between emotional and self-referential processes in healthy adults. Further investigations seem timely and crucial to determine factors of adaptive behavior and how to maintain mental health. The work presented here invites future expansion of the neurovisceral integration model to include mechanisms of mental self-referential processes that interact with emotional processes.

12.3.2 Vagal Tank Theory

The main idea of the Vagal Tank Theory is that phasic HRV indexes the efficiency in resource mobilization for self-regulatory tasks. Its fundamental aspects are based on the neurovisceral integration model, in particular, on the association between cardiac vagal control and executive processes. Therefore, the contributions to vagal tank theory proposed above will also apply to the neurovisceral integration model. The points below are discussed in the view of volitional thought control, such as intentionally memorizing or thinking about the future and past.

The results strengthen the concept of the Vagal Tank Theory by showing that cardiac vagal control is associated with the detail and vividness of future scene construction which is known to heavily rely on executive functions. It was even found that phasic HRV is the more sensitive indicator of executive functions than tonic measures further underlying the model's validity. Moreover, a few specificities were identified that are believed to substantially influence the model's predictive power:

12.3.2.1 Executive demand and adaptive function

The theory states that an increase in cardiac vagal control will be associated with better cognitive control during tasks with low physical and high executive demands. Inversely, during tasks with high physical and low executive demands, cardiac vagal withdrawal will predict better performance. In line with this concept, the evidence here underlines that this dependency on executive demands also holds for cognitive control in attention-directed thought only. Accordingly, this thesis provides support that the application of the Vagal Tank Theory can also be expanded to cognitive resource activation in complex thought relying on executive functions, such as episodic future thinking. In fact, it could be noted that a very strong involvement of executive functions is needed so that associations become visible. For example, deliberate long-term memory encoding and retrieval processes, even under time pressure, showed not to be taxing enough. A likely reason is that those processes did not sufficiently rely on inhibitory control functions that are indexed by phasic HRV. Furthermore, this work proposes that besides a requirement for high executive demands, cognitive activity needs to be aligned with a goal that is aligned with one's motivations. Vividness during negative future simulations, in contrast to positive ones, was not associated with cardiac vagal control. This leads to the assumption that an implicit motivational bias (experiencing something positive) will drive executive engagement (vivid scene construction) that is related to cardiac vagal regulation.

12.3.2.2 Fatigue and cognitive effort

The second experiment demonstrated a complex interaction between mental fatigue, heart rate reactivity, and the relationship between HRV reactivity and cognitive control over memory. Study 2 showed, in contrast to study 1, that in lower-fatigued subjects better thought control was associated with higher vagal withdrawal. But study 2 also exhibited lower task-related HRV (see [Table 5](#)). A very likely reason for the moderating effect is that experiment 1 required more cognitive effort (rapid encoding and retrieval of long stimuli lists vs mental time travel). Indeed, heart rate reactivity, which is linked to cognitive effort, was found to mask the association between HRV reactivity and cognitive control over memory. It thus seems that not only when physical demands, but also when cognitive demands reach a certain level, the prediction direction will change. This effect seems crucially dependent on mental fatigue and might be reflected in heart rate reactivity. Crucially, these results underline the importance of the phasic HRV for situated cognition as an index of neurobiological and

psychological mechanisms, like interoceptive awareness (feeling fatigued, Magnon et al., 2023), acting on cognition. They thus confirm the Vagal Tank Theory's utility to elucidate the complexity and mechanisms of self-regulatory interactions. Moreover, it seems adequate that when hypotheses based on the Vagal Tank Theory are investigated that contextual factors such as fatigue, perceived effort, motivation but also heart rate are strictly controlled for. We provide preliminary evidence that models including parallel effects HRV reactivity and heart rate reactivity can provide improved predictive power of cognitive control functions, especially in the context of varying fatigue and effort levels.

12.3.2.3 Reactivity calculation

Phasic HRV is mainly calculated by taking the difference between resting and on-task HRV. We propose that when reactivity values only are considered (i.e., not compared with recovery values within subjects), a calculation based on relative change is preferable (e.g., dividing on-task HRV by resting HRV). In both Study 2 and Study 3, reactivity values were derived from relative values and compared with the corresponding subtraction values. Several advantages for the use of relative measures emerged from this comparison:

- Values are more normally distributed and show less outliers allowing for statistically more robust tests.
- No prior data transformation is required (e.g., log-transform).
- It accounts for between-subject variability. As the authors of the Vagal Tank Theory noted, resting HRV interacts with HRV reactivity (subtraction values) such that subjects with higher resting HRV exhibit higher reactivity, and vice versa. In our data set, we observed only a very small negative correlation between resting and phasic HRV. Thus, relative values are useful to control for baseline differences.
- Avoids scaling issues when multiple reactivity terms are fitted in one model, e.g., when assessing parallel effect of HRV reactivity and heart rate reactivity as proposed above.

The data generated in this work showed that, generally, statistics based on relative and subtraction values led to the same conclusion, but in all cases, the predictive power was better for relative values.

12.3.3 Embodied cognition, long-term memory and thinking

In study 1, the Self-Regulation-Self-Referential-Memory model was introduced. In the following, we would like to update this model by expanding on the mechanisms and the cognitive processes involved ([Figure 19](#)).

The model extends the previously presented theories and empirical findings from psychophysiology, cognitive science, and neuroscience by incorporating the results found in this work. The model posits that HRV self-regulation training and biofeedback affect the autonomic and central nervous systems which in turn is in interaction with interwoven processes related to self-referential, executive, and emotional processes that underly intentional long-term memory retrieval.

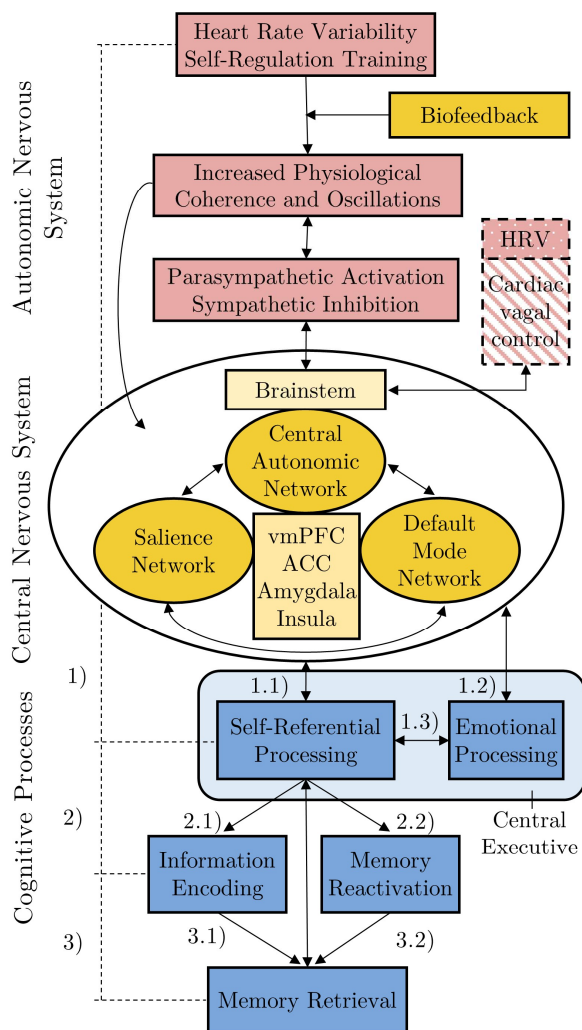


Figure 19 – The Embodied Self-Referential Thinking Model

Note. Heart rate variability (HRV) self-regulation training influences the autonomic nervous system (red, top) and the central nervous system (yellow, middle) through increases in coherence and amplitude in physiological oscillatory systems such as the cardiac rhythm. Autonomic and cognitive brain networks are intrinsically connected sharing common structures. Most notably the ventromedial prefrontal cortex (vmPFC), anterior cingulate cortex (ACC), amygdala and insula play a critical role in integrating interoceptive and exteroceptive signals for processing by cognitive systems (blue, bottom). Higher mental self-referential processing interacts with the emotional processing system and is guided by the central executive to encode and retrieve long-term memories. Cognitive systems integrate internal and external environment context (cardiac vagal control) with memory representations. Higher cardiac vagal control is associated with stronger coupling of self-referential and emotional processing that suppress negative-self representations and thus shape human thoughts.

HRV self-regulation involves techniques that increase vmHRV such as slow-paced breathing/ resonance breathing, cardiac coherence training, or mindfulness practices that are known to increase HRV. Training-evoked increases in physiological coherence and oscillation amplitudes, in particular of the heart rate, lead to enhancement of parasympathetic phasic activity and suppression of sympathetic activity, regulated by the CAN. Biofeedback moderates these physiological effects by increasing the effectiveness of the self-regulation training. Autonomic responses affect via the brainstem upper parts of the central nervous system involved in autonomic control. The CAN is intricately linked to other brain networks and circuits such as the DMN and Salience Network. Repeated training leads to functional reorganization of these structures which in turn affects autonomic regulation including tonic cardiac vagal control – indexed by HRV – and its reactivity to events. Furthermore, training effects the brain via other pathways (Mather & Thayer, 2018), such as heart beat evoked potentials which directly affects the activity in the DMN structures involved in self-referential processing (Azzalini et al., 2021; Babo-Rebelo et al., 2016).

Notable structures that are involved in this interplay of networks are the ventromedial PFC, ACC, amygdala, and insula. The ventromedial PFC is paramount to self-referential cognition but also crucially effects emotional processing due to its strong interconnection with the emotion-related amygdala. In addition, both structures are connected to the ACC which also plays a role in emotional processes and executive control. Furthermore, the DMN connects the ventromedial PFC is connected to dorsomedial PFC, posterior cingulate cortex, and memory-relevant hippocampus.

In concert these networks drive self-referential processing that influences higher-level cognition including thought and memory processing in dependence on goal and value representations and well as neurobiological and neurophysiological processes associated with the ANS. In specific, measures of cardiac vagal control reflect the functionality of brain networks. Higher cardiac vagal control is associated with a stronger interaction between self-referential and emotional processes guided by the central executive. In this line, the central executive is responsible of maintaining and monitoring goals and values and emotional representation associated with a stimulus (see Self-Memory System in Chapter 3.3.1 and 4.3, Conway, 2005). Depending on emotional and executive system, the self-referential processing system will attribute or modify “self-relatedness” to newly encoded information, activated and re-encoded existing memory and or a retrieved memory. This self-relatedness characterizes the integration of the information in the

self-system, reflecting its perceived importance or relevance for the self (e.g., goals, self-identification, future relevance). These interacting cognitive processes are in constant exchange and are dependent on the context of the internal (bodily states such as arousal or cardiac vagal control) and external environment (e.g., demands imposed by a task that determine goal setting). In this context, the insula plays a crucial role. It is essential in processing and integrating interoceptive (inner body state) and exteroceptive signals for higher mental self-processing. Furthermore, it is involved in salience processing, for example, when a negative thought occurs. Thus, it supports regulation of self-representations and integrates these with internal (body, thought) and external responses. Consequently, memory representations during encoding and retrieval are integrated with cardiac vagal control. In this line of thought, higher cardiac vagal control reflects functional activity of the nervous system which supports suppression of negative-self memory representation and enhancement of positive-self memory representation, depending on goal context. Memory retrieval, in turn, elicits activation of the self-emotion system leading to a reintegration with the current context. Likewise, thought processing and cardiac vagal control are in a bidirectional relationship. Repeated recall of negative-self representations will lead to a decrease in cardiac vagal control. Such self-representation notably also includes perceived relevance for the future self (e.g., something can happen to me). Conversely, if memory is accessed during states of high cardiac vagal control, these will be reintegrated with decreases negative-self representation, which might substantially modify the memory trace.

We postulate three potential explanations by which higher cardiac vagal is linked to modulations in self-referential processing that subserve emotion regulation:

- 1) Self-referential properties of memory are modified during retrieval, probably by the inhibition of the ventromedial PFC.
- 2) Executive control associated with HRV suppresses the recall of memories with strong negative-self representation and thus detrimental impact on the organism.
- 3) Feedback loops underpinning HRV reduce self-importance to negative events during memory processing before retrieval (i.e., (re-)encoding, consolidation).

Self-manipulation effects are mainly known to affect memory at the encoding stage, providing favor for the third option. However, overlapping lateralization of retrieval and autonomic processes to the right hemisphere indicates that mechanisms take primarily place post-encoding. It has been proposed that episodic memory retrieval is

mainly related to the right part of the prefrontal lobe, while encoding is more lateralized to the left (Tulving et al., 1994). Also, (ventromedial) PFC deactivation associated with cardiac vagal control has been argued to be lateralized to the right (Thayer et al., 2012). Such deactivation has been proposed to be the consequence of emotional stress to facilitate automatic self-regulation by prepotent responses (Arnsten and Goldman-Rakic, 1998). Since such ventromedial PFC deactivation is linked to decreased HRV and increased heart rate (Thayer et al., 2012), it seems likely that higher cardiac vagal control is associated – through increased ventromedial PFC activity – with suppressed negative memory retrieval (option 2) and/or manipulation of the negative-self memory representation (option 3).

This model can be applied broadly to the auto-noetic recollection such as during future and post mental time travel into past (episodic autobiographical memory, episodic future thinking). However, it is estimated that this model also has implications on semantic properties of thoughts (e.g., autobiographical self-knowledge, more abstract semantic future simulations). Furthermore, we do not impose that these processes directly require voluntary action and might thus also expand to spontaneous thought processes.

12.4 Limitations and Future Perspectives

12.4.1 Immediate HRV biofeedback

A major issue encountered during single session intervention was the absence of physiological and behavioral effects, which prevented a more in-depth analysis of the relationship between cognition and autonomic control. Several parameters have been identified that might have contributed to this effect, such as the experiment duration, exercise length, and fatigue. The immersion in the naturalistic VR might have further contributed to a HRV increase (Rockstroh et al., 2019) which is useful during HRV biofeedback but not necessarily during cognitive assessment. Nonetheless, it could still be useful to study effects occurring directly after HRV biofeedback to investigate congruent physiological and cognitive changes if certain parameters are considered. In the following a non-exhaustive list of experimental recommendations is provided to guide future studies:

- **Cognitive evaluation periods** should be kept very short and not mentally very charging when intermixed with the exercise (e.g., presenting single thought probes)

- **Exercise length** should be at least 30 min, eventually including short breaks if participants seem to struggle with such long exercise. Helpful could also be if participants take a semi-upright Fowler's position with a slight flexion of the torso, which can help to regulate respiration rate and tidal volume (Burns et al., 1994) and increases vagal activation (Kubota et al., 2013).
- **Experimentation time** before the exercise should be kept short to avoid interference effects of onsetting relaxation and fatigue. The time periods and exact procedure before the exercise should be reported.
- **Stressor tasks** could be implemented, as it has already been done by some experiments (Prinsloo et al., 2013; Rockstroh et al., 2019), before or during biofeedback to increase the sensitivity of reactivity measures.
- **Maximizing cardiac oscillations** should be the main target during HRV biofeedback.
- **Heart rate/ heart period** should be reported and eventually statistically corrected (de Geus et al., 2019).
- **Cognitive load** and **mental fatigue** experienced during cognitive assessment should be controlled by including subjective and objective measures, for example, eye-tracking measures (Bradley et al., 2008; Piquado et al., 2010; Yamada & Kobayashi, 2018; Zargari Marandi et al., 2018).
- **Self-regulation of breathing pace.** It could be tested how the effects of self-paced breathing vs paced breathing with HRV biofeedback differ. Interestingly, it was observed in the first study that when participants were orally paced for two minutes only and then continued regulating the breathing frequency themselves, they automatically regulated the rhythm near resonance frequency (average ≈ 6.5 cpm over 25 minutes).
- **Placebo control groups.** If motivation bias and placebo effects are not desired, an active control group should be included. For example, the one presented here is relatively easy to implement (variable pacer), which can also include a biofeedback component (respiratory/ synchronization feedback). Otherwise, the discussed *HRV-ER* trial (Yoo, Nashiro, Min, et al., 2023) provides a very interesting control condition which targets the reduction of cardiac oscillatory activity through biofeedback based on the coherence score. However, both HRV biofeedback and control biofeedback are more difficult to implement and might be not intuitive enough for a single HRV biofeedback session

12.4.2 Spontaneous thoughts

Like in many laboratory experiments, deliberate (or directed) thought processes were investigated. These are characterized by slow, attention-driven, goal-directed processes (e.g., voluntarily encoding, retrieving, or suppressing thoughts). However, very often, if not most, of memory encoding and thought occurrence (non-directed mind wandering) takes place spontaneously spontaneous (Christoff et al., 2016; Goetschalckx et al., 2019; Hale et al., 2020; Köster et al., 2014; Vingerhoets et al., 2005). Spontaneous thoughts occur more automatic and rapidly, relying on less executive control, and may potentially be the results of pre-constructed event retrieval (Cole & Kvavilashvili, 2021). The authors even proposed that spontaneous future thinking may be the default mode of prospection. Consequently, it is crucial to test whether the results presented here also extend to spontaneous thoughts, for example by assessing resting state thoughts as in study 3. Preliminary results of our last study showed that higher resting HRV during resting mind-wandering was linked to a more verbal and less visual thinking mode. These components were in turn related to a more contemplative or meditative thinking style during deliberate mental time travel (e.g., lower personal importance, reduction in negative and positive emotional valence). Such thinking modes are often associated with the practices of mindfulness and meditation, which have been shown in numerous studies to increase vmHRV during and after meditative practice (Arya et al., 2018; Kirk & Axelsen, 2020; Krygier et al., 2013; Tung & Hsieh, 2019). Consequently, it would be very interesting to investigate cardiac vagal control relates to spontaneous thought occurrences. The numerous findings of positive HRV biofeedback on stress regulation and mental health outcomes indicate that spontaneous thinking is very likely also positively affected by increased cardiac vagal control and/or HRV biofeedback. However, how HRV biofeedback may influence thought processes in healthy individuals, which may prevent the occurrence of maladaptive behavior, remains for being clear. As we have seen HRV biofeedback can have lasting effects on the cardiovascular system and even brain functionality. On the contrary, the effect of mindfulness-based interventions on elevating vmHRV still remains inconclusive (L. Brown et al., 2021). Thus, even though cardiac vagal control is indeed related to spontaneous thought, HRV biofeedback may be powerful technique to improve adaptive thinking even in the healthy population.

12.4.3 Target sample and neuroimaging data

A potential concern of this thesis is that results are limited to sample of young and healthy adults. These might not be generalizable to clinical or the elderly population. However, given previous beneficial effects of HRV biofeedback on disorders of affect (Goessl et al., 2017; Pizzoli et al., 2021) and the link between HRV and diminished cardiovascular functioning related to perseverative cognition (Ottaviani et al., 2016), we have grounds to believe that HRV biofeedback influences and cardiac vagal control indexes the interaction between self-referential and emotional processing in pathological conditions. However, there is less certainty for such conclusions towards the elderly population. As highlighted in Chapter 5.4.6, age affects the association between HRV and behavioral outcomes (for a review see on stress and emotion regulation (Thayer et al., 2021). Also, Cho et al. (2023) found differential age effects in positive memory bias in younger vs older adults. While HRV biofeedback increased overall memory recall in younger it reduced memory recall in older adults. However, the study failed to replicate the typically aging-related positivity effect (Mather & Carstensen, 2005; Reed et al., 2014), thus prohibiting to examine age effects on emotion memory. Furthermore, HRV biofeedback seems to have specific effects brain effects in the elderly. After HRV biofeedback brain volume was increased for locus coeruleus-targeted hippocampal regions in older but not in younger adults (Yoo, Nashiro, Dutt, et al., 2023). Vulnerability to stress responses specifically in the older population were found in association to cerebrovascular dysfunction, short-term fluctuations in blood pressure (Sible et al., 2023), and higher caudal locus coeruleus contrast (Bachman et al., 2023), underlining the cerebrovascular changes in aging that influence effects on the ANS. Studying the elderly and clinical populations might provide interesting insights into interaction of self-emotion processing to better understand how HRV biofeedback can contribute to mental well-being.

Unfortunately, no neuroimaging data was recorded in this work that would have surely provided important insights into neurophysiological functioning. This was not possible due to resource and methodological restrictions specifically in regard to the VR setup which complicates neuroimaging procedures. A recent acquisition by the laboratory may allow future studies to obtain EEG recordings during VR immersion. Hence, cortical activity could be recorded during HRV biofeedback and cognitive assessment. However, it is to note that many non-invasive imaging techniques, including EEG or

functional near-infrared spectroscopy, cannot reliably detect subcortical structures which constitute an essential part of the CAN.

12.4.4 Pitfalls and promises of HRV biofeedback in virtual reality

VR technology was deployed to support our experiments. However, we cannot make any firm conclusions about the VR applications in specific since no non-VR control group was included. We omitted the inclusion of such groups due to resource and time constraints, and the fact VR applications were not our primary research target but rather a medium to efficiently conduct the experiments. Hence, any predictions about VR effects remain rather speculative. However, we highlight some future recommendations of how VR could be used in the future.

An important limiting factor of this thesis was found to be fatigue. The VR-HRV biofeedback system was specifically designed to be motivating, but this might have been of limited use in short single session studies. Although overall levels of cybersickness were low it is possible that VR strained the participants (see Chapter 7.5 for a list of factors). Particularly, discomfort due to eye strain and display weight was reported. This might have canceled the desired motivation effects. It is, however, important to note that this was not specific to the HRV biofeedback but the paced breathing exercise in VR in general. An interesting possibility to counteract this problem would be the implementation of game elements or the design of a serious game (i.e., a complete game whose main focus is not entertainment). As highlighted in Chapter 2.3.1, biofeedback and feedback learning are closely tied to game theory. Game elements can be highly stimulating and thus maintain training motivation. An interesting outlook would be to design and scientifically validate an HRV biofeedback procedure that incorporates expertise from sport exercise, psychological, game, and VR theory. As an idea, yoga or Falun Gong exercises could be implemented in a VR game where body movements are synchronous with slow-paced breathing (e.g., rise and fall of the arms with the respiration) while HRV biofeedback is presented explicitly and implicitly. It is to consider, however, that motor effects on the cardiovascular system need to be controlled for, if in situ experiments are conducted, what was the main reason participants remained seated throughout the experiment. VR would also provide the means to exercise in groups while being physically separated like in a multiplayer game, which might provide synergistic group effects. In times of increasing demands for connected objects, technology could further support the training progress through

monitoring and analyzing physiological and behavior data (e.g., VR system connected to physiological sensors that record HRV along other meta-data for each session).

Furthermore, more ecological cognitive tasks could be installed. Dessy et al. (2018) noted that no study has so far investigated the potential of HRV biofeedback in real-life ecologically valid situations. For example, for Deese-Roediger-McDermott task has been successfully implemented in VR where participants are asked to recall elements after visiting a lively town (Abichou et al., 2022). Finally, increasing the degree of presence and embodiment could be further increased by creating more realistic scenarios also during HRV biofeedback and providing individualized and synchronized avatars (Penaud et al., 2023). Higher degrees of presence and embodiment contribute to the transfer of skill into real life applications (Grassini & Laumann, 2020; Sanchez-Vives & Slater, 2005). Hence, these properties are specifically interesting to train voluntary cognitive and physiological self-regulation.

12.5 Conclusion

This dissertation aimed to investigate the association between cardiac vagal control and cognitive processes of thought to shed light on the mind-body connection. VR-coupled HRV biofeedback was applied in young, healthy adults to evaluate how stimulation of cardiac vagal control influences cognition. A longitudinal and two single-session experiments were conducted to answer the following central research questions:

- Does vmHRV reflect executive, emotional, and self-referential processes involved in long-term memory and episodic future thinking, and thus self-regulation in higher cognition?
- Does HRV biofeedback promote adaptive long-term memory and episodic future thinking through vagally mediated changes in executive, emotional, and self-referential processes?

The main findings were that VR-HRV biofeedback enhanced persistently positive self-referential episodic memory and attentional control, while HRV during mental time travel was associated with cognitive and emotional regulation of thought. Overall, the results confirmed, in line with the previous literature, that vmHRV during goal-directed thinking is associated with executive, emotional, and self-referential processes that serve adaptive self-regulation. They demonstrated that HRV reactivity reflects executive processes specifically during thinking that is cognitively engaging and goal-directed,

such as positive future thinking. Moreover, tonic HRV reflected an interaction between executive, emotional and self-referential processes to suppress self-representation in negative memories. Thus, cardiac vagal control showed to play a multifaceted role in the regulation episodic past and future thought for adaptive behavior. While fatigue effects limited instantaneous HRV biofeedback effects, they provide novel insights into the interaction between neurobiological mechanisms and psychophysiological interactions relevant to embodied cognition. Results based on the longitudinal investigation underscored the interaction between self-referential and emotional processes related to parasympathetic regulation. Moreover, they showed, in line with the hypothesis and recent findings, that large-amplitude cardiac oscillations during HRV biofeedback may mediate cognitive improvements. While the small sample size limits the generalizability, the investigation highlights that only six training sessions may be sufficient to significantly change self-referential processing affecting higher cognition. This research clearly illustrates the connection between physiological regulation of the body and cognitive processes affecting the mind, and that connection can be stimulated by HRV biofeedback. But it also raises the question about the mechanistic differences between psychophysiological associations and biofeedback effects. Implications and possible extensions for the Neurovisceral Integration Model and Vagal Tank Theory are discussed. In addition, building on previous theory, we propose the Embodied Self-Referential Thinking theory. The model posits that HRV biofeedback and cardiac control influence through intricately connect neural structures, most notably the ventromedial PFC, the interaction between executive, self-referential, and emotional processing that control emotional self-representation in memory and thought. Findings of this thesis are not only relevant to psychophysiological research, but also emphasize the importance of HRV biofeedback of, and promoting cardiac vagal control in, the healthy population to prevent maladaptive thinking patterns and foster mental wellbeing. Exploratory results provide directions for future research that may examine the relevance of HRV and HRV biofeedback for spontaneous thoughts in the healthy and elderly population. The investigations of this work could be extended by validated memory tasks in virtual reality to increase ecological validity of the assessment (Abichou et al., 2022; Girardeau et al., 2023; Penaud et al., 2023). Furthermore, multidisciplinary conceptualization of gamified and scientifically validated VR-HRV biofeedback systems may provide future technology to enhance body and mind.

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Supplementary Materials

A1 BIOTRAC-2: Mental Fatigue Moderates the Relationship between vagally mediated HRV Reactivity and Cognitive Control

In the framework of the BIOTRAC-2 study, the role of fatigue as a confounder that influenced the relationship between false memory discrimination and RMSSD was investigated. These results and discussion are not featured in the publication to not further elongate the article.

Pre- to post changes in the relationship between vmHRV and cognitive control over memory scores could be observed for reactivity values (<https://osf.io/593p6/>). We assumed that relaxation and fatigue effects might have affected the psychophysiological relationship. To control for covariates that influenced the RMSSD* or cognitive control over memory, the correlation matrix was checked. Correlations showed small-to-moderate negative influences of the controls on memory variables that were mostly significant for fatigue interference. In turn, fatigue interference was moderately-to-largely correlated with the remaining control variables and might thus best capture the behavioral influences that affected the relationship between HRV and cognitive control. Indeed, generalized linear models showed that fatigue interference influenced the relationship of RMSSD*_{recognition} and d'_{lure} , $p = .023$, CC_{lure} , $p = .015$ and but not $d'_{\text{distractor}}$, $p = .327$ and $CC_{\text{distractor}}$, $p = .103$. In this context, [Figure A20](#) demonstrates how the relationship between RMSSD*_{recognition} and cognitive control over memory turned from negative (low fatigue interference) to positive (high fatigue interference). Fatigue interference had no influence on any variable at encoding ($ps > .640$). Self-reported attention did not affect relationship between any memory variable and RMSSD*, neither at encoding nor at recognition ($ps > .215$).

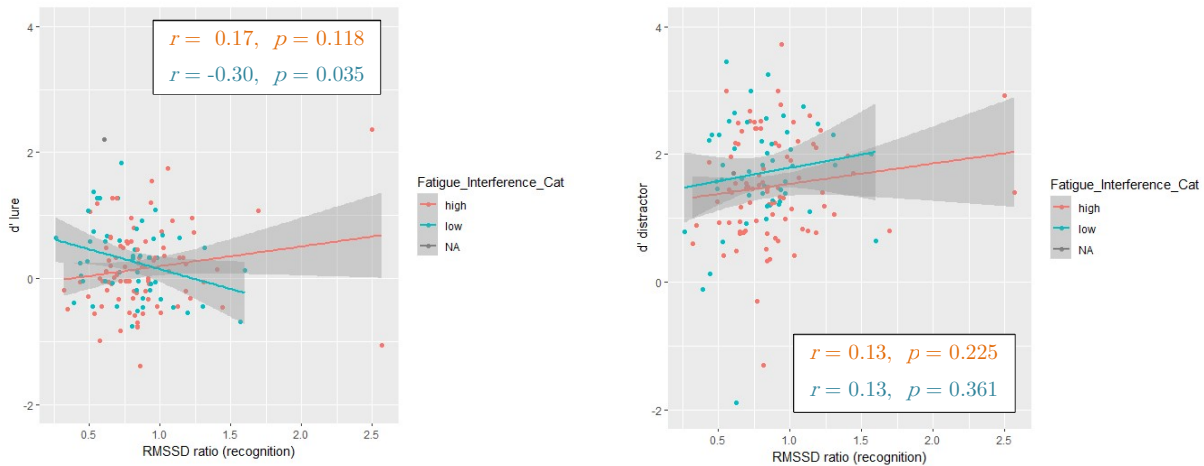


Figure A20 – Fatigue Interference Interaction Effect

Note. Fatigue interference interacted significantly with the relationship between RMSSD ratio (reactivity) and d'_{lure} (left) but not between RMSSD reactivity $d'_{\text{distractor}}$ (right). For visualization purposes only measures were equally divided into two groups when fatigue interference was highest and lowest (median-split). The results indicate that mental fatigue moderates the psychophysiological between cognitive control over memory and phasic vagally mediated heart rate variability. When mental fatigue is low cardiac vagal withdrawal will predict better true-to-false memory discrimination performance, whereas when metal fatigue is high vagal activation will predict better performance.

Physiological differences as a function of subjective fatigue were checked. Pre- and post-test measures correlated strongly for both measures of fatigue interference ($r = 0.662$) and fatigue after the task ($r = 0.671$). Participants were divided (median-split) equally into a low and high fatigue interference condition based on post fatigue interference scores because subjects that had highest level of fatigue interference during the last task were considered overall the most fatigued. Comparing fatigue interference scores using the Mann Whitney U test (low as reference condition) showed moderate-to-large differences at pre-test, $\text{delta} = 3$, $p < .001$, $r = .500$, and post-test, $\text{delta} = 4$, $p < .001$, $r = .868$. Though resting-state heart rate did not differ between fatigue interference conditions, $t(137) = 1.235$, $p = .219$, $d = .208$, resting-state RMSSD (log-transformed) was significantly smaller in the high fatigue interference group, $t(130) = -2.339$, $p = .021$, $d = -0.394$.

We posit the assumption that in line with the vagal tank theory (Laborde et al., 2018) the evaluation of vmHRV reactivity (i.e., change from baseline) may provide a deeper insight into the relationship between vmHRV and cognitive control over memory. Motivated by this idea, and to accommodate for within and between-subject baseline differences, vmHRV reactivity as well as heart rate reactivity were assessed as the

baseline change ratio percentage during encoding and recognition. It was observed that the relationship between cognitive control over memory and vmHRV reactivity was dependent on the level of fatigue interference. Participants that reported low levels of interference exhibited better cognitive control when vagal withdrawal was higher (vmHRV reactivity decreased). Inversely, at high interference levels cognitive control improved with reduced vagal withdrawal or increased vagal activation (vmHRV reactivity increased).

One possible explanation for this fatigue dependency in line with the vagal tank theory could be that the ANS played a role in counteracting the fatigue effect to maintain cognitive functioning during the task through parasympathetic activation. Similarly, prolonged executive task engagement that is likely to induce mental fatigue has been shown to increase vmHRV (Matuz et al., 2021; Van Cutsem et al., 2022). Cognitive effort is related to increased arousal and sympathetic autonomic regulation and a decrease in PNS levels (Critchley, 2005; Mathias, 2000). However, if PNS activity is already compromised (and SNS activity elevated) a further decline may not correspond to adaptive regulation in response to cognitive challenge. The same interaction between SNS and PNS in predicting cognitive outcomes has been demonstrated in previous studies (Giuliano et al., 2017; E. L. Knight et al., 2020). These showed that in young and middle-aged adults greater vagal withdrawal during a cognitive task was beneficial for cognitive functioning only when SNS activity was low. Inversely, when SNS levels were high, this relationship was attenuated. Indeed, higher levels of fatigue have been previously linked to reduced parasympathetic activity (Tanaka et al., 2015), cerebral blood flow (Boissoneault et al., 2019) and increased SNS activity (Mizuno et al., 2011). This was also reflected in the data here, as participants struggling most with the task due to fatigue tended to have lower baseline vmHRV. Greater PNS activity is indicative of increased cerebral blood flow to executive brain regions (Jennings et al., 2015). Therefore, it is possible that cognitive control over memory at a state of high fatigue, when baseline vmHRV is low, required vagal re-activation to balance the parasympathetic deficit and restore effective cortical-inhibitory-control.

A2 BIOTRAC-1: Evolution of Physiological Parameters over Sessions

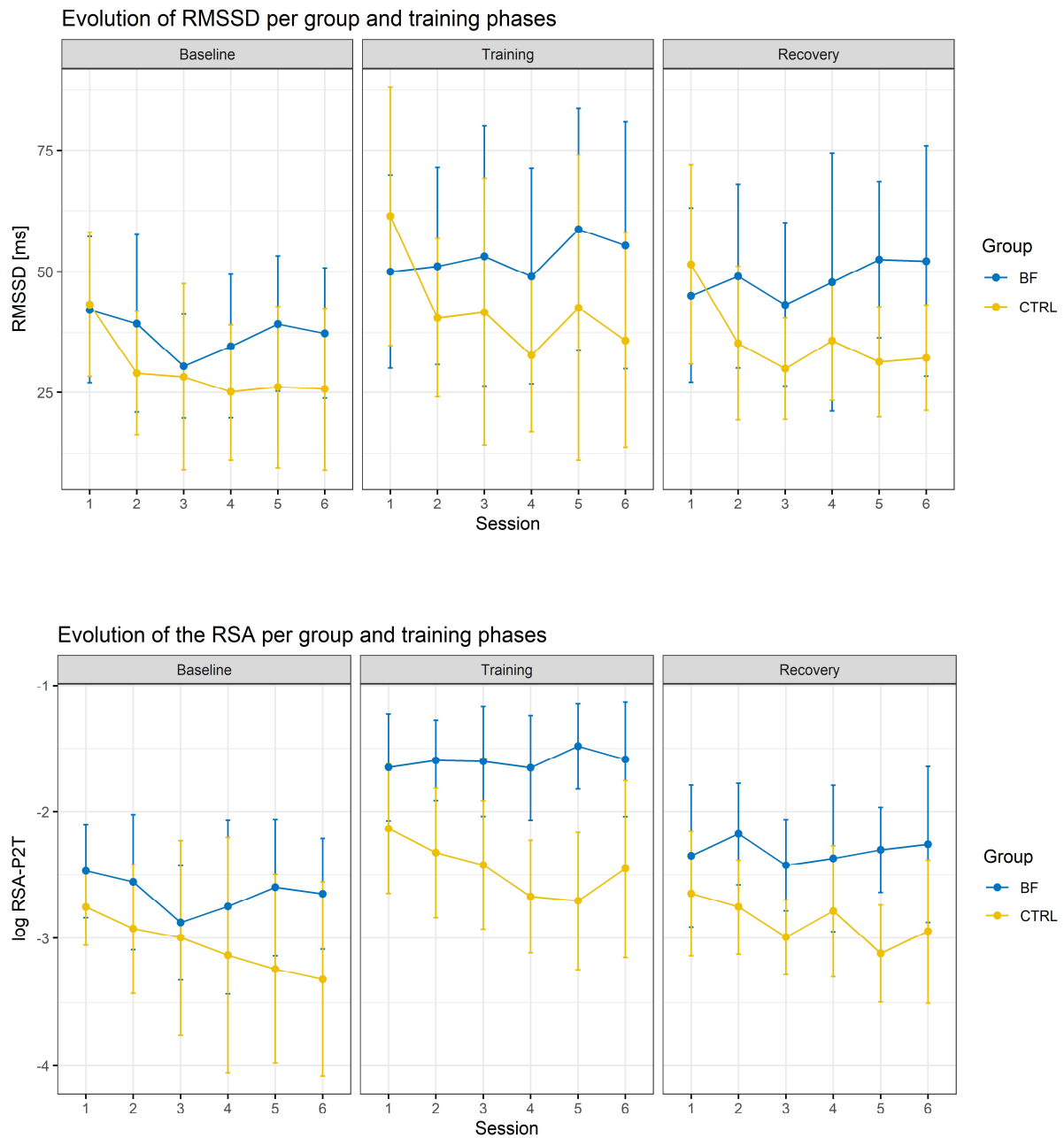
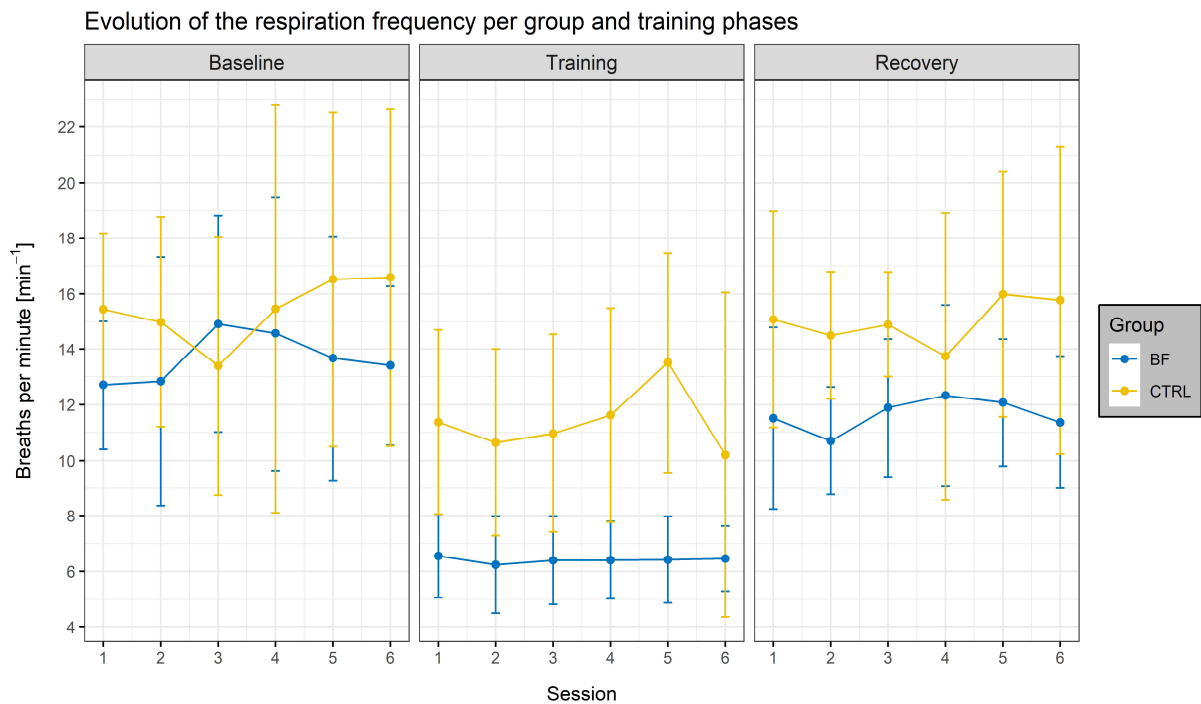
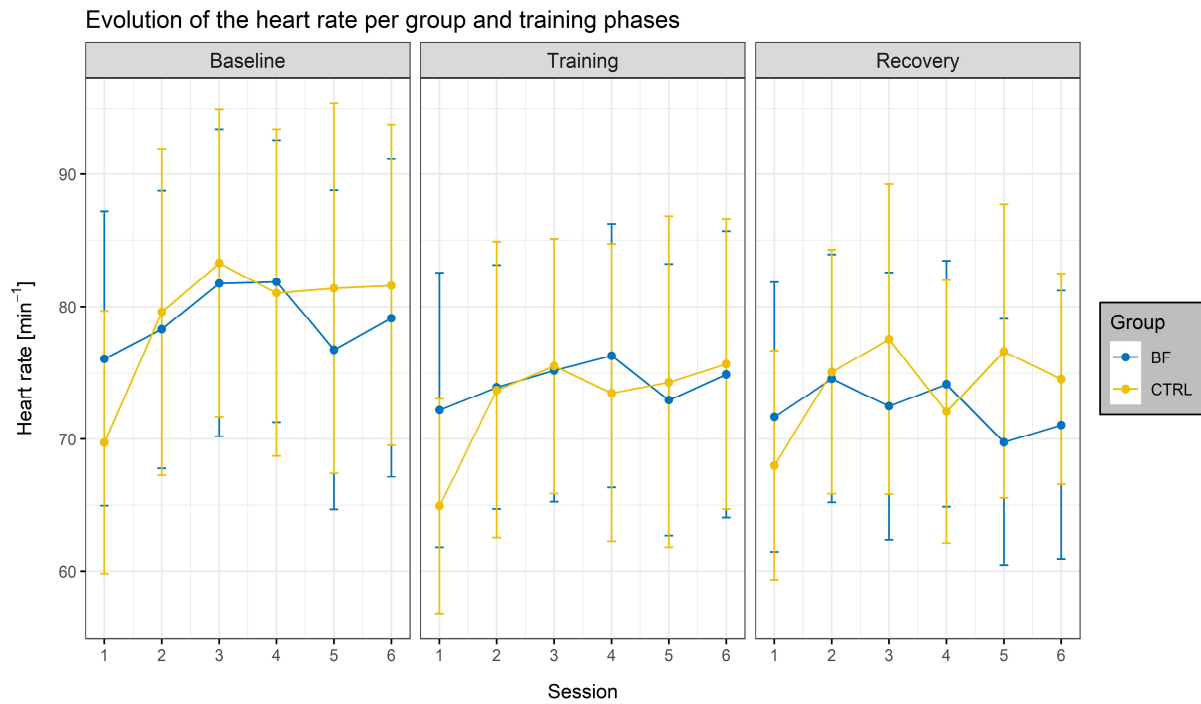


Figure A21 – Evolution of Physiological Parameters over Sessions

The figure depicts measures of root mean square in successive differences in the heart period (RMSSD), peak-to-through respiratory sinus arrhythmia (RSA-P2T), heart rate, and respirations rate recorded in study 1 across training sessions training phases within sessions. Resting-state physiological recordings were directly before (baseline) and 5 min after (recovery) self-regulation training. Participants in the ...



... biofeedback group (BF) practiced heart rate variability biofeedback, while participants in the control group (CTRL) regulated their heart rate variability based on self-paced slow breathing and mindfulness without the aid of biofeedback.

Curriculum Vitae



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- 09/2018 – 07/2019 **M2 in Bioengineering and Innovation in Neurosciences** (*bien*, average 15.8 & 3/24)
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- 04/2018 – 05/2018 **Institut Necker Enfants Malades – Cell biology Dept INSERM U1151, Paris**
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- 02/2018 – 03/2018 **Paris Descartes – Laboratoire Psychologie de la Perception UMR 8242, Paris**
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Scientific Communications

- PUBLICATION **Bögge, L.**, Colàs-Blanco, I., La Corte, V., Gaston-Bellegarde, A., & Piolino, P. (2023). Autonomic and cognitive control in memory: Investigating the psychophysiological link using virtual reality biofeedback. *Psychophysiology* [in review].
- PUBLICATION **Bögge, L.**, Colàs-Blanco, I., & Piolino, P. (2022). Respiratory sinus arrhythmia during biofeedback is linked to persistent improvements in attention, short-term memory, and positive self-referential episodic. *Frontiers in neuroscience*, 16. doi: [10.3389/fnins.2022.791498](https://doi.org/10.3389/fnins.2022.791498)
- PUBLICATION Guevara Erra, R., **Bögge, L.** (2022). Speech as a complex signal. Preprint (Version 1). doi: [10.21203/rs.3.rs-1365372/v1](https://doi.org/10.21203/rs.3.rs-1365372/v1). [In review in PNAS].
- SYMPOSIUM CHAIR **Bögge, L.**, Schumann, A., Chikhi, S., Blanchet, S., Ros, T. (2023, June 26-29). Connecting mind and body with biofeedback: innovative and rigorous approaches to cognitive enhancement. [Symposium presentation & chairing]. 21st World Congress of Psychophysiology (IOP2023), Geneva, Switzerland.
- ORAL **Bögge, L.**, Colàs-Blanco, I., La Corte, V., Gaston-Bellegarde, A., & Piolino, P. (2023, July 11-13). *Virtual reality biofeedback as a gateway to explore the interaction between cognitive control over memory and cardiac activity* [Paper presentation]. 26th Annual CyberPsychology, CyberTherapy & Social Networking Conference, Paris, France.
- ORAL **Bögge, L.**, Colàs, I., & Piolino, P. (2022, September 19–24). Virtual reality HRV biofeedback elicits persistent cognitive improvements that are linked to the level of respiratory sinus arrhythmia during training [Paper presentation]. 21st Meeting of the Biofeedback Federation of Europe (BFE), Montesilvano, Italy.
- ORAL **Bögge, L.**, Colàs, I., & Piolino, P. (2022, March 23-26). Control your heart, enhance yourself: Biofeedback training in virtual reality improves self-referential episodic memory [Paper presentation]. AAPB 53rd Annual Scientific Meeting, Irving, Texas, United States. *Note:* The talk was postponed due to the COVID19 pandemic.
- ORAL **Bögge, L.**, Colàs, I., & Piolino, P. (2021, September 22-23). Control the heart, control the mind: biofeedback training in virtual reality improves memory and attention [Paper presentation]. European Workshop on Imagery and Cognition Special Meeting (EWIC), Cambridge, United Kingdoms.
- ORAL **Bögge, L.**, Colàs, I., & Piolino, P. (2021, September 13-15). *Control the heart, control the mind: biofeedback training in virtual reality improves memory and attention* [Paper presentation]. 25th Annual CyberPsychology, CyberTherapy & Social Networking Conference, Milan, Italy.

Seven poster presentations at different scientific conferences across Europe. For example:

- POSTER **Bögge, L.**, Colàs, I., & Piolino, P. (2022, August 29 – September 01). HRV biofeedback evokes persisting improvements in attention, short-term memory, and positive self-referential episodic memory [Poster presentation]. European Society for Cognitive Psychology (ESCoP), France, Lille.
- POSTER **Bögge, L.**, Colàs, I., & Piolino, P. (2022, May 18-22). HRV biofeedback evokes persisting improvements in attention, short-term memory, and positive self-referential episodic memory [Poster presentation]. International Conference of Cognitive Neuroscience (ICON), Helsinki, Finland.

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