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Consciousness on a Spectrum: Rethinking Traditional Boundaries through Brain and Behavioral Dynamics

Başak Türker

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Sorbonne Université

École Doctorale Cerveau, Cognition, Comportement (ED3C)

Institut du Cerveau (ICM)

Physiological Investigations of Clinically Normal and Impaired Cognition (PICNIC) lab

La conscience sur un spectre :
Repenser les frontières traditionnelles à travers les
dynamiques cérébrales et comportementales

Başak Türker

Thèse de doctorat en Neurosciences

Sous la direction de Jacobo Sitt

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Devant un jury composé de :

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Rethinking Traditional Boundaries through Brain and
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Başak Türker

Dissertation for the degree of Doctor in Philosophy

Under the supervision of Jacobo Sitt

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To Meral and Nurşit

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RESUME

Le terme "état de conscience" désigne le type ou le niveau de conscience d'une personne à un moment donné. Il inclut différents aspects de l'expérience subjective tels que la perception, les pensées, les émotions et la conscience de soi. On peut classer les états de conscience selon différentes caractéristiques, comme le degré de vigilance (par exemple, être éveillé ou sous anesthésie), la présence ou l'absence de stimuli sensoriels externes (par exemple, être éveillé ou en train de rêver) et le degré de conscience de soi (par exemple, être éveillé ou sous l'influence de substances psychédéliques). À l'heure actuelle, ces états sont catégorisés de manière discrète en fonction de caractéristiques spécifiques. Par exemple, une personne éveillée peut consciemment traiter les stimuli sensoriels et y réagir, ce qui est considéré comme impossible pendant le sommeil. Dans ma thèse, je remets en question cette croyance dominante et soutiens que les états de conscience se placent sur un continuum, plutôt que constituer des états discrets. Je défends l'idée que la classification actuelle ne rend pas pleinement compte de la richesse et de la variabilité de chaque état. Pour étayer cette argumentation, j'étudie l'interaction entre les dynamiques cérébrales et la capacité à traiter les informations de manière consciente.

La première étude se penche sur les effets de la perception consciente sur les dynamiques cérébrales. Dans la vie quotidienne, nos expériences subjectives sont influencées par des stimuli complexes provenant de différentes modalités sensorielles, et l'intégration de ces éléments nous permet de comprendre le monde qui nous entoure. En utilisant l'imagerie par résonance magnétique fonctionnelle (IRMf), nous avons étudié les interactions entre différents réseaux cérébraux chez des participants ayant visionné un film audiovisuel. Les résultats suggèrent que les dynamiques cérébrales des participants se sont synchronisées lors du visionnage, ce qui renforce l'idée selon laquelle les expériences subjectives influencent les dynamiques cérébrales.

Les études suivantes se concentrent sur la relation inverse et cherchent à comprendre si nos états cérébraux peuvent influencer notre perception consciente. Notre deuxième étude combine l'IRMf et l'électroencéphalographie (EEG) pour étudier les fluctuations des expériences conscientes pendant l'éveil, un état qui permet généralement le traitement conscient de l'information. Les variations des dynamiques cérébrales de base sont liées à la perception consciente ou non d'un stimulus apparaissant ultérieurement. Les résultats montrent que certaines dynamiques cérébrales favorisent la perception consciente des stimuli. Nous

concluons que même dans un état d'éveil propice au traitement de l'information, nous pouvons observer des variations de l'activité cérébrale et du comportement, ce qui suggère que l'éveil n'est pas un état de conscience homogène.

Cette deuxième étude se focalise sur les fluctuations des expériences conscientes dans l'éveil. Mais qu'en est-il de notre perception consciente lors d'états de sommeil, pourtant considérés comme défavorables au traitement de l'information ? La troisième étude vise à comprendre si nous pouvons consciemment percevoir des stimuli pendant les différents stades du sommeil. Contrairement aux croyances largement répandues dans la littérature, nous démontrons que le cerveau endormi est capable d'accomplir des tâches complexes et de générer des réponses comportementales appropriées à tous les stades du sommeil. De plus, ces périodes transitoires de réactivité aux stimuli externes peuvent être prédites en se basant sur des marqueurs EEG pré-stimulus précédemment associés à des états conscients.

Dans l'ensemble, cette thèse fournit des preuves expérimentales démontrant que le traitement conscient de l'information fluctue à l'intérieur des états de conscience traditionnellement définis, en fonction des dynamiques cérébrales en cours. Cela souligne la nécessité de nouvelles avancées théoriques et empiriques pour redéfinir ces états traditionnels afin de comprendre pleinement leur complexité et la multitude de processus qu'ils englobent.

SUMMARY

The term "state of consciousness" refers to an individual's specific quality or level of awareness at a given moment. It encompasses various aspects of subjective experience, including perception, thoughts, emotions, and self-awareness. States of consciousness can be classified based on different features, such as the level of alertness (e.g., wakefulness versus anesthesia), the presence or absence of external sensory input (e.g., wakefulness versus dreaming), and the degree of self-awareness (e.g., wakefulness versus drug-induced states). Currently, these states are classified discretely based on the presence of specific characteristics. For instance, when someone is awake, they can consciously process and respond to sensory stimuli, which is considered impossible when they are asleep. This is evident in everyday situations where we might ask someone if they are sleeping and conclude that they are indeed asleep if they do not respond. In my thesis, I aim to challenge this prevailing belief and argue that states of consciousness exist on a continuum rather than as discrete states. I argue that the current discrete classification fails to capture the richness and variability of each state. To support this argument, I focus on the interaction between ongoing brain dynamics and the capacity to consciously process information.

The first study investigates how conscious perception influences ongoing brain dynamics using functional Magnetic Resonance Imaging (fMRI). Our subjective experiences in everyday life are shaped by complex stimuli from different sensory modalities, and the integration of these elements enables us to understand the world around us. By utilizing naturalistic movies as a model of real-world environments, we demonstrate that global brain states, characterized by interactions among different brain networks, synchronize among participants and align with ongoing subjective experiences.

Subsequent studies focus on the inverse relationship and seek to understand whether baseline brain states prior to stimulation can influence our conscious perception. Our second study combines fMRI and electroencephalography (EEG) to investigate fluctuations in conscious experiences during wakefulness, a state that typically enables conscious processing of information and behavioral responsiveness. The results show that certain brain dynamics, previously associated with conscious states, favor the conscious perception of stimuli. We conclude that even in a state of wakefulness conducive to information processing, we can observe variations in brain activity and behavior, suggesting that wakefulness is not a homogeneous state.

This second study focuses on fluctuations in conscious experience during wakefulness. But what about our conscious perception during sleep states, which are considered unfavorable for information processing? The third study aims to investigate the capacity for information processing and responsiveness during different sleep stages. Contrary to widely accepted beliefs in the literature, we demonstrate that the sleeping brain is capable of performing complex tasks and generating appropriate behavioral responses in all sleep stages. Moreover, these transient periods of responsiveness to external stimuli can be predicted based on pre-stimulus EEG markers previously associated with conscious states.

Overall, this thesis provides experimental evidence demonstrating that conscious information processing fluctuates even within traditionally defined states of consciousness, depending on ongoing brain dynamics. This highlights the need for further theoretical and empirical advances to redefine these traditional states in order to fully capture their complexity and the multitude of processes they encompass.

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LIST OF PUBLICATIONS

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CHAPTER I

GENERAL INTRODUCTION

GENERAL INTRODUCTION

Until recently, the exploration of consciousness was a subject largely considered taboo within scientific circles. Many researchers held the belief that it was beyond the realm of experimentation, relegating its investigation to philosophers. However, over the past few decades, consciousness has emerged as a genuine scientific topic. The field of cognitive science now engages in ongoing debates surrounding fundamental questions such as the nature of our awareness of the world, the underlying mechanisms of consciousness, its potential existence in non-human entities, and the possibility of machine consciousness (Dehaene et al., 2017). Advancements in neuroimaging techniques, coupled with the development of theoretical and computational models, now enable scientists to shed light on these long-standing questions. Moreover, various pathological and normal states, such as blindsight, neglect, anesthesia, sleep, hypnosis, and mind-wandering, offer valuable empirical opportunities to investigate consciousness.

Before describing these conditions and reviewing the state of the art in this scientific field, it is crucial to establish a clear framework by defining the terminology employed throughout this work. Consciousness can be defined in different ways, such as the capacity to subjectively report mental representations (including sensory, motor, semantic, episodic, or emotional) (Naccache, 2018), to be aware of something, to be able to perceive or feel things, a the state of the subject (like in the phrase “the patient is not conscious”), or the unique experience of each of us have (Chalmers, 1998). In this work, we will focus on two specific concepts: conscious perception and state-of-consciousness.

Conscious perception, or **conscious access**, refers to our ability to perceive information that can be verbally reported or expressed through gestures. For instance, when you read this paragraph attentively, your brain processes the words consciously. You can then recall, report, and manipulate the processed information in various ways, such as repeating it word for word, providing the general meaning, or saying the words backward.

State-of-consciousness, on the other hand, relates to our ability to maintain a "stream of conscious contents" (James, 1890), which is closely tied to our level of arousal or vigilance. When we are awake, we can consciously access information, but this ability declines during lower vigilance states like sleep, coma, or anesthesia. Although arousal is a necessary condition for being conscious, it is not sufficient. This distinction is particularly apparent in pathological

conditions such as the vegetative state or the minimally conscious state, where patients may exhibit signs of arousal such as opening their eyes or moving but show little or no overt signs of consciousness in their behavior. In the following sections, we will delve deeper into these two concepts and explore different scientific methods used to investigate them.

1.1. (Un)conscious perception

Perception refers to the interpretation of physical sensations, such as sight, sound, touch, smell, and taste, based on prior experiences and predictions. Whether this process happens consciously or unconsciously depends on the physical quality of the information being processed. For a stimulus to be experienced and reported, it must reach a person's awareness. However, studies have shown that perception can occur unconsciously under some experimental or clinical conditions (Mudrik et al., 2014).

In healthy individuals, unconscious perception can happen when a subliminal stimulus (i.e., below the threshold of awareness) is encoded. A subliminal stimulus cannot be consciously perceived because it conveys only a small amount of information to the cognitive system. Even if a person dedicates significant cognitive resources to the stimulus, the stimulus's strength (e.g., duration, contrast, or energy) remains insufficient to trigger conscious processing. However, an increasing body of research shows that subliminal perception, despite not being consciously experienced, can still affect subsequent behavior.

The first line of evidence comes from neuroimaging studies that show that subliminal stimuli can induce changes in brain activity. For instance, studies have demonstrated that the unconscious perception of fearful faces (Whalen et al., 1998) and fearful eye whites (Whalen et al., 2004), without explicitly noticing the stimulus, can modulate activity in the amygdala. Similarly, the presentation of masked words (see section 1.1.1.2 for details on the masking paradigm) that go unnoticed by the participant activates regions related to reading (Dehaene et al., 2001). Moreover, subliminally presented prime words decrease subsequent activation for the same word, suggesting that repetition suppression, a reduced neural response to repeated stimuli (Barron et al., 2016), can occur even after a subliminal presentation. In addition to affecting neural responses, subliminal stimuli can also induce priming effects that reduce reaction times to the same target stimulus following the prime. Subliminal repetition suppression and priming effects have been found in facial recognition domain (Kouider et al., 2009). In this study, participants were asked to determine whether the presented face belonged

to a celebrity. Using subliminal prime images, the authors showed that using the same image as a prime reduced neural response to the target image in the face processing related regions. Furthermore, reaction times to the target were shorter when the prime image belonged to the same celebrity (even if it was the exact same image or a different angle). These results indicate that subliminal primes can impact subsequent brain and behavioral responses, even if participants cannot report any perceptual experience.

A study that used the go/no-go paradigm to investigate inhibitory control has also revealed an effect of unconscious perception on reaction times (van Gaal et al., 2011). In this study, participants were presented with a target indicating left or right button-press, followed by either a stop signal (“STOP”) or a control signal (e.g., “BLUF”). Half of the trials had masked signals that were not visible, while the other half had no masks, making the signal easily perceived. Unmasked (visible) stop signals caused the expected inhibition of the response. Although masked stop signals did not lead to omission of the response, they still caused a significant increase in response times. Furthermore, masked stop signals triggered similar ERP components as the unmasked stop signal, suggesting that inhibitory control can be initiated unconsciously.

The impact of unconscious information processing on behavior has been further supported by Pessiglione and colleagues in the domain of motivation (Pessiglione et al., 2007). In an incentive force task, participants were presented with coin images indicating the value of the trial (one pound or one penny), followed by a mask image whose duration varied, making it visible only for some trials. Participants were instructed to exert force on a hand grip and were informed that the amount of money they earned on each trial depended on the force they exerted. Feedback on the exerted force was given on the screen in real time. The results showed that force exerted in the “pound” condition was greater than the force exerted in the “penny” condition, indicating that unconsciously perceived signals can influence the level of motivation and effort invested in a task.

A number of studies have also demonstrated that unconscious stimuli can be integrated over time (for a comprehensive review, see Mudrik et al., 2014) leading to the initiation of cognitive tasks without conscious awareness. For example, Reber and Henke (2012) found that new semantic associations between subliminal words can be established over time in an unconscious manner. Atas et al. (2014) showed that sequential regularities of unconsciously perceived stimuli can be learned through their non-conscious temporal integration.

Furthermore, Ric and Muller (2012) found that subliminally presented arithmetic instructions, such as addition, can be processed and applied unconsciously to supra- and sub-threshold numbers.

Taken together, these studies demonstrate that, under specific experimental conditions, stimuli processed unconsciously can elicit behavioral and brain responses regardless of subjective experience. Such a phenomenon can also be observed in certain clinical conditions, such as blindsight, where individuals are able to react to visual stimuli despite being unable to consciously perceive them due to cortical blindness (Weiskrantz et al., 1974). Following damage to the visual cortex, patients with blindsight have been shown to exhibit better than chance-level performance in detecting, localizing, or discriminating visual stimuli presented to their blind visual field. It has been shown that patients with blindsight can discriminate facial expressions despite reporting no awareness of the faces (de Gelder et al., 1999). Several case reports also revealed that valid spatial cueing of a target presented in the blind field improves task performance, suggesting that patients with blindsight can direct attention to their blind field (Kentridge et al., 1999, 2004; Schurger et al., 2008). Overall, these findings indicate that visual awareness is distinct from visual processing and that unconscious processing can be influenced by attention.

When you were reading the previous sentences on your computer, you may not have been aware of the noise your computer was making until I brought it to your attention. This was because your attention was focused on the reading rather than the computer noise. This illustrates the strong link between attention and conscious perception. A dichotomy between subliminal and preconscious stimuli has been proposed in the literature to distinguish different types of unconscious stimuli. While a subliminal stimulus is too weak to reach awareness, a preconscious stimulus carries enough bottom-up information but remains inaccessible due to a lack of top-down attentional amplification. (Dehaene et al., 2006). Examples of the latter include change blindness (Simons & Levin, 1997; Simons & Rensink, 2005) and inattention blindness (Simons & Chabris, 1999; Mack, 2003), where individuals fail to detect objects or large changes in the scene due to a lack of attention, even when the stimuli are presented in the fovea. These examples demonstrate that the strength of the stimulus alone is not sufficient for conscious perception; it needs to be coupled with attention.

1.1.1. Experimental paradigms to study conscious perception

Over the last few decades, researchers have developed various paradigms to study conscious perception and its corresponding neural correlates. In most cases, these paradigms involve comparing brain activity elicited by conscious and unconscious perception of the same stimulus in order to reveal the neural mechanisms underlying awareness. In this section, we will review the main paradigms used in this field and discuss the neural correlates that have been identified through their use.

1.1.1.1. Threshold stimulus presentation

A stimulus at the detection threshold refers to sensory input whose strength allows perception at a predetermined level of accuracy. Typically, studies that compare conscious and unconscious perception establish the stimulus strength so that the stimuli are detected in 50% of trials. This method requires identifying the individual threshold for each participant, as they may exhibit inter-individual differences. The most commonly used method for identifying individual detection or discrimination thresholds is the *staircase procedure* (Cornsweet, 1962) which involves adjusting the stimulus strength based on the participant's response. In this procedure, the participant is repeatedly presented with the target stimulus to be detected. The stimulus strength is decreased or increased by the experimenter each time the participant detects or misses the stimulus, respectively, until the stimulus strength is such that the participant can detect only half of the trials. The same procedure can be used to identify the discrimination threshold between two stimuli. In this case, the difference between the two stimuli is decreased after each correct discrimination and increased after each miss. After the threshold has been identified, the participant is repeatedly presented with stimuli at the detection threshold, and the trials are separated according to whether the stimulus is perceived or not. Brain activity before or after detection and misses are then contrasted to uncover neural correlates of conscious perception. The threshold stimulus presentation has been widely used in the auditory (Kusnir et al., 2011; Leske et al., 2015; Sadaghiani et al., 2009, 2015), visual (Busch et al., 2009; Ergenoglu et al., 2004; Pins & Ffytche, 2003; Wyart & Tallon-Baudry, 2009), and somatosensory (Palva et al., 2005; Ploner et al., 2010; Wühle et al., 2010, 2011) domains, as well as in cross-modal evaluation (Sanchez et al., 2020).

1.1.1.2. Masking paradigm

The masking paradigm involves briefly presenting a target stimulus in close spatial and temporal proximity to a second 'mask' stimulus, preventing its perception (see Figure 1.1 for an example). Although visual stimuli like words presented in isolation for tens of milliseconds can be perceived and reported by individuals, when this brief target stimulus is immediately followed by a mask stimulus, it becomes invisible (Breitmeyer & Ögmen, 2010).

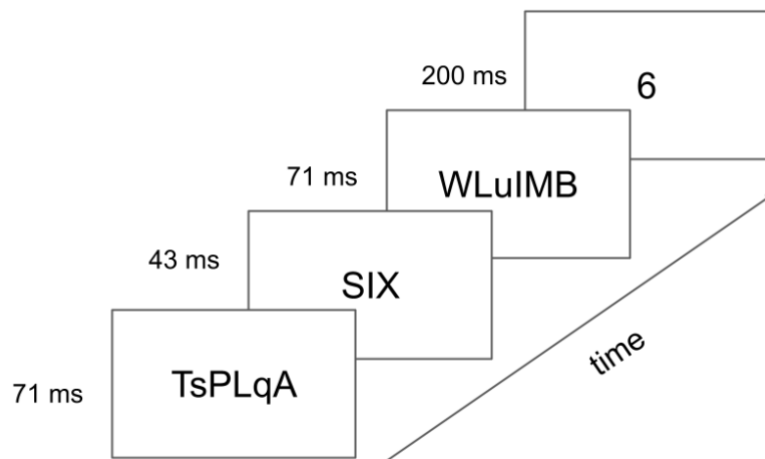


Figure 1.1. An example trial in the masking paradigm. Alphabetically written target ‘SIX’ cannot be perceived due to the preceding and following masks, even though it was presented for a duration exceeding the detection threshold. The second target ‘6’, on the other hand, remains visible due to its longer presentation time and absence of a backward mask (Adapted from Dehaene et al., 1998).

The masking paradigm has been widely employed in the literature to investigate the impact of unconscious processing on cognition. In a seminal study, Dehaene et al. (1998) demonstrated that subliminally perceived stimuli could influence motor responses. To reveal such effect, participants were required to determine whether a numerical target was larger or smaller than five. A prime number, which was either congruent (for example, if the target was bigger than five, the prime was also bigger than five) or incongruent with the target, was briefly presented and in between two visual masks, making it impossible to perceive consciously (as shown in Figure 1.1). The results revealed that response times for incongruent trials were significantly slower than those for congruent trials. Even though participants were not aware of the discrepancy between the prime and the target, it biased their motor response during the task, demonstrating the possibility of unconscious priming.

1.1.1.3. Attentional blink

The attentional blink phenomenon arises when a sequence of rapidly presented stimuli contains multiple targets that need to be processed. During visual attentional blink experiments, two targets (T1 and T2) are displayed in a series of stimuli at the same location, with T2 appearing after T1 with varying temporal intervals (Figure 1.2). Notably, detecting T2 is substantially hindered when it appears 200-500ms after T1. However, T2 detection is not affected when it is presented immediately after T1, with a delay exceeding 500ms or when detection of T1 is not required. Attentional blink paradigms are often coupled with neuroimaging techniques such as EEG (Sergent et al., 2005), MEG (Kessler et al., 2005), and fMRI (Marois et al., 2004; Kranczioch et al., 2005) to investigate neural events that correlate with conscious and unconscious perception of T2.

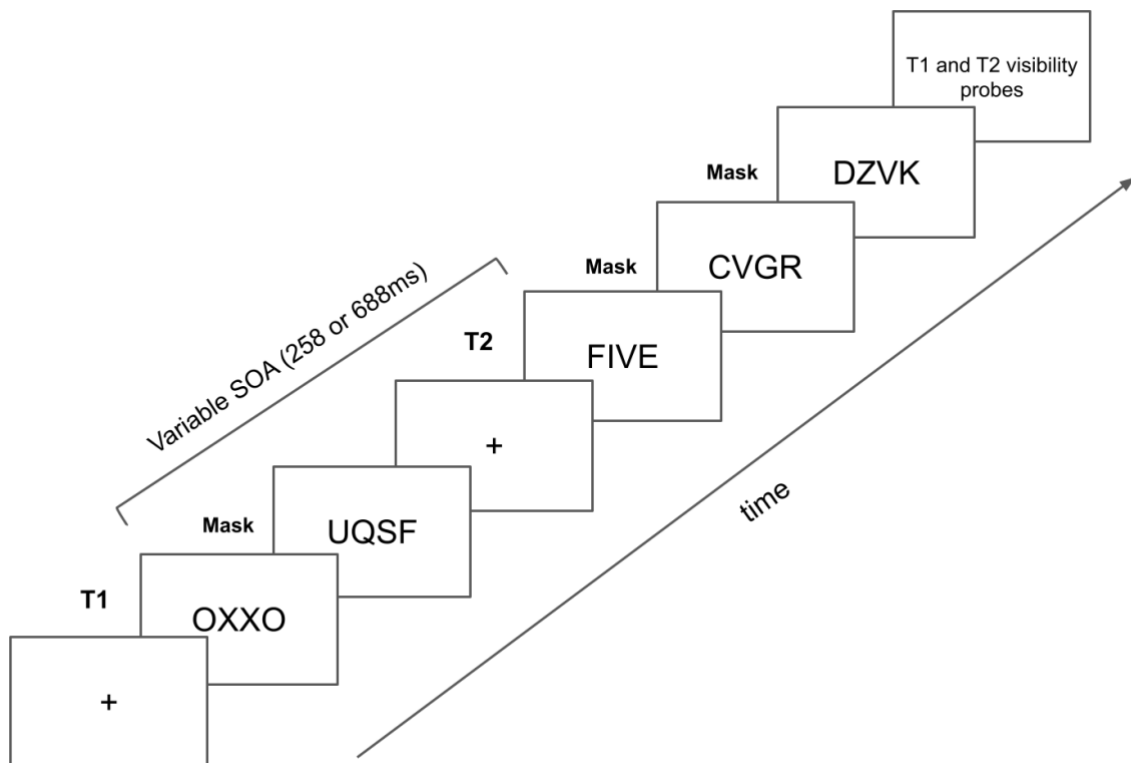


Figure 1.2. An example trial in the attentional blink paradigm. During the trial, participants are presented with a rapid succession of visual stimuli, each displayed for 43 ms. Participants are specifically instructed to attend to two specific stimuli, T1 (OXXO) and T2 (FIVE), and are asked to respond to visibility probes that appear at the end of the trial. Depending on the trial, the stimulus onset asynchrony (SOA) between T1 and T2 is either short or long (258 and 688 ms, respectively). In trials with a short SOA, the visibility of T2 is impaired due to the attentional blink phenomenon. (adapted from Sergent et al., 2005).

1.1.1.4. Ambiguous stimulus presentation

An ambiguous visual stimulus is a type of stimulus that can have multiple interpretations or meanings. For instance, the duck-rabbit illusion (Figure 1.3D) is an example of an ambiguous stimulus that can be perceived as either a duck or a rabbit. When participants observe ambiguous stimuli, their perception can spontaneously switch between the possible interpretations, even though the sensory information remains the same. In ambiguous stimulus presentation paradigms, participants are asked to indicate these changes in perception by either verbalizing them or via button presses. This paradigm allows researchers to investigate the neural activity associated with changes in conscious perception, without manipulating the stimuli or assigning any specific cognitive tasks. For a comprehensive overview of studies that use ambiguous stimuli in cognitive science, see Kornmeier & Bach, (2012).

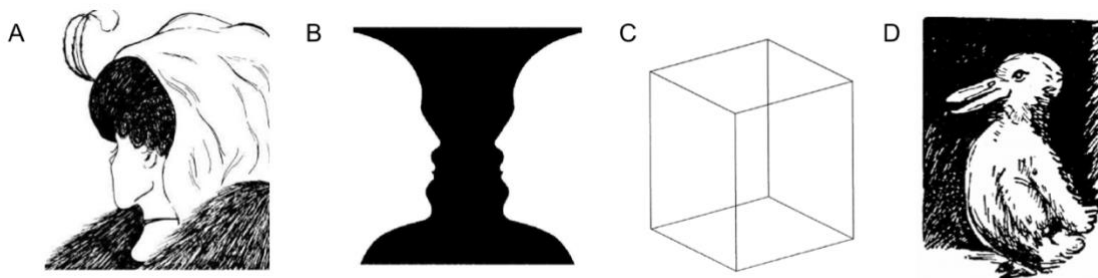


Figure 1.3. Examples of ambiguous visual stimuli. (A) The young girl/old lady illusion. (B) Rubin's face/vase illusion. (C) The Necker cube. (D) The duck/rabbit illusion (taken and adapted from Schooler, 2015).

1.1.1.5. Binocular rivalry

Binocular rivalry is a phenomenon where different images are presented to each eye, leading to a competition for visual dominance in the brain. This typically results in spontaneous switches between perceiving one image and the other, rather than fusing them into a single image (Tong et al., 2006). This perceptual competition is known as binocular rivalry. Similar to ambiguous stimulation presentation paradigms, perceptual alternations occur spontaneously and continuously over time. Participants are instructed to report percept switches, allowing researchers to measure the rate and duration of perceptual alternations. These alternations can be used to study the neural mechanisms underlying conscious perception and attention, as well as the role of top-down processes, such as attention and expectation, in modulating perceptual awareness.

One major limitation of the aforementioned paradigms is that participants are required to report their perception, making it difficult to distinguish between neural activity associated with conscious perception and neural activity associated with decision-making or reporting. To address this issue, researchers have developed new methods, referred to as the "no-report paradigm", that can detect perceptual changes without requiring participants to report their subjective experience. One such method involves using optokinetic nystagmus (OKN), a reflexive eye movement that occurs when an individual is presented with a moving visual stimulus such as a scrolling pattern. OKN is comprised of slow tracking movements followed by quick, corrective saccades. The slow tracking movements allow the eyes to follow the moving stimulus, while the quick saccades reset the eyes to their starting position for the next tracking movement.

Using this paradigm, Frässle et al. (2014) presented two gratings moving in opposite directions to each eye. The direction of the OKN followed the current percept, demonstrating rightward movement when participants perceived the grating moving to the right (and vice versa). By using eye-tracking methods, the authors were able to detect perceptual alternations without relying on subjective reports, as eye movements were found to be closely linked to subjective perception. The neural correlates of conscious perception identified in no-report paradigms are discussed in Section 1.1.2.

1.1.1.6. Continuous flash suppression

Another method for manipulating conscious perception is continuous flash suppression. Similar to binocular rivalry, this technique takes advantage of the discordance between the inputs of the two eyes. However, instead of presenting two conflicting stimuli to each eye, as in binocular rivalry, continuous flash suppression involves presenting a continuously changing image to one eye and a static image to the other eye. The dynamic image has been shown to suppress the perception of the static image, allowing researchers to modulate conscious perception without altering the static stimulus itself (Tsuchiya & Koch, 2005). Similar suppression effects can also be observed under non-stereoscopic presentation conditions, such as motion-induced blindness, which involves the suppression of the perception of stationary salient stimuli by small moving stimuli in the background (Bonneh et al., 2001).

Using continuous flash suppression, Mudrik et al. (2011) showed that integration between an object and its background can occur unconsciously. In this study, participants were presented with successive colored images in a Mondrian-like pattern to one eye, which induced

perceptual suppression of the static scenes presented to the other eye. The static scenes contained objects that were either congruent (e.g., basketball players holding a basketball) or incongruent (e.g., basketball players holding a watermelon) with the overall scene. Results revealed that incongruent scenes emerged into awareness more quickly than congruent ones, suggesting that participants were able to unconsciously evaluate the coherence of the scene.

1.1.1.7. Interventional methods

Interventional methods involve altering brain activity using magnetic fields or electrical currents to enhance or inhibit conscious perception. These techniques are often used alongside psychophysics paradigms. The most commonly used methods in healthy individuals are Transcranial Magnetic Stimulation (TMS), transcranial Direct Electrical Stimulation (tDCS), and transcranial Alternating Current Stimulation (tACS). These non-invasive techniques are used to investigate the neural correlates of conscious perception and to establish causal links between brain activity in specific regions and the capacity for conscious perception.

For example, using TMS in healthy participants, Chanes et al. (2012) demonstrated that stimulating the Frontal Eye Field (a region known to be involved in visuospatial attention) prior to presentation of threshold stimuli increased detectability and facilitated conscious perception. However, applying TMS to primary visual areas 100ms after stimulus onset has been shown to reduce performance in conscious color discrimination and to decrease unconscious priming effects (Railo et al., 2012). Using repetitive TMS (rTMS), some studies investigated the causal role of parietal regions in conscious access. Babiloni et al. (2007) found that interfering with activity in the left and right ventral posterior parietal cortex using rTMS decreased performance at a masked stimulus detection task. Moreover, Beck et al. (2006) showed that disrupting activity in the right and left parietal cortex resulted in more pronounced change blindness and longer latencies to detect changes between two similar images. Similarly, Carmel et al. (2010) reported that altering activity in the right superior parietal cortex increased switches between percepts in binocular rivalry by decreasing the duration of dominance periods.

Other studies using tACS aimed to modulate inter-hemispheric synchrony by delivering weak sinusoidally oscillating electrical currents that were either in-phase or anti-phase between the two hemispheres (Helfrich et al., 2014; Strüber et al., 2014). These studies combined 40 Hz stimulation over occipital-parietal regions with a bistable motion perception paradigm and found that increasing interhemispheric synchrony resulted in participants perceiving horizontal motion more frequently. Although interventional studies allow for inferring causal links

between brain activity and conscious perception, they are relatively rare in the literature compared to neuroimaging studies that provide a more comprehensive and coherent view of which brain regions are involved in conscious processing. In the next section, we will review the state-of-the-art in the field.

1.1.2. Neural correlates of conscious perception revealed by neuroimaging

Investigating the neural correlates of conscious processing requires combining cognitive paradigms that contrast the processing of conscious and unconscious stimuli with brain imaging techniques. While some studies conducted on monkeys using multi-neuron recordings (Supèr et al., 2001) and on healthy humans using fMRI (Tse et al., 2005) suggested that detecting a visual stimulus primarily depends on brain activity in the visual cortex, other studies on neglect patients (Vuilleumier et al., 2001) and healthy participants (Grill-Spector et al., 2000) demonstrated that activity in the visual cortex can occur without visual awareness, implying that conscious access requires contributions from other brain areas. Since then, a body of research indicated that a larger scale of brain activity may be necessary for a stimulus to reach awareness.

A study comparing brain activity evoked by presentation of masked (invisible) and un-masked (visible) words showed that while unconscious perception mainly activated visual and word-processing areas, conscious perception was also associated with widely distributed activations, including frontal and parietal areas (Dehaene et al., 2001). Functional connectivity analysis revealed a strong correlation between left fusiform region and bilateral posterior intraparietal sulci, the dorsolateral prefrontal cortex and the inferior frontal/anterior temporal cortices when the words were visible. Similar functional connectivity results were also found in an fMRI study, showing that the visibility of a stimulus was correlated with activity in higher visual areas and also in fronto-parietal regions (Haynes et al., 2005).

Studies using electrophysiological recordings further supported the observation of widespread activations during conscious perception. Sergent et al. (2005) combined EEG recording with an attentional blink paradigm, where two masked visual targets were presented sequentially (Figure 1.2). The delay between the two stimuli (SOA) was variable. The attentional blink phenomenon occurred only in the short SOA condition when participants had to pay attention to both stimuli. By comparing "seen" and "unseen" trials in the double-task condition, the authors highlighted the brain events associated with conscious access. ERP analysis revealed

that the P1 and N1 responses to ‘seen’ and ‘unseen’ trials did not differ. However, late responses to ‘seen’ and ‘unseen’ trials were different. The former engendered a greater left-lateralized posterior negativity around 270 ms (N2) and central negativity around 350 ms (N4). Importantly, a frontal negativity around 300 ms (N3), a frontal positivity around 440 ms (P3a) and late parietal positivity around 580 ms (P3b) were observed only during ‘seen’ trials. Source localization indicated that activity for ‘seen’ and ‘unseen’ trials were comparable in occipital and occipitotemporal areas until 200 ms. However later on, ‘seen’ trials evoked different activity, starting with left temporal lobe and inferior frontal regions and extending to the dorsolateral prefrontal, ventral prefrontal, anterior cingulate regions and finally over inferior parietal cortex.

Another study combining EEG recordings with a masking paradigm yielded similar results. Del Cul et al. (2007) briefly presented a numerical target followed by a mask surrounding the target location with a variable SOA (16, 33, 50, 66, 83, or 100 ms). Participants were asked to compare the numerical target to five and rate its visibility on a continuous scale. The results showed a sigmoidal pattern of performance, with performance increasing nonlinearly as a function of the duration of the stimulus onset asynchrony (SOA) between the target and the mask. Consistent with the findings of the attentional blink experiment by Sergent and colleagues, the N1 and P1 components were not affected by shorter SOAs and thus, did not differ between ‘seen’ and ‘unseen’ trials. However, the amplitude of later components such as the N2 and P3 correlated with the duration of SOA, with longer SOAs yielding higher amplitudes. Notably, the amplitude of the P3 response showed a sigmoidal relation that was identical to the fraction of seen trials as a function of SOA. Furthermore, the amplitude of the P3 component was statistically different for seen and unseen trials at a given SOA.

Altogether, converging results from these two studies using different experimental paradigms suggest that the P3 component is one of the neural signatures of conscious perception. Activity across a distributed fronto-parietal network is implicated in conscious access, supporting the Global Neuronal Workspace Theory (GNWT) (Dehaene & Naccache, 2001; Baars, 2005; Dehaene & Changeux, 2011a; Mashour et al., 2020). According to this theory, unconscious information is processed in parallel by different neural networks. For information to become conscious, it needs to be broadcasted and made accessible to other brain networks. Attentional amplification facilitates this broadcasting process, generating coherent and sustained patterns of large-scale brain activity. The fronto-parietal network is proposed to play a crucial role in

this broadcasting mechanism, which is not modality-specific but rather a common mechanism for conscious access to information across modalities (visual, auditory, tactile, access to memories or to emotions).

In line with this idea, a recent MEG study by Sanchez et al. (2020) evaluated conscious perception in visual, auditory, and tactile modalities. The study found common features in the neural activity across modalities, suggesting a supramodal mechanism for conscious perception and the late global broadcasting of information. A decoding algorithm trained to classify perceived and unperceived stimuli in one modality was able to generalize to other modalities. This modality-independent activity even included activity in sensory regions corresponding to different modalities, indicating the presence of a shared mechanism for conscious perception.

GWNT was further supported by studies using multi-unit recordings in monkeys demonstrating that late frontal activity is associated with conscious perception. van Vugt et al. (2018) trained animals to detect and report visual stimuli by making saccades. They compared post-stimulus activity for detected and undetected stimuli in V1, V4 and prefrontal cortex and found similar activity in the visual areas in both cases. However, they observed a late and sustained frontal activity only in detected trials. Interestingly, false detections, where the monkeys reported perceiving a stimulus that was not there, also elicited prefrontal activity.

These studies provide converging evidence for the involvement of a distributed fronto-parietal network in conscious access and support the idea that conscious perception relies on the broadcasting of information across different neural networks. The P3 component and late frontal activity have been suggested as neural correlates of conscious perception, and the findings across modalities suggest a supramodal mechanism for conscious access. However, the role of the prefrontal cortex in conscious perception has been a subject of debate in the field. Some researchers argued that prefrontal activity is not purely linked to conscious perception but rather to processes such as attention, expectation, monitoring, and report (Koch et al., 2016; Pitts et al., 2014; Tsuchiya et al., 2015). According to this view, in order to uncover the true correlates of conscious perception, one must eliminate all other processes, including subjective reports.

Frässle et al. (2014) conducted a study using a no-report paradigm tackle this issue. They employed binocular rivalry and optokinetic nystagmus to infer the conscious content of participants without relying on subjective reports (see Section 1.1.1.5 for methodological

details) and found frontal activations when participants were asked to provide reports, consistent with previous studies. However, when participants did not provide any report and the perceptual content was derived from the direction of optokinetic nystagmus, frontal activities disappeared. Based on these findings, the authors concluded that frontal activity was linked to report or introspection rather than conscious perception itself.

A recent study tackled the same question with a model-based approach (Sergent et al., 2021). Participants were presented with auditory stimuli at different signal-to-noise ratios (SNRs) and were asked to either report the stimuli (active session) or simply pay attention to them without providing any reports (passive session). The authors hypothesized that the brain activity following the presentation of threshold stimuli would exhibit high inter-trial variability, indicating bifurcation dynamics, as some stimuli would be detected and increase brain activity while others would not. The results supported this hypothesis, showing bifurcation dynamics in both active and passive sessions. Furthermore, the late post-stimulus EEG activity could be utilized to classify whether a high SNR stimulus was presented using time generalization decoding (King & Dehaene, 2014). The projected brain activity, which represents the distance between the trial's location in the multivariate decoding space and the decision boundary, mirrored the bifurcation dynamics observed in the original neural data. To further investigate the role of frontal cortex in conscious perception, the study trained a model in the passive condition and tested it in the active condition, and vice versa, to classify stimulus presence (maximal SNR) versus absence trials. The findings revealed that the late activity in the passive sessions reflected mechanisms implicated in conscious perception, along with decision-making and reporting mechanisms. Comparisons of neural activations elicited by highest SNR stimuli in the active and passive sessions revealed that certain frontal areas, such as the inferior frontal cortex, remained activated, while others, like the supplementary motor area, were disengaged when no reports were needed. These results suggest that the frontal cortex is involved in task-free conscious processing, but a broader frontal network comes into play when decision-making and motor planning are necessary.

These studies contribute to the ongoing debate regarding the minimal core neural activity needed for conscious perception. By employing different populations (animals and humans), neuroimaging techniques (EEG, MEG, fMRI, intracranial recordings), and innovative no-report paradigms, they shed light on the neural processes underlying conscious perception.

While the involvement of the prefrontal cortex in conscious perception is acknowledged, its specific role may depend on task demands and the need for decision-making and reporting.

1.2. States of (un)consciousness

A state of consciousness refers to an individual's level of awareness of both internal factors, such as proprioception, memories, and emotions, as well as external information, including perception of the surrounding world. The subjective experience of an individual depends on the specific states they are in. Various states of consciousness can be differentiated based on the level of alertness (e.g., wakefulness vs. anesthesia), the presence or absence of sensory input (e.g., wakefulness vs. dreaming), and the degree of self-awareness (e.g., wakefulness vs. drug-induced states).

States of consciousness encompass normal wakefulness, sleep, disorders of consciousness, anesthesia, mind-wandering, hypnosis, drug-induced altered states, and meditation. In this section, our focus will be on disorders of consciousness and sleep.

1.2.1. Disorders of Consciousness (DoC)

Disorders of consciousness (DoC) encompass various pathological alterations in consciousness resulting from severe brain injuries, including traumatic brain injuries, post-anoxic encephalopathies, and stroke. DoC can be classified into three main categories: coma, vegetative state, and minimally conscious state.

Coma refers to a state where a patient is completely unresponsive, with closed eyes and no signs of arousal. If these patients start displaying some signs of arousal, such as opening their eyes or exhibiting motor behavior, they may transition into a vegetative state (VS), also known as unresponsive wakefulness syndrome (UWS). Although patients in a VS show spontaneous eye openings and sleep-wake cycles, they do not demonstrate any adaptive response to the external environment (Jennett & Plum, 1972), indicating a lack of awareness. On the other hand, patients in a minimally conscious state (MCS) exhibit some evidence of awareness through cognitive behaviors like visually tracking a person who is speaking, following simple commands, or providing gestural or verbal yes/no responses. MCS was initially described as 'a condition of severely altered consciousness in which minimal but definite behavioral evidence of self or environmental awareness is demonstrated' (Giacino et al., 2002). MCS is a highly heterogeneous syndrome, varying greatly between and within patients. Patients often

fluctuate in their display of signs of awareness. Some authors have suggested further subcategories within MCS, distinguishing between MCS- and MCS+ patients based on the absence or presence of signs of language function, respectively (Bruno et al., 2011). Patients who regain functional communication and the ability to use objects are considered to be in an emergence/exit MCS (EMCS).

The gold standard for diagnosing different states of consciousness is a clinical evaluation using the Coma Recovery Scale – Revised (CRS-R) (Giacino et al., 2004). The CRS-R scale consists of six domains (auditory perception, visual perception, motor function, verbal abilities, communication, and arousal) and assesses 23 different items. A clinician administers the CRS-R to evaluate a wide range of behaviors, from reflexes (such as withdrawal motor response to pain) to following commands and object use. A patient is diagnosed with MCS if their CRS-R score exceeds 10. If functional object use or communication is observed, the patient is considered to be in EMCS.

Although the CRS-R is the primary diagnostic tool for DoC, distinguishing between UWS and MCS based on behavior remains challenging, with misdiagnosis rates of up to 43% (Schnakers et al., 2009). To improve diagnostic accuracy, new clinically feasible evaluations have recently been proposed as complementary to the CRS-R. For instance, Hermann et al. (2019) asked multiple nursing staff members to provide their subjective assessments of patients (referred to as DoC-feeling scores) over a week and demonstrated that these scores may enhance diagnostic and prognostic accuracy. The same authors also showed that assessing the auditory startle reflex in DoC patients could differentiate between VS and MCS patients (Hermann et al., 2020). The startle reflex is an automatic reaction (such as eye blinks) to sudden or intense stimuli. If the stimulus is repeated and predictable, this reflex response diminishes, a phenomenon known as habituation. In their study, Hermann and colleagues examined the habituation of the auditory startle reflex in DoC patients and found that while most MCS patients displayed startle reflex habituation when repeatedly stimulated, most VS patients did not.

It is important to note that behavioral evaluations of patients can sometimes be misleading, as patients may have sensory deficits such as blindness, deafness, or sensorimotor impairments that prevent them from responding to stimuli. For instance, locked-in patients with cognitive-motor dissociation cannot respond to stimulation due to impaired motor function, even though they are fully conscious and possess nearly normal cognitive abilities (Schnakers, Majerus, et

al., 2008). Other innovative protocols utilizing neuroimaging tools have also been proposed to supplement CRS-R scoring in detecting preserved consciousness in locked-in patients. This will be further discussed in the following section.

1.2.1.1. Assessing residual capacity in DoC patients using neuroimaging

Recently, several neuroimaging approaches have been developed either to aid in the diagnostic process of MCS/VS patients or to identify locked-in patients who can consciously perceive external information but are unresponsive in their behavior.

One such approach, known as the Local-Global Paradigm (Bekinschtein et al., 2009), relies on the evaluation of Event-Related Potentials (ERPs) triggered by auditory irregularities. In this paradigm, the stimuli consist of repeated auditory notes that exhibit two levels of hierarchical regularities (Figure 1.4). The first level, called local regularity, becomes apparent within a few hundred milliseconds when the same note is repeated multiple times. Occasionally, a note is altered, resulting in a local irregularity. These local irregularities elicit early brain responses such as mismatch negativity (MMN), which is considered an automatic response associated with unconscious processing. Previous studies have demonstrated the persistence of MMN in unconscious states like anesthesia (Heinke et al., 2004) and coma (Fischer et al., 1999). On the other hand, the second level of regularity, known as global regularity, operates on many sequences of five tones. Detecting violations of the global regularity requires the maintenance of information in working memory and thus implies conscious processing. Global irregularities evoke a late brain response called P3b, which is considered a potential marker of conscious processing.

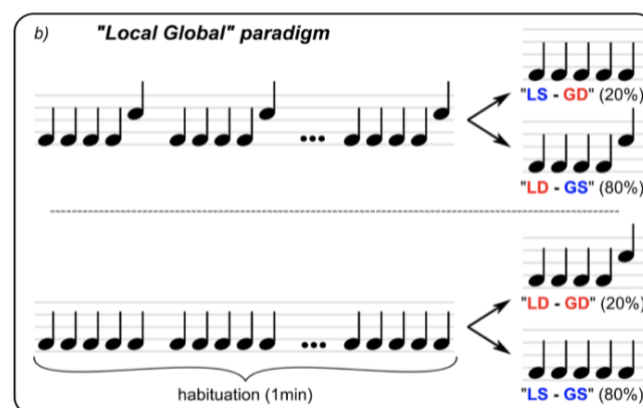


Figure 1.4. Local Global Paradigm. In each trial, four identical sounds are followed by either the same (Local Standard - LS) or a different sound (Local Deviant - LD). The global regularity is determined by the repetition of five sounds, which can either be identical to the previous series (Global Standard - GS) or different (Global Deviant - GD) (Taken from Rohaut & Naccache, 2017).

In each trial of the experiment, a sequence of five short sounds is presented. The first four sounds are identical, while the fifth sound can either be identical (locally standard trials) or different (locally deviant trials) from the preceding sounds. The global regularity, on the other hand, is determined by the relative frequency of these two types of sequences. Global standard trials make up 80% of the trials, while global deviant trials occur only in 20% of the trials. Using this passive auditory paradigm in DoC patients, Bekinschtein and colleagues showed that while brain responses to local irregularities could be observed in both VS (3 out of 4), MCS and EMCS patients, the P3b response to global irregularities was only present in EMCS and MCS patients. Additionally, a subsequent study reported the occurrence of the P3b effect for global irregularities in two VS patients who later regained consciousness (Faugeras et al., 2011). These findings indicate that when combined with the Coma Recovery Scale-Revised, the Local-Global Paradigm can offer supplementary information about a patient's remaining cognitive abilities and potential prognosis.

An alternative approach for assessing covert cognition in patients with DoC involves command following protocols. These paradigms are primarily used to detect *locked-in* patients who can consciously carry out cognitive tasks following instructions, without displaying any observable behavioral signs. In a groundbreaking study, Owen et al. (2006) discovered that a patient diagnosed as being in a vegetative state (based on their CRS-R score) was able to perform mental imagery and spatial navigation tasks. The participant was instructed to either imagine playing tennis or walking in their house while their brain activity was monitored using fMRI. The brain activations observed during these tasks were indistinguishable from the ones of healthy individuals who performed the same tasks. These findings demonstrated that despite the patient's diagnosis, they were capable of comprehending spoken language, willingly following commands, and exhibiting brain activity similar to that of a healthy individual, indicating awareness.

A subsequent study replicated these results by demonstrating that out of 54 patients diagnosed with DoC, five exhibited modulation of brain activity during the tasks (4 out of 23 VS). This study also highlighted the potential for communicating with these responsive patients by decoding their responses to yes/no questions through brain activations during mental imagery (Monti et al., 2010). Building upon these groundbreaking findings, several other experimental command following procedures have been developed, including motor commands (Bekinschtein et al., 2011), word counting/working memory tasks (Monti et al., 2009) and

attention switching tasks (Monti et al., 2013). For a comprehensive review of different protocols, refer to Fernández-Espejo & Owen (2013). Furthermore, a study utilizing naturalistic stimuli compared the brain activity evoked by movie watching in healthy individuals and two DoC patients (Naci et al., 2014). Participants were instructed to watch the movie without any additional tasks. The study revealed that movie watching synchronized brain activity across visual, auditory, and fronto-parietal networks in healthy participants. More significantly, one of the DoC patients, who was later identified as having locked-in syndrome (unknown during the experiment), also exhibited synchronized brain activity with the healthy controls. Taken together, these findings indicate that fMRI activity in clinically diagnosed DoC patients can provide reliable information about their remaining cognitive abilities, including language, sustained attention, working memory, and integrating information.

While the results demonstrate the effectiveness of fMRI in detecting task-induced brain activity changes in DoC patients, conducting fMRI scans in a clinical setting remains challenging due to limited availability of scanners, high costs, and susceptibility to movement artifacts. Therefore, it is crucial to develop similar command following protocols using EEG to make this tool accessible for assessing remaining cognitive abilities at the bedside. Several studies have demonstrated the feasibility of such protocols in EEG. For instance, one study found that patients in a MCS exhibited larger P3 ERP components when they heard their own names compared to other names (Schnakers, Perrin, et al., 2008). Similar to control participants, they also displayed larger P3 responses when asked to count the number of times they heard their names, as opposed to a passive listening condition. In contrast, patients in a vegetative state (VS) did not show any differences in the P3 response. Similar to local global paradigm, such late response could be used to distinguish VS and MCS patients. Other studies employed motor commands to assess covert awareness in VS (Cruse et al., 2011; Cruse, Chennu, Fernández-Espejo, et al., 2012) and MCS (Cruse, Chennu, Chatelle, et al., 2012) patients who were instructed to imagine moving their hands. 19% of the VS patients and 23% of the MCS patients exhibited consistent EEG responses to the motor commands. Although the results from VS patients could not be replicated in a subsequent study that re-analyzed the same data using alternative statistical models (Goldfine et al., 2013), a later study using similar motor commands confirmed covert responses in 15% of a large cohort of 104 unresponsive patients (Claassen et al., 2019).

The aforementioned studies employing neuroimaging techniques have consistently demonstrated task-induced brain activity changes in patients diagnosed with DoC, providing valuable insights into their language comprehension, command following abilities, and the presence of healthy-like brain activity indicative of awareness. The incorporation of neuroimaging techniques into the traditional clinical assessments, provides a more accurate diagnosis and prognosis. Such an enhanced diagnostic approach holds great importance in guiding appropriate treatment decisions, optimizing patient care, and ensuring the best possible outcomes for individuals with DoC.

1.2.1.2. Neural correlates of (un)conscious states

In addition to the cognitive task-based and command following studies discussed earlier, researchers have also explored structural and resting-state recordings to identify neural markers that vary with states of consciousness. These investigations have provided insights into the potential use of structural brain differences in accurately diagnosing patients with DoC. Diffusion Tensor Imaging (DTI), which maps the diffusion process of molecules to visualize white matter tracts, has shown promising results in differentiating MCS and VS patients by accurately classifying them into their respective clinical categories based on the CRS-R score, achieving a 95% accuracy (Fernández-Espejo et al., 2011). Furthermore, the severity of the diagnosis has been found to correlate with the impairment of structural connections in the Default Mode Network (DMN), where more intact pathways are associated with more complex behavioral signs of awareness in these patients (Fernández-Espejo et al., 2012).

Electrophysiology recordings have also revealed distinct characteristics in the EEG signals among these patient populations. Specifically, higher delta and theta power have been observed (Lechinger et al., 2013), along with reduced complexity particularly pronounced in patients with VS compared to those with MCS, when compared to healthy individuals (for comprehensive reviews, see Bai et al., 2017 and Duszyk-Bogorodzka et al., 2022). Moreover, long-range connectivity within different brain networks has been proposed as a prerequisite for conscious processing (Dehaene & Naccache, 2001; Baars, 2005; Dehaene & Changeux, 2011a; Mashour et al., 2020). Quantifying the extent of inter-areal communication can therefore provide information about an individual's ability to process information and, consequently, their state of consciousness. Building upon this idea, King et al. (2013) introduced a functional connectivity measure called weighted Symbolic Mutual Information (wSMI). This measure captures both linear and non-linear coupling between sensors and relies on a symbolic

transformation of the EEG signal. The authors demonstrated that wSMI was capable of distinguishing between different states of consciousness, particularly when calculated in the theta-alpha (4-10 Hz) frequency range.

While these individual EEG markers correlate with consciousness levels at a group level, they lack the robustness required for diagnosing individual patients. However, combining multiple spectral, complexity, and connectivity markers can offer a more comprehensive understanding of a patient's current condition. Using machine learning classification algorithms, Sitt et al. (2014) aimed at predicting clinical diagnosis of 113 DoC patients based on several EEG markers extracted from resting-state recordings. This procedure accurately classified the patients' consciousness states (based on their CRS-R scores), achieving an AUC of 78%. Furthermore, VS patients who exhibited richer brain activity (higher complexity and connectivity) were more likely to regain consciousness in the subsequent weeks. These findings were later replicated in a separate study using data from different sites and protocols, demonstrating the robustness of EEG-based classifications of consciousness states (Engemann et al., 2018).

EEG has also been combined with TMS to evaluate the effective connectivity of residual cortical networks in patients with DoC. This approach involves stimulating a specific cortical region using repeated TMS pulses and observing the spread of electrophysiological activity triggered by the stimulation via EEG. In the initial study employing this method, Massimini et al. (2005) targeted the rostral right premotor cortex. They demonstrated that while TMS induced sustained brain responses with recurrent TMS-locked activity during wakefulness, TMS-evoked responses in non-REM sleep (N2 and N3) only showed an initial large response without subsequent activity. Similar results were observed in other states of unconsciousness, such as anesthesia (Ferrarelli et al., 2010). TMS-induced brain activity has also been found to differentiate patients with DoC, with localized and brief responses in VS and more widespread and sustained responses in MCS (Rosanova et al., 2012; Ragazzoni et al., 2013). In the same year, Casali et al. (2013) developed a measure called the perturbational computational index (PCI) to estimate the activity induced by TMS at the individual level. PCI quantifies the degree of signal segregation and integration in TMS-evoked responses. This measure is based on the Integrated Information Theory, which posits that information integration is a prerequisite for consciousness and that the level of consciousness depends on the system's ability to integrate information beyond what its constituent parts can integrate alone (Oizumi et al., 2014; Tononi

et al., 2016). Importantly, PCI has demonstrated a sensitivity of 94.7% in detecting patients in MCS (Casarotto et al., 2016), highlighting the strong relationship between the level of consciousness and the brain's capacity for efficient functional connectivity. These findings align with the notion that long-range connectivity plays a crucial role in consciousness and are consistent with previous empirical findings indicating higher wSMI in conscious states.

Long-range resting-state functional connectivity profiles have also been investigated in non-human primates (Barttfeld et al., 2015; Uhrig et al., 2018), as well as conscious and unconscious humans (Demertzi et al., 2019) using fMRI. By employing unsupervised learning clustering methods, these studies revealed distinct recurring functional connectivity patterns that are correlated with different states of consciousness. Specifically, they observed that conscious individuals exhibit brain connectivity patterns that deviate from anatomical connectivity and display both positive and negative correlations among distant brain regions (high coordination patterns). Conversely, these high coordination patterns were reduced in states of unconsciousness (Figure 1.5). On the other hand, less diverse connectivity patterns lacking negative inter-areal correlations (low coordination patterns) were more frequently observed in patients with DoC, with more prevalence in VS than MC.

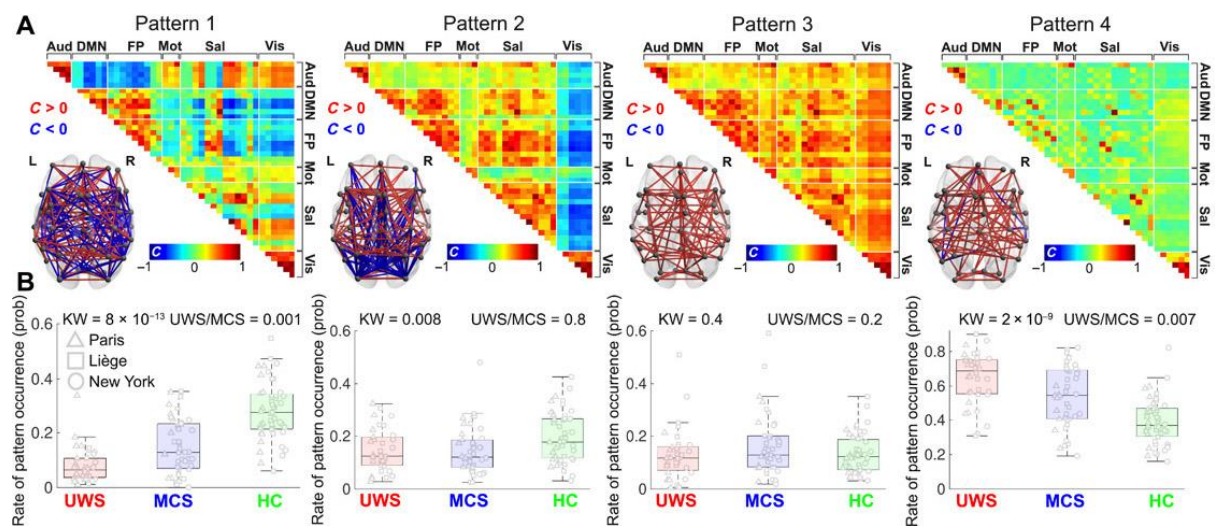


Figure 1.5. The prevalence of functional connectivity patterns depends on the states of consciousness. (A) Four recurrent functional connectivity patterns found in Demertzi et al. (2019). Pattern 1 (high coordination pattern) shows both positive and negative correlations between brain regions whereas Pattern 4 (low coordination pattern) mirrors anatomical connectivity and lacks negative correlations. (B) Occurrence rate of patterns in unresponsive wakefulness syndrome (UWS/VS), minimally conscious state (MCS) and healthy controls (HC). Note that Pattern 1 and 4 show differences in their occurrence rate depending on the level of consciousness (taken from Demertzi et al., 2019).

Significantly, patients diagnosed with VS but who showed signs of covert cognition (*locked-in* patients) were less likely to exhibit the low coordination pattern. Moreover, when all patients, including those emerging from MCS (EMCS), were anesthetized, the frequencies of the connectivity patterns became similar, with the low coordination pattern being the most prevalent regardless of clinical diagnosis. In a subsequent study, deep brain stimulation targeting the thalamus with the aim of restoring consciousness in anesthetized non-human primates has also been found to restore the high coordination patterns (Tasserie et al., 2022). Collectively, these findings demonstrate that conscious states are associated with intricate, long-range functional connectivity profiles that diminish in unconscious states.

1.2.2. Sleep

Another state of consciousness we experience on a daily basis is sleep. Sleep can be defined as a reversible condition where arousal is suppressed, resulting in reduced interaction with the environment, decreased information processing capacity, and limited behavioral reactions. Sleep plays a crucial role in maintaining healthy cognitive functioning, as its deprivation can negatively impact memory (Rasch & Born, 2013), attention (Lim & Dinges, 2008), cognitive control (Gevers et al., 2015), and, in extreme cases, even lead to death (Everson et al., 1989). Sleep exhibits a high degree of heterogeneity in terms of neural activity and subjective experiences associated with it, comprising various sub-states known as sleep stages. These stages, N1, N2, N3, and REM sleep, are defined by established guidelines from the American Academy of Sleep Medicine (AASM) (Berry et al., 2017) based on polysomnography (PSG), which includes recordings of EEG, electromyography (EMG), and electrooculography (EOG).

1.2.2.1. Sleep stages and sleep architecture

Wakefulness. When the eyes are open, the PSG shows rapid-frequency EEG activity (15-60Hz beta and gamma activity), frequent eye movements (saccades or pursuit), and high muscle tone. When the eyes are closed and the individual is relaxed but still awake, alpha band activity (8-12Hz) becomes dominant in the EEG.

N1 Sleep. N1 sleep serves as a transitional state between wakefulness and sleep. It is characterized by a gradual decrease in alpha power and an increase in theta band activity (4-7 Hz). Eye movements can be observed in the EOG recordings. N1 sleep reoccurs briefly during the night between awakenings and sleep and represents the smallest portion of overnight sleep. It is associated with dream-like visual and auditory experiences known as hypnagogic

(“*leading into sleep*” in Greek) hallucinations (Rowley et al., 1998) and has been shown to promote creativity (Lacaux et al., 2021).

N2 Sleep. N2 sleep is characterized by two grapho-elements, namely spindles and K-complexes, occurring alongside baseline theta band activity. Spindles are bursts of sigma band (11-16 Hz) activity that last between 0.5 to 2 seconds and are primarily observed in the central EEG electrodes. K-complexes consist of a sharp negative wave followed by a slower positive component lasting at least half a second. They are predominantly recorded on the frontal electrode and are a response to sensory stimuli, although they can also occur spontaneously. They are believed to protect sleep from the arousing effects of sensory stimuli (Halász, 2005). N2 sleep is also characterized by decreased muscle tone, absence of eye movements, and represents the largest portion of the night's sleep (~55%).

N3 Sleep. Also referred to as slow-wave or deep sleep, N3 sleep accounts for 20% of the sleep period. It is characterized by high-amplitude ($> 75 \mu\text{V}$) delta waves (0.5 - 4 Hz), increased muscle atonia, and reduced eye movements compared to N2 sleep. N3 sleep is associated with decreased heart rate, body temperature, and physical restoration. It has also been shown to play a role in the consolidation of declarative memory (Rasch et al., 2007; Born & Wilhelm, 2012).

REM Sleep. Rapid Eye Movement Sleep, also known as Paradoxical Sleep, derives its name from the rapid, conjugate, and distinct eye movements that occur alongside muscle atonia (with less pronounced effects on facial muscles, Rivera-García et al., 2011) and occasional muscle twitches. EEG activity during REM sleep resembles wakefulness to some extent, displaying a mixture of alpha and theta activity and an absence of delta activity. REM sleep can also be accompanied by penile erections (Fisher et al., 1965) and clitoral engorgement (Abel et al., 1979). It constitutes 20% of the entire sleep period and has been associated with high dream recall frequency (Siclari et al., 2013) and emotional regulation (Gujar et al., 2011).

A typical night of sleep consists of multiple sleep cycles lasting between 90 to 110 minutes each (Hirshkowitz, 2004). Each sleep cycle encompasses all sleep stages, which occur in a specific sequence. The cycle begins with N1 sleep, with the transition from wakefulness to sleep. As time progresses, the individual moves through N2, N3, and REM sleep. The cycle concludes with a period of arousal before the next cycle begins. During the initial portion of the night, N3 sleep predominates, while the later part of the night is primarily comprised of REM sleep. Polysomnographic recordings are used to identify sleep stages, and they are scored

in 30-second epochs. Each epoch is assigned the sleep stage that dominates for more than half of the epoch. Consequently, this scoring method does not account for transient changes that may occur within an epoch.

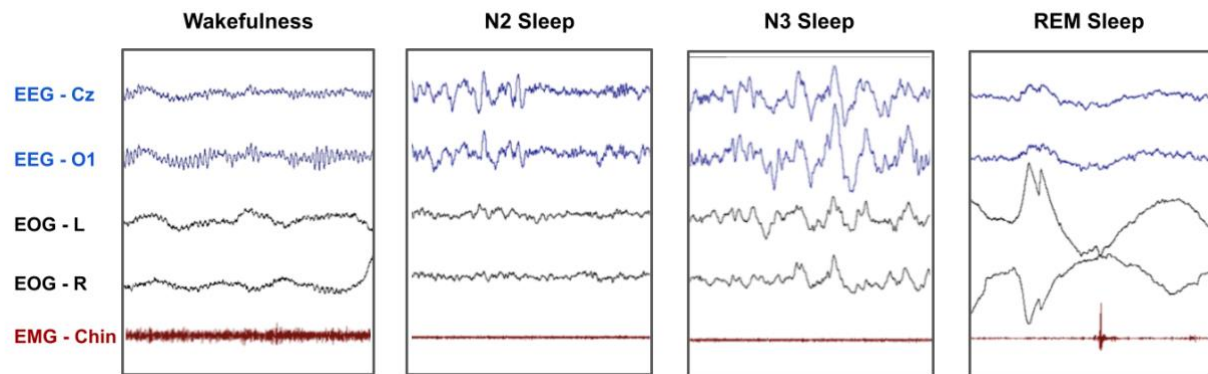


Figure 1.6. Polysomnographic recordings illustrating various sleep stages. The recordings include EEG (blue), EOG (black), and EMG (brown) activity during wakefulness, N2, N3, and REM sleep. In wakefulness, with closed eyes, alpha band activity and high muscle tone are prominent. As we transition into N2 and N3 sleep, brain activity progressively slows down. N2 sleep is characterized by the presence of K-complexes and spindles, which can be observed in the figure. REM sleep is distinguished by rapid eye movements, muscle atonia, and twitches, all of which are visible in the figure.

Although this classification is important for research purposes and clinical practice to categorize sleep's global aspects, it does not fully capture the diversity and fluctuations within each sleep stage. As we will discuss in more detail in Chapter IV, sleep stages are not stable and homogeneous but exhibit variations in terms of brain activity, cognition, and subjective experiences. One phenomenon that exemplifies this point is Sleep State Misperception (SSM), which occurs when individuals report not having slept despite polysomnographic evidence indicating sleep. SSM is referred to as a misperception because subjective reports do not align with the "objective" polysomnographic assessment of sleep. However, a recent study demonstrated that although polysomnography could not differentiate between "normal" sleep and SSM, a more detailed evaluation of EEG revealed sleep deterioration in patients with SSM, characterized by reduced slow wave activity and increased rapid frequencies (Andrillon et al., 2020). Sleep microstructure exhibited clear differences between normal sleep and SSM, while meso- and macro-sleep structures assessed through polysomnography did not provide informative distinctions between the two conditions. This study underscored that polysomnographic evaluation based on AASM criteria alone is insufficient to capture subtle changes within a sleep stage, which can affect both sleep quality and subjective experience.

1.2.2.2. Abnormal sleep

Abnormal sleep refers to deviations from the typical patterns and characteristics of healthy sleep. It encompasses various sleep disturbances, disorders, and conditions, including insufficient or excessive sleep, abnormal sleep structure, and atypical sleep behaviors. For instance, hypersomnia is a sleep disorder characterized by excessive daytime sleepiness, prolonged sleep duration, and difficulty awakening from sleep. Individuals with hypersomnia may struggle to stay awake and alert, even after getting a full night's sleep. Another group of disorders associated with abnormal sleep behaviors are parasomnias. Parasomnias involve unusual or abnormal behaviors, movements, or experiences during sleep. Examples include sleepwalking, sleep talking, night terrors, and REM sleep behavior disorder (RBD), where individuals act out their dreams.

A wide range of sleep pathologies encompasses diverse sleep disorders and conditions that can significantly impact an individual's sleep patterns and overall well-being. Diagnosis and classification of abnormal sleep rely on clinical evaluation, sleep assessments, and polysomnography conducted by healthcare professionals specializing in sleep medicine. In this section, our primary focus will be on narcolepsy, a neurological disorder that disrupts the brain's regulation of sleep-wake cycles, as we will use it as an experimental model in Chapter IV.

Narcolepsy is primarily characterized by excessive daytime sleepiness and cataplexy, which is the sudden and temporary loss of muscle tone. It frequently includes hypnagogic hallucinations, sleep paralysis, and lucid dreams. Narcolepsy results from a deficiency of orexin, a hormone that regulates arousal, caused by an autoimmune process that destroys orexin-producing neurons in the hypothalamus.

International criteria for diagnosing narcolepsy include:

- (1) **Experiencing excessive daytime sleepiness daily for at least 3 months.** Sleepiness occurs intermittently throughout the day, with sleep attacks commonly happening during non-stimulating situations such as immobility, waiting, reading, or driving.
- (2) **Having an average sleep latency of less than or equal to 8 minutes and exhibiting two or more sleep onset REM sleep periods during the multiple sleep latency test.** Patients with narcolepsy can fall asleep in less than 8 minutes (in some cases, as quickly

as 1 to 2 minutes). Furthermore, unlike healthy individuals, they rapidly enter REM sleep (typically within less than 15 minutes) during naps.

(3) Cataplexy is a specific symptom of type 1 narcolepsy. The duration of cataplexy episodes is usually brief, ranging from a fraction of a second to 2-3 minutes. The frequency of cataplexy episodes can vary widely, from several per day to only a few throughout a patient's lifetime.

(4) No other evident cause that can better explain these findings, including sleep apnea syndrome, insufficient sleep, delayed sleep phase disorder, depression, the influence of medication or substances, or their withdrawal.

In addition to these symptoms, individuals with narcolepsy commonly experience a heightened frequency of lucid dreams (Dodet et al., 2015). Their propensity and ability to fall asleep multiple times throughout the day make them an ideal population for gathering multiple instances of lucid dreams in a laboratory setting (Oudiette et al., 2018). This point will be further discussed in the upcoming section.

1.2.2.3. Dreams

Dreams are the experiences that occur while we sleep, involving sensory elements, thoughts, emotions, and concepts. Currently, the only way to access these experiences is through subjective reports. Essentially, a dream must first be experienced, encoded in memory, and then expressed using words, gestures, drawings, or any other form of communication in order to be shared. This makes dreams a particularly challenging subject to study scientifically. Firstly, dreams can be distorted or forgotten during the process between experiencing them and reporting them. A dream that is not encoded in memory cannot be recalled, making it inaccessible. Moreover, dreams can be altered during the encoding phase or censored and adapted during the reporting process (Schwartz et al., 2005). Therefore, the evaluation of dream content heavily relies on subjective reports, which can be influenced by biases.

The second major challenge in the field of dream research is determining when exactly dreams occur. Initially, it was believed that dreams only took place during REM sleep (Aserinsky & Kleitman, 1953), but this idea is now widely rejected (Siclari et al., 2013). Indeed, serial awakening paradigms that involve repeatedly waking individuals from different stages of sleep and probing their mental content, have revealed that dreams can occur in all sleep stages, with a higher frequency in REM sleep compared to N1, N2, and N3 sleep. However, the precise timing of dreams within sleep is still unknown. While we have reliable physiological markers

to detect sleep and its different stages (as defined by international guidelines), there are no easily observable and universally agreed-upon markers for dreams (Ruby, 2020).

A recent study investigated the EEG correlates of dream reports using a serial awakening paradigm (Siclari et al., 2017). In this study, participants indicated upon awakening whether they had a dream experience with recalled content, an experience without recalled content, or no experience at all. By comparing EEG activity prior to awakening, the authors found that dream recalls were associated with a decrease in low-frequency activity in the occipital-parietal cortex during both REM and NREM sleep, as well as an increase in gamma activity in the frontal regions during REM sleep. The results also suggested that similar brain regions might be involved in experiences (such as seeing a face) during wakefulness and dreams. It is important to note that these findings could not be replicated in a blinded study conducted by another research team (Wong et al., 2020).

Although the combination of the serial awakening paradigm with neuroimaging provides valuable insights into the brain state preceding a dream report, it does not directly differentiate between dream and non-dream experiences. At this stage, it is difficult to determine whether the observed effects solely reflect dream activity or if they also involve processes related to encoding or reporting, as the exact timing of the dream (whether it occurred just before awakening or several minutes prior, for example) cannot be known. To overcome this challenge, researchers have developed creative methods that allow for the identification of dreaming periods, such as the study of lucid dreaming. In the next section, we will explore the current state of research on lucid dreaming and how it can aid in identifying periods of dreaming.

1.2.2.3.1. Lucid dreams

Lucid dreaming refers to the ability to become aware that one is in a dream and, in some cases, to have control over the dream's events. Experienced lucid dreamers can alter the dream environment, such as changing the color of walls or making it snow, perform actions that are impossible in real life, like flying, or manipulate the dream characters, such as making the king of England appear or disappear. The first detailed descriptions of lucid dreaming emerged in the 19th century through the work of Hervey de Saint Denys, a French oneirologist who documented his own lucid dreaming experiences in a book titled "*Dreams and the Ways to Direct Them: Practical Observations*". However, the scientific confirmation of lucid dreaming became possible only after the invention of polysomnography.

Significant progress in the field occurred with the development of a communication code between the lucid dreamer and the experimenter, which relied on eye movements (Hearne, 1978; LaBerge et al., 1981). Researchers instructed lucid dreamers to produce specific eye movements, such as moving their eyes from left to right three times, once they realized they were in a dream. By using EOG recordings, they were able to detect these eye movements during polysomnographically-verified sleep, providing an objective measure of lucid dreaming for the first time. Since then, numerous studies have explored various aspects of lucid dreaming. For instance, lucid dreamers have demonstrated the ability to consciously control their breathing in dreams, matching their reports upon awakening (Oudiette et al., 2018). The execution of motor sequences in lucid dreams appears to take a similar amount of time as in wakefulness (Erlacher & Schredl, 2004, 2008), and the ability to visually track movements, which is only possible when a target is present, persists during lucid dreaming but not during wakeful imagining (LaBerge et al., 2018). These findings suggest that, in addition to the phenomenological similarities to wakefulness, lucid dreaming also involves wake-like cognitive processes.

While approximately 55% of the population experiences at least one lucid dream in their lifetime, frequent lucid dreamers, who have at least one lucid dream per month, account for only 23% of the general population (Saunders et al., 2016). Moreover, scientific studies on lucid dreaming require participants who can reliably and frequently experience lucid dreams or can induce them on command, making it feasible to conduct research in laboratory settings. Individuals with narcolepsy, characterized by early REM sleep onset and increased frequency of lucid dreams, present an ideal population for capturing this rare phenomenon in a research environment (Dodet et al., 2015). Due to the scarcity of expert lucid dreamers in the general population, only a limited number of studies have been able to investigate the neural correlates of lucid dreaming (for a review, see Baird et al., 2019).

By combining lucidity signals and fMRI scans, Dresler et al., (2012) recorded brain activity during a lucid dream episode and observed increased activity in the bilateral precuneus, parietal lobules, and prefrontal cortex. These brain regions are involved in self-awareness and executive functions, which are typically deactivated during regular REM sleep. However, it is possible that the increased frontal activity reflects cognitive processes related to maintaining lucidity rather than lucidity itself. In other studies using EEG recordings, lucid dream episodes were associated with elevated gamma band activity in frontal regions among healthy participants

(Voss et al., 2009), but this effect was not observed in a larger cohort of patients with narcolepsy (Dodet et al., 2015). A subsequent study that induced 40 Hz gamma activity in frontal regions using tACS suggested an increase in lucid dreaming during stimulation (Voss et al., 2014). However, it's important to note that this study did not employ the gold standard eye movement signals to indicate lucidity but relied on a questionnaire filled out upon awakening to assess lucidity. A recent study utilizing objective eye movement signaling failed to replicate these findings (Blanchette-Carrière et al., 2020) and a tDCS study that stimulated the dorsolateral prefrontal cortex only found a weak effect in experienced lucid dreamers (Stumbrys et al., 2013). The observed gamma band effects in the initial studies might be attributed to other factors, such as artifacts resulting from increased eye movements during lucid REM sleep compared to regular REM sleep (LaBerge et al., 1986). Overall, the findings in this field are still limited, and further research is needed to uncover the neural correlates of lucid dreaming.

In addition to investigating the characteristics of lucid dreaming, the lucidity signaling procedure also enables researchers to determine the timing of dream occurrences, which is currently not possible in regular sleep. However, when comparing lucid (with signals) and non-lucid (without signals) REM episodes, one must consider that different scenarios could be involved: (i) lucid dreams versus non-lucid dreams, (ii) lucid dreams versus no dreams, (iii) lucid dreams with and without signals. New protocols are required to differentiate these possibilities and identify the neural correlates of dreaming.

1.2.2.4. Information processing in sleep

Until recently, sleep was commonly believed to be a state of complete disconnection from the outside world, as sleeping individuals do not respond to stimuli or recall them upon awakening. However, studies using intracranial recordings in rats during auditory stimulation have shown that responses to stimuli in the primary auditory cortex are maintained throughout all sleep stages, suggesting that sensory disconnection occurs in later stages of information processing (Nir et al., 2015). In humans, neuroimaging studies have also demonstrated that low-level stimulus processing remains intact during different sleep stages. ERP studies have shown that the brain of sleepers responds preferentially to their own name compared to others' (Perrin et al., 1999), detects unexpected deviant stimuli in oddball (Bastuji et al., 1995; Ruby et al., 2008) and local-global paradigms (Strauss et al., 2015), recognizes the cry of their own baby (Formby, 1967), and distinguishes the semantic congruency of word pairs (Perrin et al., 2002;

Ibáñez et al., 2006). Recent studies have even demonstrated that in a cocktail party paradigm, where participants hear intelligible speech in one ear and nonsensical speech in the other, the brain prioritizes processing of the intelligible speech, which can be decoded from neural activity during both N2 (Legendre et al., 2019) and REM (Koroma et al., 2020) sleep.

Moreover, the presentation of sensory cues associated with previously learned information during sleep has been shown to enhance the recall of that information upon awakening (Rudoy et al., 2009; for an exhaustive review, see Oudiette & Paller, 2013). For example, re-exposure to the same odor presented during the learning of object locations in a visuospatial task improves performance upon awakening, specifically if the re-exposure occurs during N3 sleep (Rasch et al., 2007). The sleeping brain also has the ability to form new associations within (Züst et al., 2019; Ruch et al., 2022) and across different sensory modalities (Arzi et al., 2012). Interestingly, these learned associations can influence subsequent behavior upon awakening (Arzi et al., 2014; Ruch et al., 2022). For example, Arzi and colleagues showed that exposing individuals to unpleasant odors immediately after presenting cigarette odors during N2 and REM sleep resulted in aversive conditioning, leading to a reduction in smoking behavior among participants in the subsequent week.

Furthermore, processed stimuli can be integrated into dream scenarios (see Solomonova & Carr (2019) for a comprehensive review). Although the extent of incorporation varies drastically across studies and sleep stages, the incorporation has been shown for auditory (Rahimi et al., 2015), visual (Paul et al., 2014), olfactory (Trotter et al., 1988) and tactile (Leslie & Ogilvie, 1996; Paul et al., 2014) stimuli to some degree. However, it is important to note that the amount of stimulus incorporation in dreams is hard to quantify. Determining the precise semantic boundary between a stimulus and its associated dream content can be challenging. For instance, when water is splashed on a sleeper's face, it may evoke dream elements such as rain or taking a shower, which are relatively straightforward associations. On the other hand, if the sleeper reports swimming, running (and potentially sweating), drinking water, or feeling thirsty, the association becomes less clear and more ambiguous. Therefore, although I am convinced that stimulus incorporation in dreams is possible (see my personal anecdote in page 95), I believe that it remains rare and difficult to quantify precisely.

Finally, studies have found that the sleeping brain can not only process verbal stimuli at a low level but also make semantic discriminations and prepare for motor responses (Kouider et al., 2014; Andrillon et al., 2016). In these studies, participants were instructed to categorize

auditory stimuli as either objects or animals and indicate their response via button-press. The results revealed that lateralized readiness potentials, an indicator of motor preparation, were present in light non-REM (NREM) sleep for all stimuli and in REM sleep for previously heard stimuli. These findings suggest that the sleeping brain is capable of generating appropriate responses to environmental stimuli, although this does not translate into observable behavior. One possible reason for the lack of behavioral response is the loss of muscle tone during sleep. In the following section, we will discuss the literature on behavioral responsiveness during sleep and demonstrate that in certain conditions, such as N1 sleep and lucid dreaming, behavioral responses can be observed.

1.2.2.5. Behavioral responsiveness in sleep

Given that behavioral responsiveness was believed to be linked to wakefulness and was not thought to occur during sleep, only a limited number of studies have attempted to assess responsiveness during sleep, particularly during the transitional state between wakefulness and sleep known as sleep onset. Cote et al. (2002) discovered that participants who were instructed to press a button upon hearing a rare and unusual auditory stimulus were able to detect and respond to 47% of the targets in polysomnography-scored N1 sleep. Another study, conducted by Strauss et al. (2015), also found behavioral responses to global deviant stimuli in the local-global paradigm during N1 sleep. In a subsequent study, the same research team observed behavioral responses in 14.3% of early N2 sleep trials, which were not present in consolidated N2 sleep (Strauss et al., 2022).

Another group investigated behavioral responses during drowsiness (Canales-Johnson et al., 2020). Instead of using polysomnographic assessment, which requires scoring the sleep stage in 30-second epochs, they employed an automated algorithm to distinguish between alertness (wakefulness), mild drowsiness (early N1 sleep), and severe drowsiness (late N1/early N2 sleep) (Jagannathan et al., 2018). Participants performed an auditory Stroop task, where they heard the words "left" or "right" in either the left or right ear and were asked to indicate the word through a button press. The congruency between the word and the ear could either be consistent or inconsistent. The authors discovered that behavioral responses persisted during drowsiness; however, participants made more errors and took longer to respond compared to when they were alert. Importantly, they also observed conflict adaptation (the moderating effect of previous conflict on the current one) in both alertness and drowsiness, suggesting that the drowsy brain responds to conflict similarly to the awake brain. Similar results were found

in a spatial attention task, where participants were instructed to locate auditory stimuli (coming from different angles) as either left or right (Jagannathan et al., 2022). Once again, behavioral responses were observed during drowsiness, with increased reaction times and error rates for left stimuli.

All the converging studies mentioned above indicate that sleepers can exhibit behavioral responses to external stimuli during sleep onset (N1 sleep, drowsiness). However, no behavioral responses have been observed during deeper sleep stages, with the exception of the study by Strauss et al. (2022), which found rare responses in early N2 sleep. Nevertheless, it is possible that behavioral responses are indeed possible during deeper sleep stages (N2, N3, and REM), but they are masked by increasing muscle atonia. In fact, all the aforementioned studies utilized limb movements (button presses) as the response modality. Other muscle groups, such as facial muscles which are less affected by muscle atonia (Rivera-García et al., 2011), could be better suited for observing behavioral responses during sleep.

In a recent collaborative study, we provided the first evidence of responsiveness to stimuli during lucid dreaming in polysomnography-verified REM sleep (Konkoly et al., 2021). In this study, four independent scientific teams from France, Germany, the Netherlands, and the USA demonstrated that lucid dreamers were capable of perceiving instructions from the experimenter and responding to them behaviorally, either through eye movements or contractions of facial muscles. For instance, a participant with narcolepsy who was highly experienced in lucid dreaming was able to respond to auditory and tactile stimuli. The participant was instructed to contract their corrugator muscles the same number of times they were tapped on the hand, with the number of taps ranging from 2 to 4 and being delivered randomly. Using EMG electrodes placed on the corrugator muscles, we were able to observe accurate responses to the stimulation (Figure 1.7). Importantly, the participant had indicated their lucidity prior to the stimulation through eye movements and remembered having performed the task upon awakening.

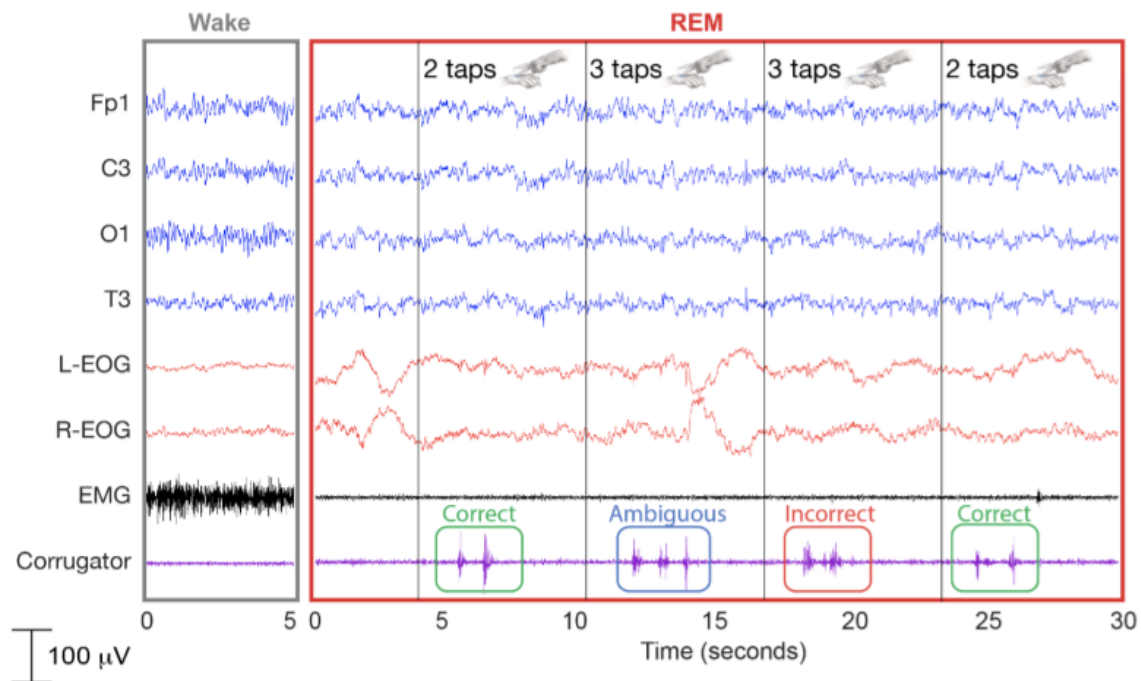


Figure 1.7. Behavioral responses to tactile stimuli observed during REM sleep. The participant was instructed to contract their corrugator muscles (shown in violet) the same number of times they were tapped on the hand. The EEG (theta-band activity), EOG (eye movements), and EMG (loss of muscle tone) indicate the presence of REM sleep (taken from Konkoly et al., 2021).

The participant was also able to answer verbally presented yes/no questions (such as "Do you like chocolate?" or "Do you watch football?") through contractions of the zygomatic (yes) and corrugator (no) muscles. Once again, they remembered the questions and the answers they provided upon awakening. Healthy participants from the other teams were also able to perform similar tasks during lucid REM sleep. They were able to solve simple mathematical equations presented verbally or visually (with LED flashes) and respond to them using eye movements. These findings demonstrate that sleepers can perceive instructions from different modalities, perform complex tasks, and respond behaviorally, at least during lucid REM sleep. In Chapter IV, we will present evidence that behavioral responsiveness can extend to all other sleep stages and can also be observed in non-lucid healthy participants during sleep. We will also discuss the brain dynamics that allow for such responsiveness.

1.3. Present work: hypotheses and objectives

In this chapter, we have introduced various aspects of consciousness, including conscious perception and states of consciousness. We have delved into the methods used to investigate these aspects and provided an overview of the current understanding of their neural correlates. Additionally, we have distinguished different states of consciousness such as wakefulness, disorders of consciousness, different sleep stages, and lucid dreaming. In the three upcoming chapters, our focus will be on experimental work that explores the intricate interplay between ongoing brain activity and conscious perception in different states of consciousness. The goals of this research are to assess several general hypotheses (Figure 1.8):

- (i) Conscious processing influences ongoing brain dynamics.
- (ii) Conscious processing of information is a fluctuating phenomenon that can vary even within traditionally defined states of consciousness.
- (iii) Ongoing brain dynamics impact the capacity for conscious perception, with some brain states facilitating such processing while others do not.
- (iv) Traditional definitions of states of consciousness do not fully capture the richness and variability within each state.

First, we will focus on hypothesis (i), aiming to examine the impact of conscious perception on ongoing brain dynamics. Cognitive neuroscience extensively investigates the impact of sensory stimulation on brain activity. While most studies have primarily rely on non-ecological stimuli and examine local brain activation in specific cortices, it is important to acknowledge that cognitive processes extend beyond localized regions. Instead, they emerge through the coordination and integration of various brain networks that process and exchange information. Moreover, in our daily lives, our conscious experience is shaped by complex stimuli from multiple sensory modalities, and it is the coherent integration of these elements that enables us to make sense of the world around us. Therefore, in Chapter II, we will adopt a more dynamic and ecological perspective and assess how global brain states, characterized by brain network interactions, track ongoing subjective experience. To achieve this, we will employ naturalistic movies as a model for real-world environments, allowing us to explore how the processing of complex and ecologically valid stimuli influences the dynamics of brain network interactions.

By investigating these dynamics, we hope to gain insights into how they support information processing and contribute to our overall perception and understanding of the world.

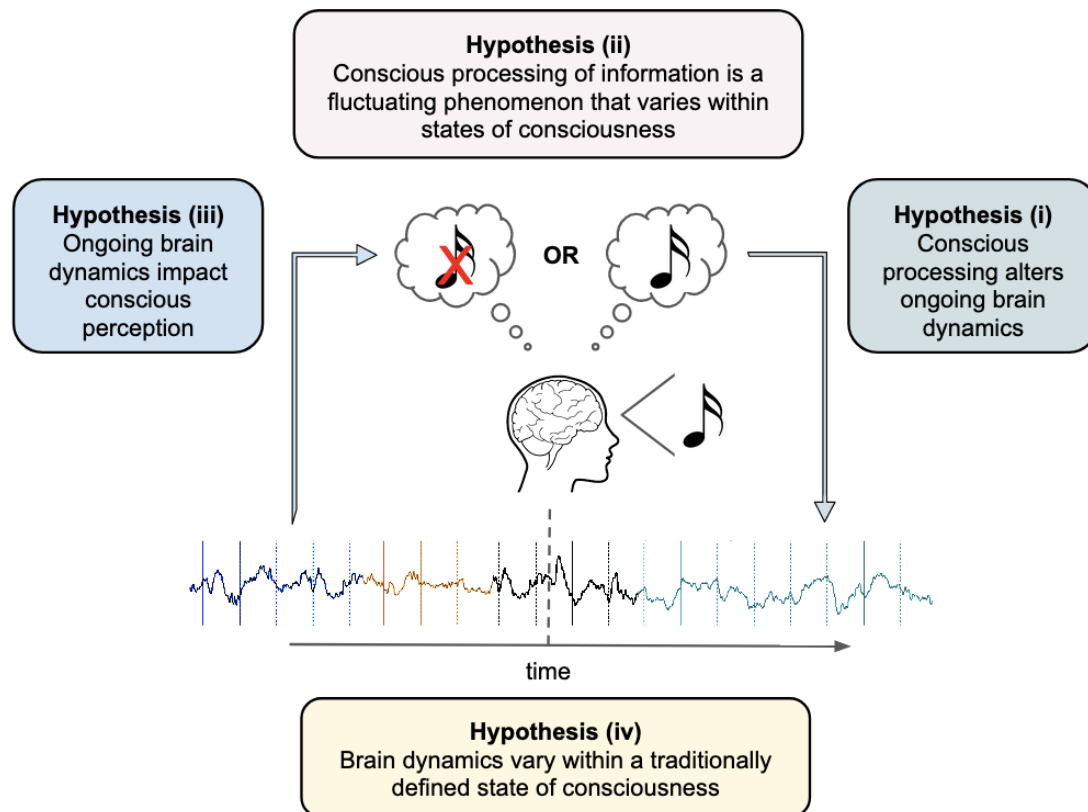


Figure 1.8. A visual representation of the hypotheses examined in this thesis. A stimulus (such as an auditory note) can be consciously perceived or not (hypothesis ii), depending on the ongoing brain dynamics before the stimulus is presented (hypothesis iii). These dynamics, which vary over time (hypothesis iv), play a role in determining whether the stimulus is consciously perceived or not. The conscious processing of the stimulus itself has an impact on the ongoing brain dynamics (hypothesis i), establishing an interactive loop of reciprocal influence.

In the following two chapters, we will delve into hypotheses (ii), (iii), and (iv), shifting our focus towards exploring the reciprocal relationship between ongoing brain activity and conscious perception. Even when resting, our brains are in a constant state of oscillation, transitioning between different brain states. In the field of consciousness research, we often prioritize examining the brain's response to external stimuli, overlooking the moments when no stimulus is present, such as prior to stimulus presentation. However, the processing of stimuli may vary depending on the specific brain state we are in. Here, we argue that our baseline brain states before stimulation significantly impact our capacity for conscious experiences. In Chapter III, we will examine the fluctuations in conscious experiences during

wakefulness. Although wakefulness is a state that typically enables conscious information processing and interaction with the environment, we will demonstrate that access to external information actually varies based on ongoing brain dynamics. Previous research has indicated that specific patterns of brain connectivity, characterized by long-range interactions and anticorrelations, are associated with conscious states and diminish when consciousness is lost (Demertzi et al., 2019). Using fMRI recordings during a threshold stimulus detection task, we will investigate the functional role of these brain patterns in shaping conscious experiences by altering participants' ability to process external information. Our findings will uncover that certain brain patterns correlating with conscious states also promote greater susceptibility to the external world.

In Chapter IV, we will expand our investigation to encompass other states of consciousness, particularly focusing on the capacity for information processing during sleep. Traditionally, sleep has been associated with a lack of awareness of the external world and reduced responsiveness. However, we will demonstrate that the sleeping brain is capable of performing complex tasks and generating appropriate behavioral responses not only during N1 sleep (as previously shown in the literature) but also during N2 sleep, as well as during lucid and non-lucid REM sleep. Additionally, we will reveal that these transient windows of reactivity to external stimuli can be predicted by utilizing pre-stimulus EEG markers that have been previously shown to be associated with conscious states. Based on our findings, we will argue that baseline brain states can lead to variations in the capacity to process information not only during wakefulness but also within other globally defined states of consciousness.

Finally, in the last chapter, we will discuss the overarching findings from the three studies and their implications for consciousness research.

CHAPTER II

COMMON SUBJECTIVE EXPERIENCES ELICIT COMMON BRAIN DYNAMICS

“It was the beginning of my PhD. I was telling Lao how I had ended up in this field by chance, and that it was not my original plan. I was telling him that I had studied cinema in Turkey and that I had come to France to study psychology, thinking that it would help me write screenplays. During my first year of undergraduate studies in Lyon, I was asked to choose a “minor” in addition to my psychology “major”. The options included sociology, anthropology, linguistics, education, and cognitive science. I chose cognitive science because I had no idea what it was and thought it would be fun. I liked it so much that I ended up doing a bachelor's, master's, and PhD in it, and I gave up cinema. Lao told me, “Maybe one day you will mix science and cinema”. We laughed. A couple of months later, the pandemic started. We had to come up with a new study that did not require data collection. Luckily, we had amazing collaborators who had some data on movie watching. Now, I feel grateful that my favorite movie director, Hitchcock, featured in my first PhD study. Lao was right after all.”

PROCESSING OF THE SAME NARRATIVE STIMULI ELICITS COMMON FUNCTIONAL CONNECTIVITY DYNAMICS BETWEEN INDIVIDUALS

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2.1. Abstract

It has been suggested that conscious experience is linked to the richness of brain state repertoires, which change in response to environmental and internal stimuli. High-level sensory stimulation has been shown to alter local brain activity and induce neural synchrony across participants. However, the dynamic interplay of cognitive processes involved in moment-to-moment information processing remains poorly understood. In this study, we utilized naturalistic movies as a realistic experimental model to explore how the perception of intricate real-world stimuli affects the dynamics of brain network interactions and facilitates information processing. Participants underwent fMRI scans while watching movies, watching scrambled versions of the movies, and resting. By measuring the phase synchrony between different brain networks, we analyzed whole-brain connectivity patterns. Our findings revealed distinct connectivity patterns associated with each experimental condition. During movie watching, there was a higher degree of synchronization in brain patterns among participants compared to rest and the scrambled movie conditions. Additionally, synchronization levels increased during the most captivating parts of the movies. The synchronization dynamics among participants were particularly related to suspense; scenes with higher levels of suspense induced greater synchronization. These results suggest that processing the same high-level information elicits shared neural dynamics across individuals, and that whole-brain functional connectivity tracks variations in processed information and subjective experience.

2.2. Introduction

The content of our conscious experience changes depending on the environment and ongoing task. Both external and internal information are processed and integrated to give rise to our conscious experiences. The dynamic interplay of cognitive processes that underlie our moment-to-moment experience of the world remains poorly understood. Using naturalistic movies as an ecological laboratory model of the real world, previous studies have shown that audio-visual clips have a similar impact on brain activity across individuals, reflecting their shared conscious experiences and holistic understanding. Movie watching can synchronize brain activity in the cortex (Hasson et al., 2004; Jääskeläinen et al., 2008; Kauppi et al., 2010; Nummenmaa et al., 2012; Naci et al., 2014; Lankinen et al., 2018), establish time-resolved correlations between pairs of regions (Di et al., 2022), and elicit consistent whole-brain activations across participants (Meer et al., 2020). Moreover, studies have shown that the quality of encoding of the movie's content is correlated with inter-subject synchronization during movie watching (Hasson et al., 2008; Simony et al., 2016). However, the descriptions of local activations offer only a limited summary of the dynamic processes that give rise to coherent understanding over time.

In recent years, dynamic descriptions of brain activity have gained prominence as they might better account for the participant's mental state. Focusing on how different brain networks interact over time, rather than the classic description of local activity, could provide a better understanding of conscious processing. The interaction between brain regions has been widely investigated using static functional connectivity (Fox et al., 2005; Damoiseaux et al., 2006; Cole et al., 2014; Laumann et al., 2015) computed over the entire fMRI scan (for a comprehensive review see van den Heuvel & Hulshoff Pol, 2010). More recently, dynamic functional connectivity measures came into use, revealing transient brain states that vary in time (Honey et al., 2007; Tagliazucchi et al., 2012; Hutchison et al., 2013; Allen et al., 2014; Cabral et al., 2017), reflecting ongoing cognitive processes (Gonzalez-Castillo et al., 2015; Gonzalez-Castillo & Bandettini, 2018). It has been suggested that the richness of conscious experience can be directly linked to the richness of brain state repertoires. Indeed, individuals who lack consciousness present brain states that are less diverse, with fewer long-range interactions and no anticorrelation between brain areas (Barttfeld et al., 2015; Uhrig et al., 2018; Demertzi et al., 2019). Furthermore, active interventions, such as deep brain stimulation, aimed at restoring consciousness have been found to increase the diversity of brain state repertoires (Tasserie et al., 2022).

A recent study utilizing a latent space representation of brain network interactions found increased overall similarity between participants who actively tried to comprehend a scrambled movie (Song et al., 2021). However, the movie features that drive inter-subject synchronization of brains states are poorly understood. Given the evolving nature of movie plots, high-level cognitive processing of the movie varies significantly over time. Therefore, it is crucial to unravel the relationship between similar brain state dynamics across participants and the dynamic features of a particular narrative to understand how brain processes contribute to movie comprehension over time.

To address this gap, our study investigates how the processing of plot-driven naturalistic movies dynamically influences the repertoire of brain states, as assessed through interactions among dynamic brain networks. We examine whole-brain connectivity patterns that emerge during resting-state, movie watching, and scrambled movie watching in healthy participants. Our findings demonstrate that certain brain patterns are more prevalent during movie watching, while others are more prominent in non-movie conditions. Furthermore, by analyzing the average and dynamic synchronization of connectivity patterns between participants over time, we show that narrative stimuli induce higher inter-subject synchronization, particularly during suspenseful scenes. Altogether, these results suggest that processing of the same narrative stimuli elicits common functional connectivity configurations between individuals, and the dynamics of these brain states track variations in the high-level properties of the processed information.

2.3. Method

2.3.1. Participants and Procedure

In this study, we used a previously published dataset (Naci et al., 2014) in which 27 participants underwent functional MRI recordings. During the acquisition, 15 participants (18-40 years; 7 males) watched an 8-minute black and white movie clip taken from a TV show entitled “Alfred Hitchcock Presents—Bang! You’re Dead”. The same participants also went through a resting-state scan. A second group of 12 participants (18-30 years; 4 males) watched the same movie but in a scrambled order. In this condition, the movie was cut into 1-second segments and shuffled, ensuring that participants viewed all the scenes without comprehending the plot. To evaluate how suspense varied in the movie, a third group of 15 participants (19–29 years; 5 males) watched the movie clip outside of the scanner and rated the suspensefulness of each 2-second segment using an 8-point scale. All participants were right-handed native English

speakers with no history of neurological or psychiatric disorders. They provided written informed consent prior to the experiment and were remunerated for their participation. This study followed the principles prescribed by the declaration of Helsinki and was approved by the local ethics board of the Western University. Further information on the participants or experimental procedure can be found in Naci et al. (2014).

2.3.2. MRI acquisition parameters

MRI data were acquired on a 3T Siemens Tim Trio System. T2*-weighted whole-brain images were recorded during resting-state (256 volumes), movie (246 volumes) and scrambled movie (238) watching with a gradient-echo EPI sequence (33 slices, slice thickness: 3 mm, interslice gap of 25%, TR/TE: 2000 ms/30 ms, voxel size: $3 \times 3 \times 3$ mm, flip angle: 75°). A mirror box allowed participants to see the movie that was presented on a projection screen behind the scanner. Noise cancellation headphones (Sensimetrics, S14) were also used for sound delivery. An anatomical volume was also acquired using T1-weighted MPRAGE sequence in the same acquisition sessions (154 slices, matrix size: $240 \times 256 \times 192$, TE: 4.25 ms, voxel size: $1 \times 1 \times 1$ mm, flip angle: 9°).

2.3.3. fMRI preprocessing

Raw MRI data were preprocessed and denoised using CONN functional connectivity toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012) implemented in MATLAB (The MathWorks). The first 5 volumes were discarded to ensure stable magnetization. The preprocessing procedure included realignment, slice-time correction, outlier detection, segmentation, normalization into the MNI152 space (Montreal Neurological Institute), and spatial smoothing using a Gaussian kernel of 6-mm full width at half-maximum. For outlier correction, images with more than 0.3 mm framewise displacement in one of the x, y, z directions, more than 0.02 rad rotational displacement, or global mean intensity exceeding 3 standard deviations were included as nuisance regressors in the generalized linear model (GLM). White matter and cerebrospinal fluid masks were also included as nuisance parameters in the GLMs. Average time-series from 42 regions of interest were extracted after applying a 0.008 to 0.09 Hz band-pass filter to the signal. Regions of interest were defined as 10 mm-diameter spheres around the given MNI coordinates (Table S1).

2.3.4. Time-varying functional connectivity patterns

All computations were performed in MATLAB following the procedure from Demertzi et al. (2019). After the preprocessing, the extracted ROI time-series were represented in the complex space using their analytic representation, consisting of the original signal as the real part and the Hilbert transform as the imaginary part. The instantaneous phase is computed as the inverse tangent of the ratio of the imaginary and real components and wrapped into the $[-\pi, \pi]$ interval using the angle function implemented in MATLAB. This allowed us to have a time-series of instantaneous phases for each ROI. Note that to avoid edge artefacts, the first and last 9 time points have been discarded from the time series. Then, phase differences between each ROI pair (a total of 861 pairs) were calculated at each time-point using cosine similarity. This allowed the representation of the whole-brain connectivity configuration at each time point as an observation in an 861-dimensional space. The data from all sessions (a total of 42 sessions: 15 resting-states, 15 movies, and 12 scrambled movies) were concatenated, and k-means ($k = 3, 4, 5, 6, 7$) clustering with 1000 repetitions using Manhattan distance was applied to uncover recurrent "prototypical" connectivity configurations across all experimental conditions. The silhouette method indicated that 4 clusters provided the best classification. Connectivity configuration at each time point was then labeled with one of the 4 cluster centroids to which the configuration belonged. Finally, participants' brain activity during the scans was expressed as a sequence of the 4 centroids (42 by 42 phase coherence matrix).

2.3.5. Inter-subject similarity index

We computed an Inter-subject Similarity Index (ISI) in order to assess the resemblance between the participants' pattern sequences using the following formula

$$ISI(A, B) = \frac{\sum_{i=1}^k \left(P(A = i, B = i) - P(A = i)P(B = i) \right)}{\sum_{i=1}^k \left((P(A = i) + P(B = i))/2 - P(A = i)P(B = i) \right)}$$

where $P(A = i)$ and $P(B = i)$ are the occurrence probabilities of Pattern i (among total number of k patterns, in this study $k = 4$) in participants A and B respectively. $P(A = i, B = i)$ corresponds to the joint probability of exhibiting Pattern i by participants A and B at a given time-point. The ISI measures the co-occurrence of brain patterns between two participants (A and B) while accounting for the overall occurrence probability of each connectivity pattern.

Positive values of ISI indicate higher co-occurrence of patterns compared to chance ($SI = 0$). The synchronization level of each participant is defined as their average ISI with all the other participants of their group.

2.3.6. Suspense rating

The suspense ratings were obtained from the 15 participants who watched the movie outside of the scanner. After viewing each 2-second segment, participants rated the suspense level on an 8-point scale. To smooth out rapid variations within scenes and highlight changes in the movie plot, a moving average of 7 ratings (equivalent to 14 seconds) was calculated. The average suspense ratings can be found in Figure 2.3B.

2.3.7. Instantaneous co-occurrence

We used entropy as a measure of instantaneous pattern co-occurrence between participants. The entropy $H(X)$ of the connectivity patterns at a given time point was computed using the following formula:

$$H(X) = - \sum_{i=1}^4 P(x_i) \log_2 P(x_i)$$

where $P(x_i)$ is the occurrence probability of pattern i among the participants at a given moment. Since there are four distinct patterns, the maximum entropy value is 2, indicating a uniform distribution of pattern probabilities (each pattern exhibited by 1/4 of the participants). Conversely, lower entropy values indicate that majority of the participants had the same pattern at the given time point. This co-occurrence measure is not pattern specific: increased co-occurrence of any patterns would decrease the entropy values. To assess the relationship between suspense variations and instantaneous co-occurrence, a moving average of 7 entropy values was calculated, similar to the suspense ratings.

2.3.8. Temporal pattern consistency

Following a previously published method (Meer et al., 2020), we assessed which patterns contributed the most to the inter-subject co-occurrence of the patterns. This method consists in counting the number of participants having a given pattern at least once in a time window and in determining the pattern that manifested the most. Here we used a sliding window of 7

consecutive time points to construct the time windows similarly to all our other analyses. The dominant patterns during movie watching and scrambled movie watching can be found in Figure 2.3D in the center and bottom panels respectively. The percentage of consistency indicates the percentage of participants having the dominant pattern at a time point. In order to exclude consistency that might appear by chance given the natural occurrence probabilities of the patterns, we subtracted the occurrence percentage of a pattern during the movie and scrambled movie-watching scans from the percentage of consistency of this pattern at a given time-point in these conditions.

2.3.9. Statistical analyses

Occurrence probabilities of the patterns and changes in the similarity index across conditions are assessed with linear models using lme4 (Bates et al., 2015), car (Fox & Weisberg, 2019), and emmeans (Lenth, 2021) packages in R (R Core Team, 2021). Wilcoxon rank-sum tests on the suspense ratings and the temporal consistency values, as well as the Spearman's correlation between the suspense values and the entropy were performed on MATLAB (The MathWorks). All tests are corrected for multiple comparisons using the Bonferroni procedure except for the sign-tests on Pattern coherence levels which were corrected using the Benjamini–Hochberg procedure.

2.4. Results

We investigated how high-level sensory information processing influences ongoing brain activity arises from the coordination of different brain regions. 15 participants underwent fMRI recordings during movie watching and rest. A second group of 12 participants watched the same movie but scrambled to prevent them from understanding the plot while still viewing every scene. Using Hilbert transform and k-means clustering, we computed whole-brain connectivity patterns for each fMRI volume in each condition (Figure 2.1). The clustering procedure has resulted in four distinct connectivity patterns. While Pattern 1, 2 and 3 showed both positive and negative correlations between different brain networks, Pattern 4 lacked long-range connectivity (Figure 2.2A).

First, we hypothesized that some whole-brain connectivity patterns would be associated with a particular experimental condition and would vary in frequency accordingly. A linear model revealed a Pattern*Condition interaction ($F(6) = 7.17, p < 0.0001$). Pattern 2 showed increased occurrence during movie watching (median: 28.4%) compared to resting-state (median: 11.2%,

$t(156) = 3.94$, $p = 0.0004$, after Bonferroni correction), and scrambled movie watching (median: 11.4%, $t(156) = 4.77$, $p < 0.0001$). By contrast, Pattern 1 was less frequent during movie watching (median: 13.0%) compared to resting-state (median: 22.3%, $t(156) = -3.48$, $p = 0.0019$) and scrambled movie (22.1%, $t(156) = -3.38$, $p = 0.0027$) (Figure 2.2A). We didn't find any difference between the resting-state and scrambled movie watching for Patterns 1 ($t(156) = -0.099$, $p = 1.00$) and Pattern 2 ($t(156) = 1.05$, $p = 0.88$). Patterns 3 and 4 exhibited similar occurrence probabilities across all conditions.

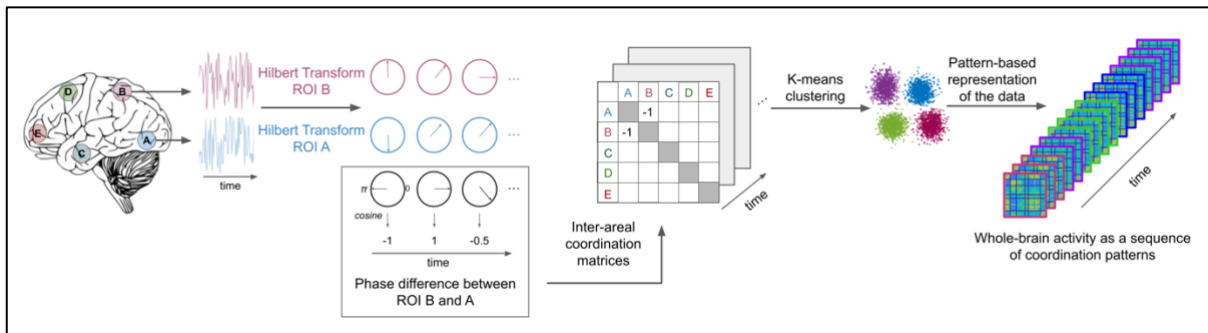


Figure 2.1. Summary of the method used to compute inter-areal connectivity patterns. After preprocessing the fMRI data, we extracted BOLD signal time-series from 42 regions. Following the preprocessing of the fMRI data, BOLD signal time-series were extracted from 42 regions of interest (ROIs) belonging to 6 different networks (visual, auditory, saliency, default mode, fronto-parietal, and motor). The Hilbert transform was applied to all time-series in order to extract the instantaneous phase at each fMRI volume (pink and blue circles in the figure). At each time point, we calculated phase differences between each pair of ROIs (in this example, between ROI A and B), represented by the black circles in the figure. Using cosine similarity, we ranged the phase synchronies between -1 and 1; -1 indicating a complete phase opposition and 1 indicating a complete phase coherence between the two ROIs. Then, phase synchrony values were used to construct a 42 by 42 inter-areal coordination matrix for each time-point (fMRI volume). Using k-means clustering, we classified the coordination matrices into 4 *prototypical patterns*. Finally, the fMRI data of each participant was represented as a sequence of these 4 patterns.

Given the movie-specific modulation of Patterns 1 and 2, we further investigated how they differed in their inter-ROI coherence profiles. Pattern 2, which occurred more frequently during movie watching, showed positive coherence between the saliency network (SAL), fronto-parietal (FP) and visual (VIS) networks, and negative coherence between the default-mode network (DMN) and fronto-parietal (FP), saliency (SAL) and visual (VIS) networks (Figure 2.2B, left panel). On the other hand, Pattern 1, which occurred more frequently in the non-movie conditions, exhibited negative coherence between SAL - DMN and SAL - VIS, and positive coherence between DMN - FP and DMN - VIS (Figure 2.2B, middle panel). The

contrast between Pattern 2 and Pattern 1 (Figure 2.2B, right panel) revealed that Pattern 2 contained more negative coherence between DMN - FP and DMN - VIS, and more positive coherence between FP - VIS and SAL - VIS compared to Pattern 1.

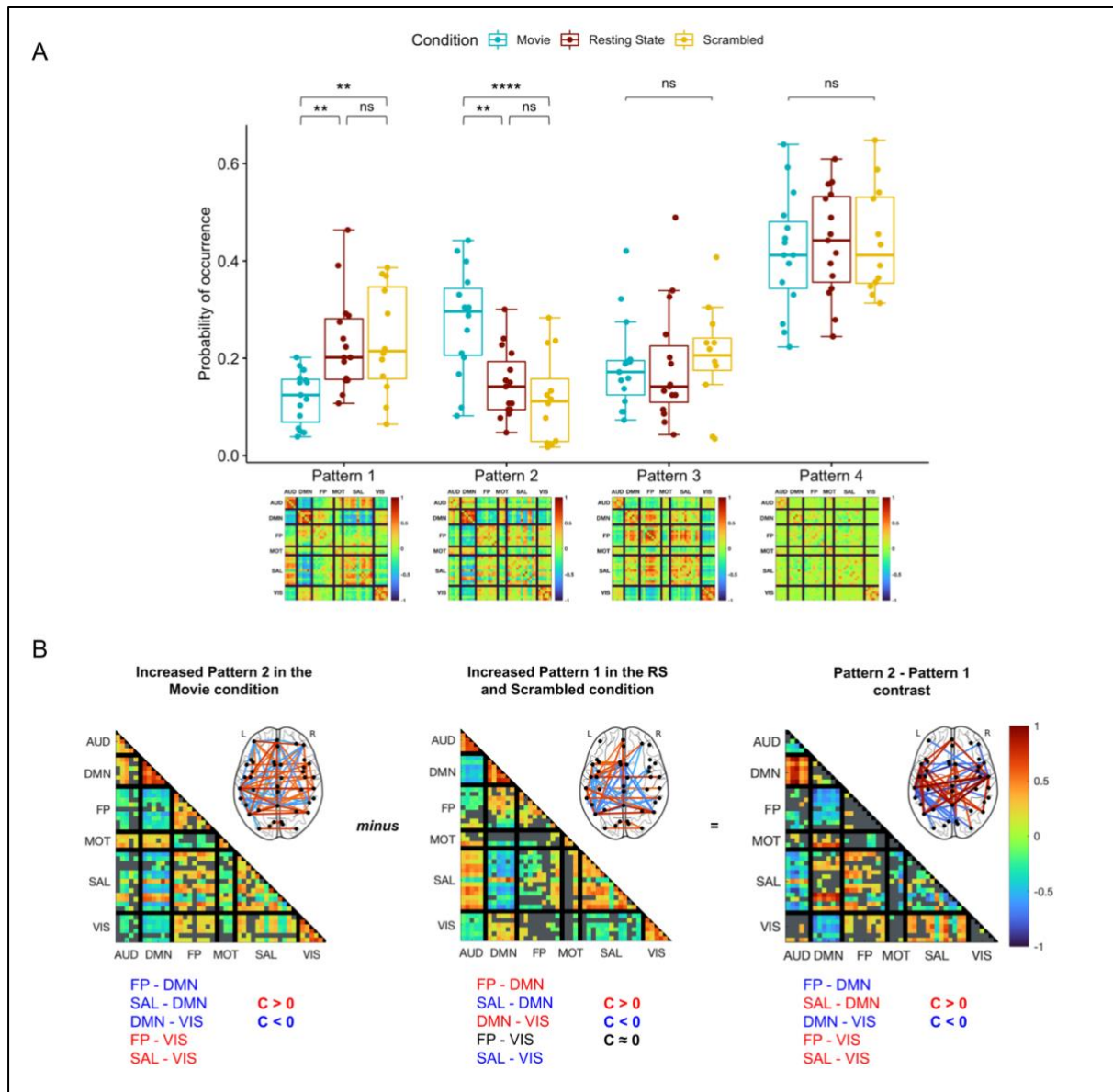


Figure 2.2. Condition specific variation of the whole-brain connectivity patterns. (A) Occurrence probability of the 4 patterns during movie watching (blue), rest (brown) and scrambled movie watching (yellow). Patterns 3 and 4 displayed similar occurrence probabilities across the three conditions. However, Patterns 1 and 2 exhibited condition-specific modulation. Pattern 2 was more frequent during movie watching, while Pattern 1 occurred more frequently during resting-state conditions and scrambled movie watching. Stars indicate statistical significance after correction for multiple comparisons using the Bonferroni procedure. (B) Description of the differences between Pattern 2 (more frequent in movie condition) and Pattern 1 (more frequent in non-movie conditions). Coherence values are depicted using blue shades for negative coherence ($C < 0$) and red shades for positive coherence ($C > 0$) after

applying the Benjamini-Hochberg procedure for multiple comparisons (Sign test; $p < 0.001$). Gray color represents coherence that is not significantly different from zero. Note that brain templates show the top 5% coherence for visualization purposes. Pattern 2 (left), which was more frequent in the movie condition, displayed negative phase coherence between the default-mode network (DMN) and fronto-parietal (FP), saliency (SAL) and visual (VIS) networks while the visual network had positive coherence with fronto-parietal (FP) and saliency (SAL) networks. Pattern 1 (center), which had more occurrence in non-movie conditions, was characterized by positive coherence between default-mode network (DMN) and fronto-parietal (FP) and visual (VIS) networks and negative coherence between saliency network (SAL) and visual (VIS) and default-mode networks. The contrast between patterns (Pattern 2 - Pattern 1; right) revealed more negative coherence between default-mode network (DMN) and fronto-parietal (FP) and visual (VIS) networks in Pattern 2 (increased with movie) than Pattern 1 (increased with non-movie conditions). Moreover, saliency (SAL) and visual (VIS) networks showed more positive coherence in Pattern 2 compared to Pattern 1. Gray color indicates p values greater than 0.001 after FDR correction in a mixed linear model.

Next, we hypothesized that functional connectivity dynamics would be similar across participants during movie watching when the same narrative drives brain activity. We computed an inter-subject similarity index (ISI) that allows us to assess the inter-subject co-occurrence of the patterns in the three experimental conditions. Since we were describing the brain activity with only four patterns, co-occurrence of patterns could arise by chance, even though participants were under different conditions and their brain activity was completely independent. The ISI indicates how much more co-occurrence participants have compared to chance-level co-occurrence. As expected, we found ISI values around zero during rest (Wilcoxon signed rank test after Bonferroni correction: $V = 35$, $p = 0.51$) and scrambled movie watching ($V = 64$, $p = 0.16$), indicating that the co-occurrence of patterns during those conditions was at chance level. We observed a significant increase in the ISI during movie watching (median ISI = 0.05, S.E. = 0.005, $V = 120$, $p = 0.0002$) compared to rest (median SI = 0, S.E. = 0.003, $t(39) = 9.56$, $p < 0.0001$, after Bonferroni correction) and scrambled movie watching (median SI = 0.01, S.E. = 0.004, $t(39) = 6.74$, $p < 0.0001$), indicating higher co-occurrence when participants watched the movie (Figure 2.3A).

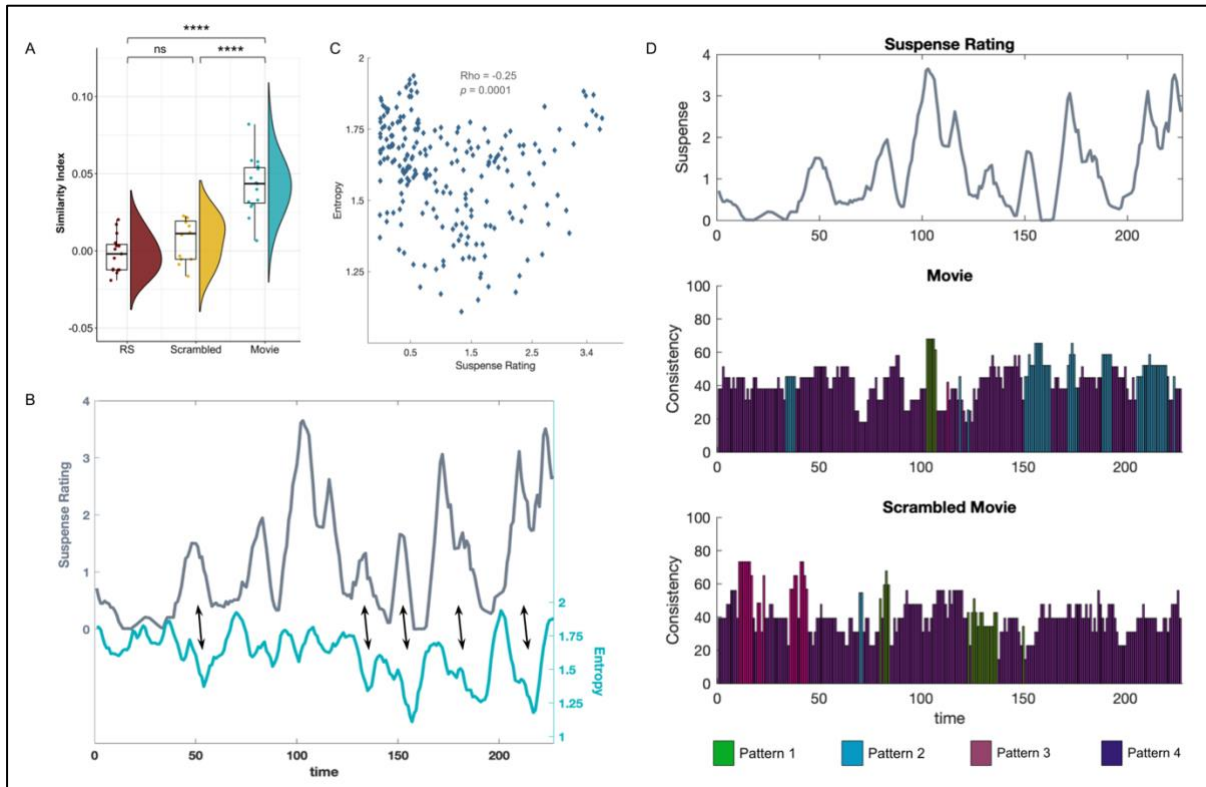


Figure 2.3. Movie watching induces inter-subject synchronization by increasing the co-occurrence of the movie-related whole-brain connectivity pattern. (A) Average inter-subject similarity index of each participant in resting-state (RS), scrambled movie, and movie watching conditions. Similarity indices were not different than zero in non-movie conditions, indicating a chance-level co-occurrence of patterns among participants throughout the whole duration. On the other hand, participants in the movie condition showed higher similarity index values, indicating increased co-occurrence of the patterns compared to chance. Stars denote statistical significance after correction for multiple comparisons using Benjamini–Hochberg procedure. (B) Suspenseful scenes increase pattern co-occurrence during movie watching. The dark gray line shows the variations in the average suspense rating. Entropy (light blue line) of the pattern distribution among participants at each time point is used as an instantaneous co-occurrence measure. Lower entropy values indicate higher co-occurrence. Note the negative relationship between the suspense rating and the entropy values: scenes with higher suspense ratings are followed by a decrease in entropy and thus an increased co-occurrence of the patterns among participants. (C) Scatter plot of the average suspense rating and the subsequent entropy values (6 seconds after the suspense rating). We found a significant negative correlation between the two measures ($\rho = -0.25$; $p = 0.002$). (D) Instantaneous co-occurrence during suspenseful scenes is associated with the movie-specific pattern. Temporal consistency of the whole-brain connectivity patterns in the movie (middle panel) and scrambled movie (bottom panel) watching condition. Variations in the average suspense rating can be found in the top panel. The dominant pattern at a given time point is indicated by a color code. The y-axis shows the percentage of across-participant consistency. The overall occurrence probability of each pattern in the conditions (Figure 2.2A) is

subtracted from the instantaneous consistency in order to assess consistency exceeding random occurrence. Note the higher consistency values in the movie condition compared to the scrambled movie condition. Pattern 2 (blue) was the dominant pattern during increased suspense, reaching up to 65% excess consistency during movie watching.

Moreover, we predicted that the co-occurrence of the patterns would be more important during the most engaging parts of the movie, during which the movie plot captures the viewers' attention. We took advantage of the suspenseful nature of the movie and utilized an existing dataset where a separate group of 15 participants had rated the suspense of the scenes on an 8-item scale outside of the scanner¹. We noted higher suspense values in the second half of the movie compared to the first half (mean: 1.3 vs 0.9, Wilcoxon rank-sum test: $z = 2.43, p = 0.01$). As predicted, ISI values were higher only in the second half of the movie ($F(2) = 44.34, p < 0.0001$) and did not differ between conditions during the first half of the recordings ($F(2) = 1.73, p = 0.2$) (Figure S2.1). The same was true for the patterns' occurrence probabilities in the three conditions, which only differed in the second half of the recordings (Figure S2.2). For a finer assessment of inter-subject brain state synchronization, we used entropy as a measure of instantaneous pattern co-occurrence among participants at each time point. Lower entropy values indicate higher co-occurrence between participants. We observed a negative relationship between the average suspense ratings and the entropy values: scenes with higher suspense were followed by a decrease in entropy, indicating a higher co-occurrence across participants (Figure 2.3B). The relationship between the suspense and entropy was further confirmed by a significant Spearman's correlation ($\rho = -0.25, p = 0.0002$), taking a 6 second fMRI response lag (3 TRs) relative to the time of suspense rating into account (Figure 2.3C). This relationship was not found in the resting-state ($\rho = -0.08, p = 0.25$) and scrambled movie conditions ($\rho = 0.09, p = 0.21$) (Figure S2.3).

Finally, we examined whether the increased co-occurrence during suspenseful scenes was driven by a specific connectivity pattern or if all patterns contributed equally to the increase. Following a previously published method⁸, we determined the most frequently expressed pattern at each time window during movie watching and scrambled movie conditions and evaluated their consistency across participants (Figure 2.3D). We subtracted the *time-averaged* occurrence probabilities of each pattern during the movie and scrambled movie watching (Figure 2.2A) from the consistency level in these conditions to reveal consistency exceeding mean session occurrence. Overall, we found higher consistency values during movie watching compared to scrambled movie watching (mean: 44.1 vs 38.6, Wilcoxon rank-sum test: $z = 3.65$,

$p = 0.0003$). Furthermore, Pattern 2, which showed increased occurrence during movie watching, was the dominant pattern during the moments of suspense in the second half of the movie, reaching up to 65% excess consistency.

To summarize, our findings demonstrate that: (i) dynamic connectivity patterns show condition-specific modulation in their occurrence frequency, with Pattern 2, characterized by positive coherence between the VIS and FP networks and negative coherence between the DMN and VIS, FP, and SAL networks, exhibiting increased occurrence probability during movie watching compared to non-movie watching conditions; (ii) participants exhibit synchronization in their dynamic functional connectivity profiles during movie watching; (iii) this synchronization is significantly associated with the narrative of the movie, with higher synchronization observed during suspenseful moments; and (iv) Pattern 2 contribute the most to the synchronization during suspenseful moments. Altogether these results suggest that processing of the same high-level information elicits similar functional connectivity dynamics that reflect and track changes in the properties of the processed information.

2.5. Discussion

In the current study, we investigate how the processing of an engaging audio-visual stimulus alters ongoing brain activity and induces common functional connectivity dynamics across viewers. Until now, most studies investigating inter-subject synchronization during naturalistic stimuli viewing focused on local static activations (Hasson et al., 2004, 2008; Jääskeläinen et al., 2008; Kauppi et al., 2010; Nummenmaa et al., 2012; Naci et al., 2014; Simony et al., 2016). In contrast, our study takes a global and dynamic perspective on neural activity and reveals that watching a plot-driven and captivating movie shapes the interaction of brain networks and synchronizes the network dynamics across-individuals. Importantly, we also demonstrate that the neural synchronization among participants is not constant but rather fluctuates over time. Indeed, the dynamics of the network interactions vary with the suspense of the scenes, resulting in a higher inter-subject synchronization when participants are immersed in the movie.

In light of these results, we propose that suspense ratings may be used as a proxy for the allocation of attention. Suspenseful scenes capture attention which enhances the processing of the scenes, resulting in a higher inter-subject synchronization during these scenes. Compatible with our results, previous studies have found that increased suspense in the narrative induces higher activity in the ventral attention network (Bezdek et al., 2015, 2017). Our results go

beyond this finding and show that increased attention in turn, modulates the ongoing processing similarly across individuals.

The two patterns that showed condition-specific modulation present both positive and negative phase coherence between different brain regions that coordinate according to the ongoing task (Figure 2.2B). For example, positive coherence between visual and FP networks and negative coherence between DMN and FP networks during movie watching suggest that while attention networks coordinate with sensory areas, they decouple from the regions that are implicated in internal thought generation (Mason et al., 2007; Fox et al., 2015). These results align with previous studies reporting a juxtaposition between DM and FP networks during movie watching (Haugg et al., 2018) and during switches between internal and external awareness (Vanhaudenhuyse et al., 2011), and furthermore show that this decoupling occurs simultaneously with the coupling of sensory and attention networks. Interestingly, studies show that patterns which exhibit both positive and negative coherence between different brain regions are predominant in healthy populations and diminish in unconscious states (Barttfeld et al., 2015; Uhrig et al., 2018; Demertzi et al., 2019; Tasserie et al., 2022). Our results add to this literature by showing that, in healthy participants, these rich coherence patterns can be divided into similar yet distinct sub-patterns reflecting the cognitive processes implicated in the ongoing task.

One could ask why scrambled movie watching and resting-state induce similar connectivity patterns although the two conditions differ drastically, especially at the sensory level. This might be due to the fact that participants could not follow the plot in the scrambled movie condition and therefore, may instead, have directed their attention to their self-generated thoughts, as they did during resting-state scans (Mason et al., 2007). Since the whole-brain patterns capture the global brain state and not region-specific activations, they are likely more sensitive to participants' ongoing mental activity than detailed sensory-driven processes, and thus, pick up on the similarities between the mental states elicited by these apparently different conditions.

In summary, our study provides valuable insights into the impact of ecologically valid stimuli on brain activity and inter-subject synchronization. By adopting a global and dynamic approach, we demonstrate that watching a plot-driven and captivating movie shapes the interaction of brain networks, resulting in synchronized network dynamics across individuals. The fluctuation of this synchronization over time, varying the suspense of the scenes, highlights

the role of attention in modulating neural processing. Overall, our study highlights the importance of considering dynamic network interactions and the high-level stimulus characteristics when investigating inter-subject synchronization during naturalistic stimuli viewing.

2.6. Supplementary information

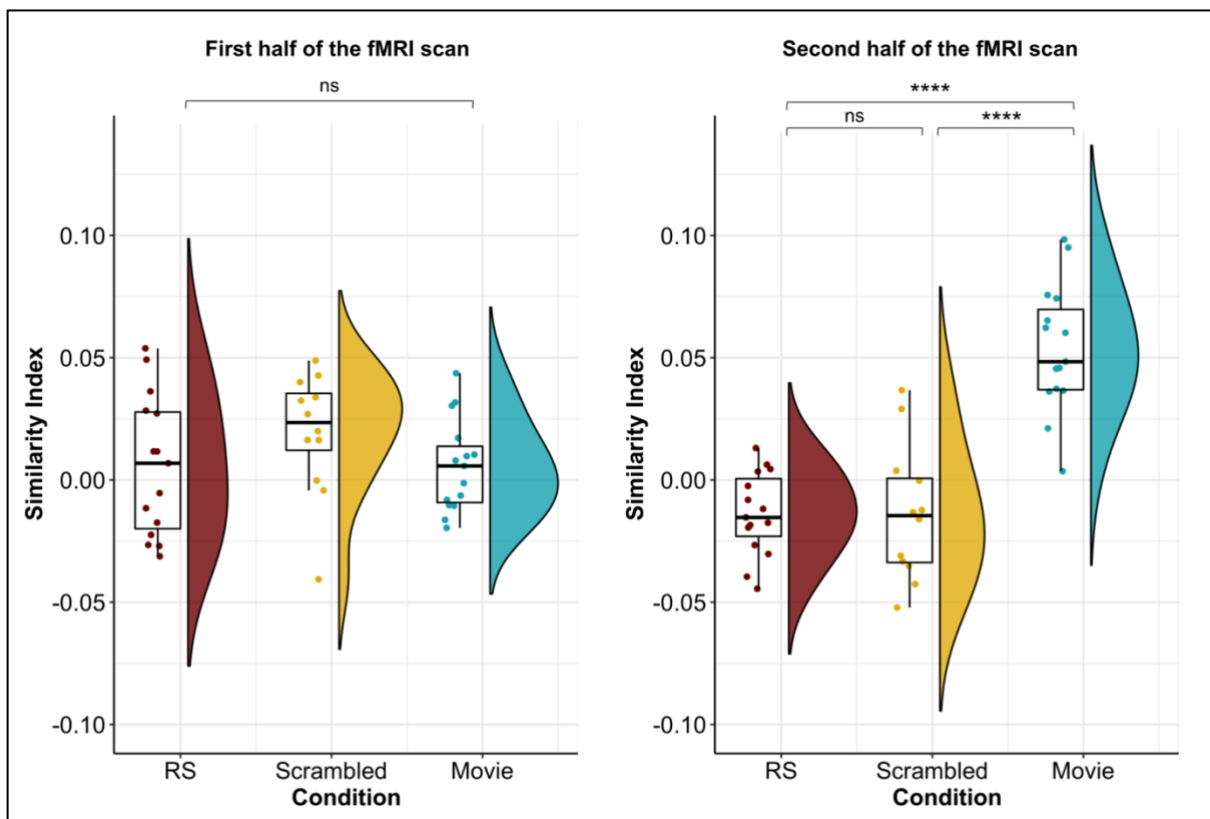


Figure S2.1. Increased inter-subject similarity index only during the second half of the movie.

Average similarity index (SI) of each participant computed over the first (left) and second (right) half of the fMRI scan during resting-state, scrambled movie watching, and movie watching conditions. While SI did not differ between condition during the first half of the fMRI scan ($F(2) = 1.73, p = 0.19$), SI during movie watching was significantly higher compared to resting-state ($t(39) = 8.49, p < .0001$) and scrambled movie ($t(39) = 7.6, p < .0001$) conditions. SI during resting-state and scrambled movie conditions were not statistically different ($t(39) = 0.41, p = 1$). Each dot represents a participant.

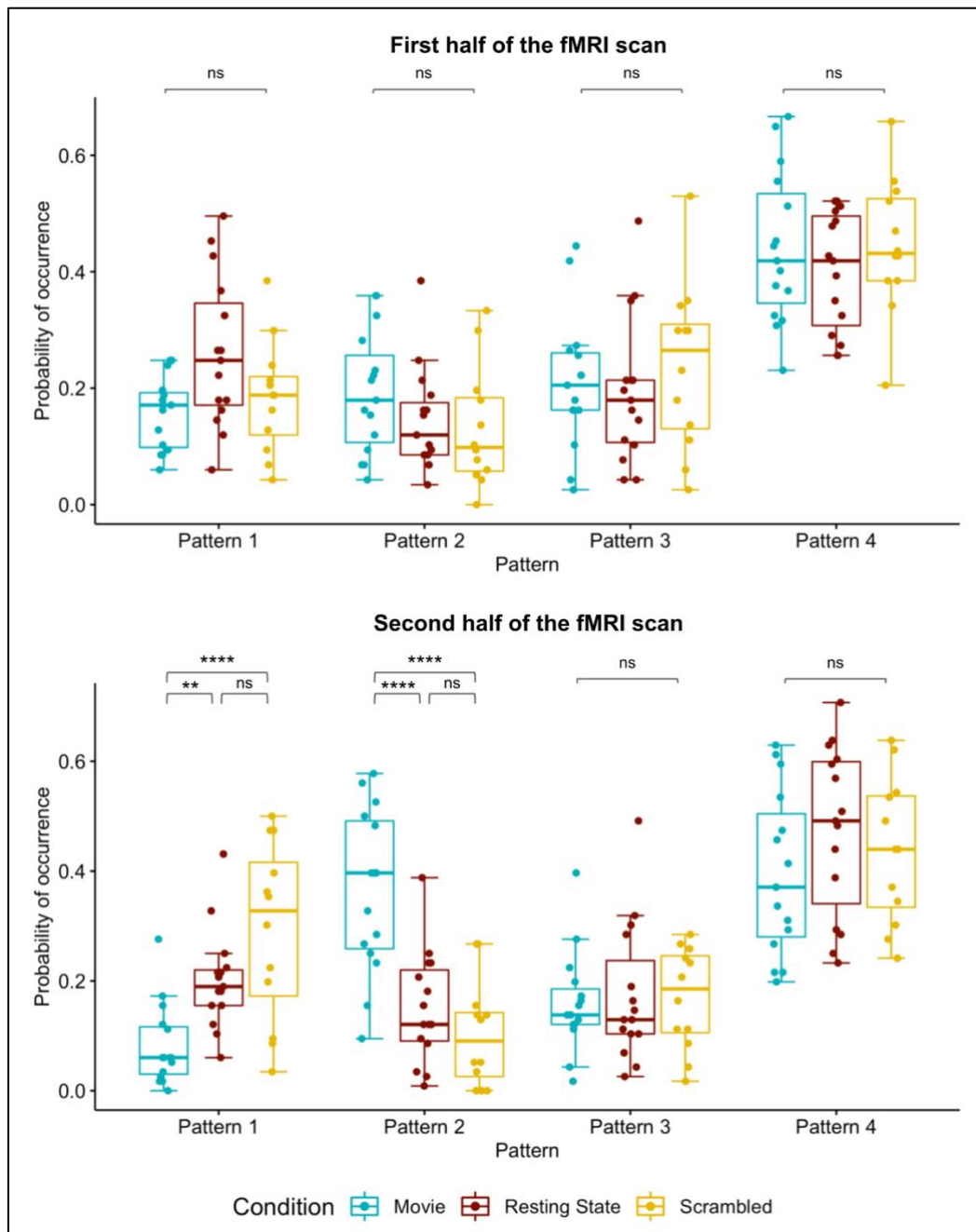


Figure S2.2. The occurrence probability of the patterns differs between conditions only during the second half of the fMRI scan. The occurrence probability of the patterns during the first (left) and the second (right) half of the fMRI recording in movie watching, resting-state and scrambled movie watching conditions. While no significant interactions were found between the condition and the pattern probabilities during the first half of the scan ($F(6) = 1.81, p = 0.1$), a significant interaction was observed in the second half ($F(2) = 13.00, p < .0001$). Pattern 2 showed increased probability during movie watching compared to resting-state ($t(156) = 5.09, p < .0001$) and scrambled movie watching ($t(156) = 6.43, p < .0001$) and Pattern 1 was more frequent during scrambled movie watching ($t(156) = 5.20, p < .0001$) and resting-state ($t(156) = 3.82, p = .0006$) compared to movie watching. Patterns 3 and 4 did not differ between conditions.

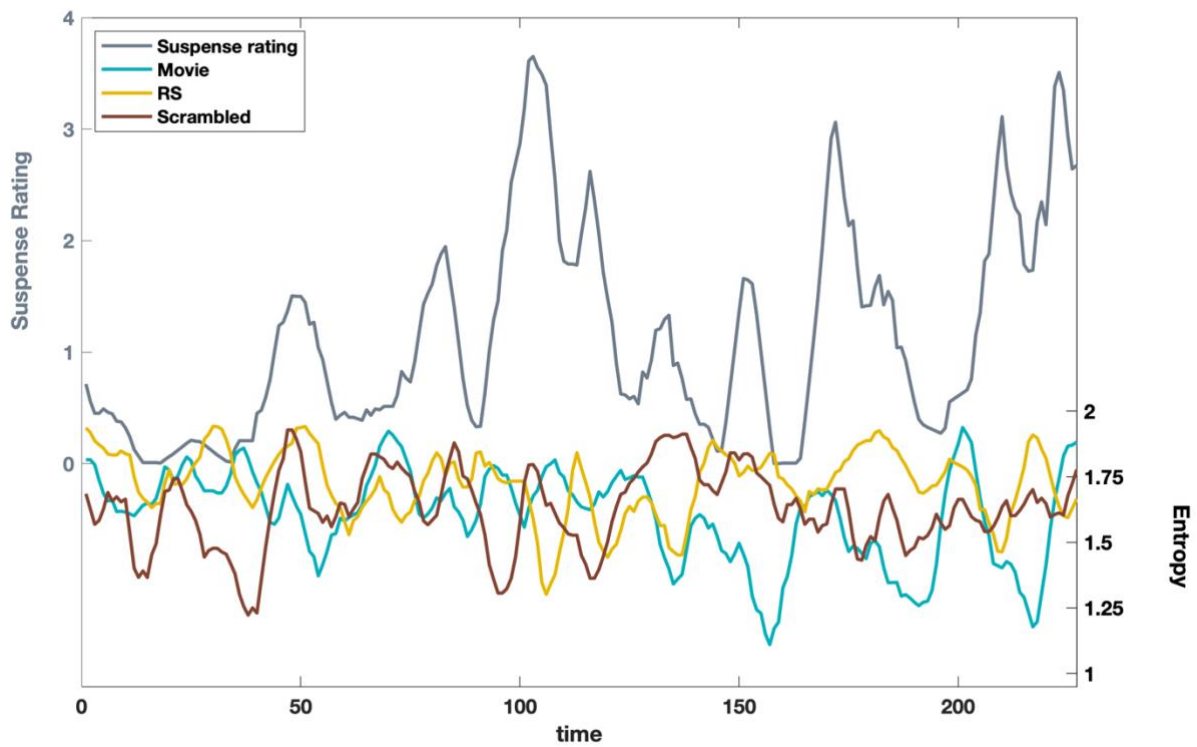


Figure S2.3. The relationship between the suspense rating and the entropy values in the movie (blue lines), resting-state (red lines) and scrambled movie (yellow lines) conditions. Moments with increased suspense was followed by a decrease in the entropy values in the movie watching condition. This negative relationship was not found in the resting-state and the scrambled movie watching conditions.

Table S2.1. 42 regions of interest used in the inter-areal coherence analyses. The regions were defined as 10mm-diameter spheres around the given x,y,z coordinates.

Region of Interest (ROI)	Seed MNI coordinates [x, y, z]
Auditory Network (AUD)	
Anterior cingulate cortex	[6, -7, 43]
Precentral gyrus [left] [right]	[-53, -6, 7] [58, -6, 11]
Superior transverse temporal gyrus [left] [right]	[-44, -6, 11] [44, -6, 11]
Default Mode Network (DMN)	
Inferior temporal cortex [left] [right]	[-61, -24, -9] [58, -24, -9]
Lateral parietal cortex [left] [right]	[-46, -66, 30] [49, -63, 33]
Medial prefrontal cortex	[-1, 54, 27]
Posterior cingulate cortex	[0, -52, 27]
Fronto Parietal Network (FP)	
Angular gyrus [left] [right]	[-31, -59, 42] [30, -61, 39]
Midcingulate cortex	[0, -29, 30]
Premotor cortex left [left] [right]	[-41, 3, 36] [41, 3, 36]
Inferior parietal lobule [left] [right]	[-51, -51, 36] [51, -47, 42]
Dorsolateral prefrontal cortex [left] [right]	[-43, 22, 34] [43, 22, 34]
Motor Network (MOT)	
Supplementary motor area	[0, -21, 48]
Primary motor cortex [left] [right]	[-39, -26, 51] [38, -26, 48]

Saliency Network (SAL)	
Dorsolateral prefrontal cortex [left] [right]	[-38, 52, 10] [30, 48, 22]
Ventrolateral prefrontal cortex	[42, 46, 0]
Parietal operculum [left] [right]	[-60, -40, 40] [58, -40, 30]
Supplementary motor area [left] [right]	[-5, 14, 48] [5, 14, 48]
Dorsal anterior cingulate	[-6, 18, 30]
Paracingulate cortex	[0, 44, 28]
Temporal pole [left] [right]	[-50, 14, -14] [51, 16, -19]
Orbital frontoinsula [left] [right]	[-40, 18, -12] [42, 10, -12]
Visual Network (VIS)	
Associative visual cortex [left] [right]	[30, -89, 20] [-30, -89, 20]
Secondary visual cortex [left] [right]	[-6, -78, -3] [6, -78, -3]
Primary visual cortex [left] [right]	[-13, -85. 6] [8, -82, 6]

CHAPTER III

BRAIN AND BEHAVIORAL DYNAMICS IN WAKEFULNESS

“It was 2019 and I was working as a research engineer at the PICNIC lab. I took bus 27 from the lab to my home at the time, on Claude Bernard street. It was dark and raining outside. The bus was approaching my street, I had 2 stops left. Suddenly, I realized that I was on the street walking towards home. I looked around me. I was between my stop and the stop before. I understood that I must have gotten off the bus one stop before my usual stop, and started walking towards home. I was very confused because I had no memory of getting off the bus, only random, unrelated thoughts that had invaded my brain. I felt like I had been in autopilot mode, like a sleepwalker. I had then started walking in the right direction: my behavior was thus correct, but I felt like I did not ‘live’ that one minute preceding my pseudo-awakening. People around me were not looking at me, so I could conclude that my behavior was not strange and that I looked like a regular, awake person. But it did not feel that way. It was frightening to feel as if I had disappeared from this world for a short period of time. It was the first time I explicitly thought that ‘awake’ was a simple word for such a rich state.”

BRAIN STATES WITH HIGH CONNECTIVITY ENHANCE CONSCIOUS PERCEPTION OF THRESHOLD STIMULI

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3.1. Abstract

Previous research has shown that brain connectivity patterns featuring long-range interactions and anticorrelations are associated with conscious states and diminish with loss of consciousness. In this study, we investigate the functional role of these brain patterns in shaping conscious experiences by altering participants' ability to process external information. During an auditory detection task, participants underwent simultaneous fMRI and EEG recordings. Using phase-coherence-based functional connectivity dynamics and k-means clustering, we were able to identify five recurrent brain patterns corresponding to those observed in previous studies, including the highly connected pattern (high-pattern). As hypothesized, we found a significant increase in detection rates for threshold stimuli when participants exhibited a high-pattern at the time of presentation. In addition, the occurrence of the high-pattern increased following detection, with participants being more likely to transition to a high-pattern after stimulus detection. Our findings suggest that certain ongoing brain configurations facilitate conscious perception, and that conscious access, in turn, influences ongoing brain activity by increasing the frequency of highly connected patterns. In the future, targeting these moments of high connectivity patterns in patients with disorders of consciousness (DoC) may help us identify windows of greater susceptibility to the outside world and pave the way for individualized patient care protocols.

3.2. Introduction

Our interactions with the environment are determined by an interplay between ongoing neural activity and our neural responses to external stimuli. Each moment, our brains process and integrate a wide variety of internal and external stimuli of different modalities. While some of these stimuli are processed consciously and contribute to our subjective experiences, most remain unconscious (Dehaene et al., 2006; Dehaene & Changeux, 2011a). Neural events that follow conscious perception are widely investigated in the literature, mainly by comparing the conscious and unconscious perception of the same stimulus using various paradigms such as masking (Del Cul et al., 2007), threshold stimuli presentation (Pins & Ffytche, 2003), and attentional blink (Sergent et al., 2005). These studies have shown that the same stimulus with a fixed intensity can induce different brain responses depending on the subjective experience.

One of the prerequisites for conscious perception is to be in a *conscious state*, such as wakefulness (high arousal and high awareness), as opposed to unconscious states, such as under anesthesia or coma (no arousal, no awareness), or disorders of consciousness (arousal without limited awareness). Recent studies of anesthetized non-human primates (Barttfeld et al., 2015; Uhrig et al., 2018), and (un)conscious humans (Demertzi et al., 2019) investigated functional connectivity dynamics at rest and revealed distinct connectivity patterns correlating with different states of consciousness. Additionally, thalamic deep brain stimulation that aimed at restoring consciousness in anesthetized non-human primates has been found to restore the aforementioned connectivity patterns (Tasserie et al., 2022). However, the functional role of these brain patterns in conscious processing and the formation of subjective experience remains unknown. In this study, we investigate whether ongoing connectivity patterns alter the processing of external information, allowing it to be represented in a conscious manner.

The effect of spontaneous baseline brain activity fluctuations on perceptual outcome has been previously explored in different domains by contrasting perceived and unperceived trials. Electrophysiological recordings have shown that the pre-stimulus phase (Busch et al., 2009) and power (Ergenoglu et al., 2004; Wyart & Tallon-Baudry, 2009) of alpha activity, as well as the phase (Monto et al., 2008) and dynamics (Baria et al., 2017) of (infra-) slow cortical oscillations in the task specific regions, correlate with the perceptual outcome on trial-by-trial basis. In an attentional blink paradigm, pre-stimulus activity in the frontal electrodes predicts both conscious access to the T2-stimulus and the amplitude of post-stimulus event-related potentials (ERPs) such as P3b (Pincham & Szűcs, 2012). Functional magnetic resonance

imaging (fMRI) studies have found that cue-induced pre-stimulus activity reflects attentional allocation (Sapir et al., 2005) and task preparation (Ekman et al., 2012) and predicts task performance. Moreover, behavioral performance in Stroop (Coste et al., 2011) and motion discrimination tasks (Hesselmann, Kell, & Kleinschmidt, 2008) as well as the perceptual outcome of ambiguous vase/face stimuli presentation (Hesselmann, Kell, Eger, et al., 2008) seem to vary depending on prior activity fluctuations in task-specific regions such as color-sensitive visual areas, motion-sensitive middle temporal region, and fusiform face area, respectively. In the nociception domain, pre-stimulus brain activity in the default-mode and fronto-parietal networks (Boly et al., 2007), along with the functional connectivity between brain areas involved in pain perception (Ploner et al., 2010), are correlated with the subsequent perception of pain. And finally, ongoing activations in sensory and attentional areas (Sadaghiani et al., 2009) and functional connectivity between different brain regions (Sadaghiani et al., 2015) have shown to predict perceptual performance in an auditory threshold stimulus detection task.

These studies consistently suggest that fluctuations in baseline brain activity can have a significant impact on our conscious perception of the external world. However, most studies have primarily focused on individual activations within specific brain regions related to a task. The contribution of coordinated activity across different brain networks to conscious perception remains unknown. As a result, these studies cannot be directly linked to research on conscious states, which has revealed that the configuration of whole-brain activity varies with consciousness (Demertzi et al., 2019). Although these results provide insights into the neural basis of conscious perception, taking a hypothesis-driven approach based on the results of studies on conscious states, rather than a data-driven approach, could help bridge the gap between these two research areas that are inherently interconnected.

Our study aims to bridge the literature on conscious states and conscious perception by exploring how brain connectivity patterns that are linked to conscious states influence the formation of conscious experience, specifically by affecting the ability to process external information. Combining simultaneous fMRI and EEG acquisitions, we found that participants were more likely to detect auditory threshold stimuli when they exhibited connectivity patterns previously associated with conscious states (Demertzi et al., 2019). We also observed a higher occurrence of these connectivity patterns following stimulus detection, with participants more likely to transition to these patterns. Finally, we explored the relationship between these

connectivity patterns and the subjective mental states of participants. Our findings demonstrate the intricate interplay between complex and dynamic brain patterns and conscious perception and unify the literature in the two important lines of consciousness research.

3.3. Method

3.3.1. Participants

Twenty-six healthy participants were recruited for this study (13 women, mean age: 24.6 ± 4.2 years, 25 right-handed). All participants were native French speakers with good hearing and without any neurological or psychiatric disorders. They gave written consent prior to the experiment and were remunerated €70 for their participation in the study. One male participant was excluded from the study due to technical issues during the MRI acquisition. The protocol had been approved by the local ethics committee (promoted by the INSERM, CPP Ile-de-France 6, C13-41).

3.3.2. Experimental design and procedure

Participants underwent simultaneous MRI and EEG recordings while performing an auditory detection task. They were asked to detect a French vowel (/a/) embedded in continuous noise (Sergent et al., 2021), at 3 different signal-to-noise ratios (SNR -11, SNR -9 and SNR -7) around the detection threshold. Stimuli were delivered in a randomized fashion every 14 seconds (+/- 1 second) using MRI-compatible headphones. Participants had their eyes closed in the fMRI scanner and pressed a button with their right thumb when detected a stimulus. The sound level was adjusted for each participant via a staircase procedure prior to the task to ensure 50% detection at SNR -9. This resulted in higher detection rates at SNR -7 and lower detection rates at SNR -11. The task consisted of 6 blocks of 8 minutes separated by a small rest period. Thirty stimuli were presented in each block (ten per SNR level) in addition to 3 catch trials. Thus, the whole task contained 198 trials (33 per block). After each block participants were asked to verbally indicate on a scale of 7: (i) how tired they felt, (ii) how successful they think they were during the block, and (iii) their attentional focus during the block (1 for complete mind-wandering and 7 for complete focus on the task). Participants also underwent a 10-minute resting state with eyes closed before the task and a 5-minute anatomical scan after the task. Simultaneous EEG and fMRI were recorded throughout the whole experimental session including the staircase procedure and the resting state. The total experimental session took approximately 2 hours.

3.3.3. Neuroimaging parameters

3.3.3.1. MRI acquisition parameters

All MRI data were acquired on a 3T Siemens Prisma System. T2*-weighted whole brain resting state images were acquired with a multi-band gradient-echo planar imaging (EPI) sequence (600 volumes, 48 slices, slice thickness: 3 mm, TR/TE: 1000 ms/30 ms, voxel size: $3 \times 3 \times 3$ mm, multiband acceleration factor: 3, flip angle: 60°). Functional MRI images during the detection task were acquired using the same sequence. The cardiac and respiratory activities were also recorded during the fMRI acquisitions. An anatomical volume was acquired using a T1-weighted MPRAGE sequence in the same acquisition session (192 or 256 slices, slice thickness: 1 mm, TR/TE: 2.300 ms/ 2.76 ms, voxel size: $1 \times 1 \times 1$ mm, flip angle: 9°). The helium pump and the ventilation were turned off during the acquisitions in order to limit the artifacts on the EEG data.

3.3.3.2. EEG acquisition parameters

Electroencephalography data were recorded using Brain Vision Recorder (Brain Products, Gilching, Germany) with a 66-channel MRI-compatible 10-10 montage cap (BrainCap MR, Brain Products GmbH, Gilching, Germany) including 63 EEG channels, a reference channel at FCz, a ground channel located at AFz, and one ECG channel. Additional ECG data was also acquired using 2 ECG electrodes placed on the left side of the chest, one below the collarbone and the other below the armpit. All signals were recorded simultaneously at a 5000 Hz sampling rate and amplified through MR-compatible amplifiers (BrainAmp MR and BrainAmp ExG MR, Brain Products GmbH, Gilching, Germany) with a bandpass filter of 0.016–250 Hz. The EEG amplifiers were placed at the back of the MRI scanner and the cables linking them to the EEG cap were stabilized by sandbags. The impedances were measured after each run and were verified to be under 10 k Ω .

3.3.4. Neuroimaging preprocessing

3.3.4.1. fMRI preprocessing

The raw MRI data underwent preprocessing and denoising using custom MATLAB (The MathWorks) scripts. The preprocessing included segmentation using CAT12 (Gaser et al., 2022), realignment, co-registration, and normalization into the MNI152 (Montreal Neurological Institute) space as implemented in SPM12 (Penny et al., 2011). We did not perform slice-timing correction as our TR was already short (1 second). We also avoided spatial

smoothing of our data. The susceptibility-induced off-resonance field distortions were corrected using the *topup* procedure (Andersson et al., 2003) as implemented in FSL (Smith et al., 2004), providing a more accurate representation of the brain. Peripheral physiological data recorded during the scans such as respiration and cardiac pulsation were extracted using PhysIO Toolbox (Kasper et al., 2017). White matter masks, realignment parameters as well as their first and second order derivatives, cardiac and respiratory signals were included as nuisance regressors in the generalized linear model (GLM) in order to denoise the data. Average time-series were extracted from 42 regions of interest (ROIs) defined as 5mm radius spheres centered at specified MNI coordinates (as listed in Table S2.1).

3.3.4.2. EEG preprocessing

The EEG data were acquired simultaneously with the fMRI throughout the whole experimental session including the staircase procedure, resting state, and detection task. Brainvision Analyzer software (Brain Products GmbH, Munich, Germany) was used to correct cardio-ballistic and gradient artifacts in the EEG data via the template subtraction method (P. J. Allen et al., 2000). Following the artifact correction, the data were band-pass filtered between 0.1 and 45Hz (with an additional 50Hz notch filter), average referenced, and epoched while decimating to 250 Hz. To further clean the data, we used the autoreject algorithm (Jas et al., 2017), which calculated an optimal global rejection threshold for each electrode using a cross-validation approach and interpolated bad channels in a given epoch while rejecting bad epochs if interpolation was not feasible. Epochs from different experimental blocks were cleaned separately. All EEG preprocessing and analyses are performed using MNE package (Gramfort et al., 2013) in Python (Van Rossum & Drake, 2009).

Time-frequency analysis. For the preliminary time-frequency analysis, we epoched the data from -1s to +2s relative to the stimulus onset. Using Morlet wavelets, we computed a stimulus-locked time-frequency representation for each detected and undetected trial at the Cz electrode. We selected 30 wavelet frequencies on a logarithmic scale between 3 Hz and 45 Hz, with the number of cycles adapted for each frequency ($n_{\text{cycles}} = \text{frequency}/2$). We also applied a log-ratio baseline correction relative to the -0.5s to -0.2s time period.

Event-related potentials. To compare the ERPs in detected and undetected trials, we epoched the data from -0.35s to +1s relative to the stimulus onset and conducted a baseline correction using a time window from -0.25s to 0s. To compare the early potentials (0 to 600ms post-stimulus) evoked by stimuli with different SNRs and conducted baseline correction using a

time window from -0.1s to 0s. We chose to use a shorter baseline in the latter as the period of interest was also shorter.

3.3.5. Time-varying functional connectivity patterns

Resting state. After preprocessing, the extracted ROI time-series were converted into a complex representation using their original signal and the Hilbert transform. The instantaneous phase was calculated by taking the inverse tangent of the ratio of the imaginary and real parts and then by "wrapping" into the $[-\pi, \pi]$ interval. This created a series of instantaneous phases for each ROI. Next, the phase differences between each ROI pair were determined at each time point using cosine similarity, allowing the brain's connectivity configuration at each time point to be represented in an 861-dimensional space (each dimension represented the coherence of a pair of ROIs). Data from all participants were combined and k-means clustering (with k values of 3, 4, 5, 6, and 7) was applied with 1000 repetitions using the Manhattan distance to identify recurrent connectivity configurations. The silhouette method determined that five clusters provided the best classification. The connectivity configuration at each time point (a 42 by 42 phase coherence matrix) was then labeled with one of the 5 cluster centroids. Finally, the participants' brain activity during the scans was represented as a sequence of the five centroids.

Detection task. For each fMRI volume, inter-areal coherence matrices were calculated using the Hilbert transform and cosine similarity as described above. These matrices were then assigned to the closest of the five clusters that were computed using the resting state data.

3.3.6. Statistical analysis

Statistical analyses were conducted in R (R Core Team, 2021) using lme4 (Bates et al., 2015), emmeans (Lenth, 2021), and car (J. Fox & Weisberg, 2019) packages. To account for multiple comparisons, all statistics were corrected using the False Discovery Rate (FDR) Benjamini-Hochberg procedure. Linear mixed models with subject ID as a random factor were used to investigate SNR and Pattern ID on detection rates and reaction times. The statistics for both detection rates and reaction times were calculated at the individual subject level, and the observations in the model were weighted based on the number of trials performed by each participant. Importantly, an arcsine transformation was applied to the detection rates and an inverse transformation was applied to the reaction times (1/RT) to better meet the model assumptions. The assumptions of the linear models were assessed visually through residual distributions and Q-Q plots, and the significance of individual factors was evaluated using

Wald X-Tests. Subject-averaged post-stimulus pattern probabilities were compared between detected and undetected trials using paired Wilcoxon signed-rank tests. Finally, the relationship between pattern probabilities and subjective reports was assessed using Spearman correlations rather than Pearson correlations since they are more suited for ordinal scales such as subjective ratings.

3.4. Results

We investigated how ongoing brain activity emerging from the coordination of different brain regions influenced the perception of threshold auditory stimuli. 25 participants underwent simultaneous EEG and fMRI recordings during an auditory detection task (Figure 3.1). The task involved listening to French vowel (/a/) that were embedded in continuous noise at 3 different signal-to-noise ratios (SNR -11, SNR -9 and SNR -7) around the detection threshold. The sound level was adjusted for each participant via a staircase procedure prior to the task to ensure that they could detect a stimulus with an SNR of -9 in 50% of the trials. They also underwent a resting-state scan before the task.

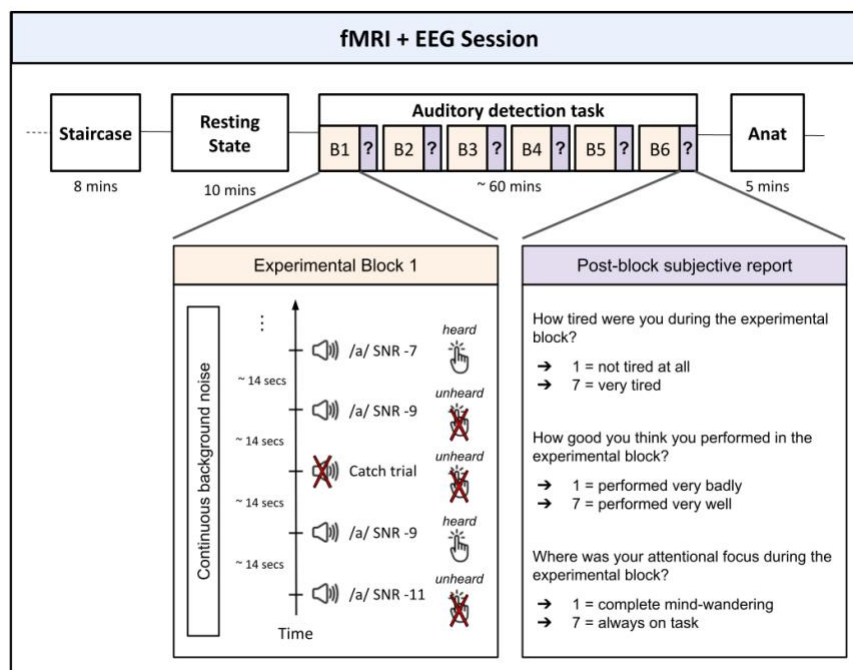


Figure 3.1. Experimental procedure. The experimental session began with a staircase procedure which allowed participants to become familiar with the task and to adjust the stimulus volume such that a stimulus with an SNR of -9 would be detected in 50% of the trials. Following a 10-minute resting state acquisition, participants completed an auditory detection task, during which they heard stimuli embedded in a continuous noise at different SNRs (-7, -9 and -11). They were instructed to press a button if they detected a stimulus. Stimuli were delivered randomly every 14 seconds (± 1 second).

At the end of each experimental block, participants verbally indicated on a scale of 7: (i) how tired they felt, (ii) how successful they think they were during the block, and (iii) their attentional focus during the block (1 for complete mind-wandering and 7 for complete focus on the task).

Using Hilbert transform and k-means clustering, we computed whole-brain connectivity patterns in each fMRI volume obtained during the resting-state scan (Figure 3.2). Our clustering procedure yielded five distinct connectivity patterns. The centroids of the clusters were then used to label the task data. Each task fMRI volume was assigned to the nearest cluster based on their distance to the cluster centroids.

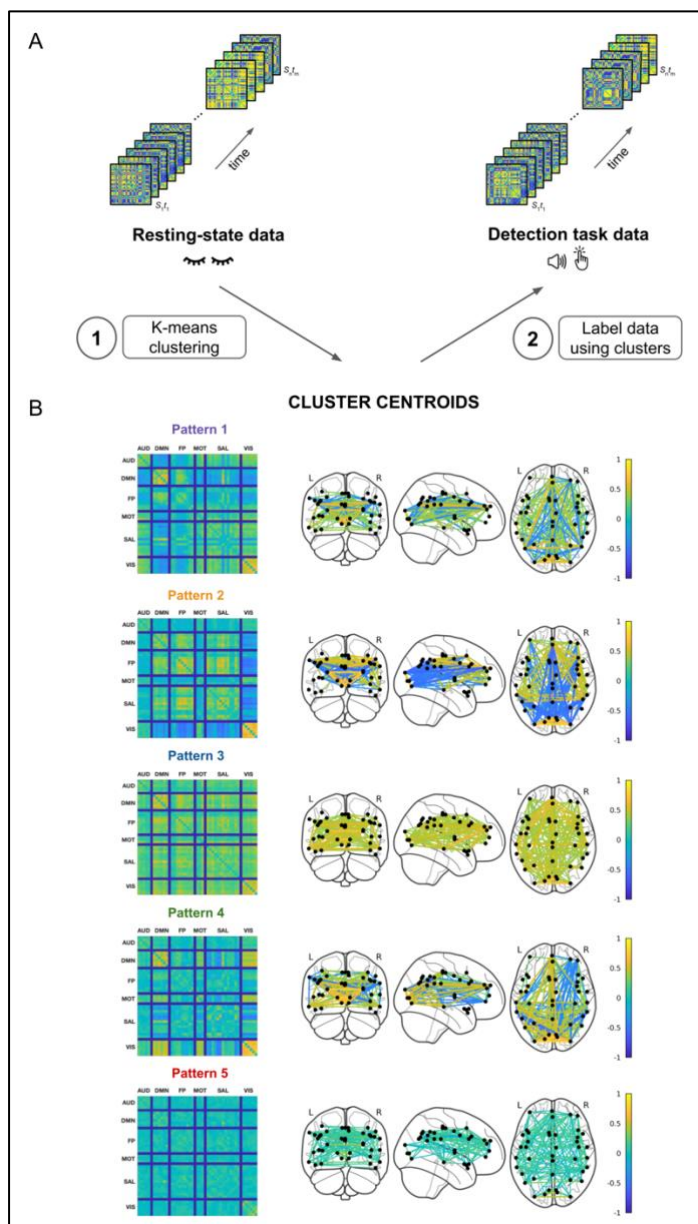


Figure 3.2. Clustering procedure and the cluster centroids. (A) Inter-areal connectivity matrices are computed for each resting state and task fMRI volume. Resting state connectivity matrices are divided into five distinct clusters using k-means clustering (1). The found cluster centroids are then used to classify the task data (2). By calculating the distance between each connectivity matrix from the task and the cluster centroids from the resting state data, the connectivity matrices from the auditory detection task are assigned to the closest of the five clusters. (B) Cluster centroids.

Our first goal was to verify that our clustering method could extract meaningful information from the data. Examples of connectivity configurations resulted from the Hilbert transform as well as the centroids of their respective clusters can be found in Figure 3.3. Although the connectivity configurations were rather sparse and noisy, our clustering procedure successfully identified commonalities among them and resulted in centroids (Patterns) with functional connections respecting the network borders. Interestingly, while Patterns showing inter-areal connectivity (Pattern 1-4) had similar occurrence rates during resting state, Pattern 5 which lacked connectivity, exhibited higher fractional occupancy. To ensure that the identified Patterns were truly representative of the data and not an artifact of the methodology, we generated a surrogate data set and repeated the coherence-based connectivity analyses and the clustering procedure. By randomly shifting the time-series from each ROI and participant, we broke the temporal relationship between different ROIs while preserving the temporal order within each time series. As expected, the connectivity configurations resulting from the surrogate data were sparser than those obtained from the original data. Moreover, the clustering procedure yielded almost identical centroids that lacked inter-areal connectivity and had uniformly distributed occurrence rates (see Figure 3.3, right panel). This control analysis demonstrated that the Patterns identified in the original data were indeed reflective of the brain's connectivity configurations and not driven by the methodology.

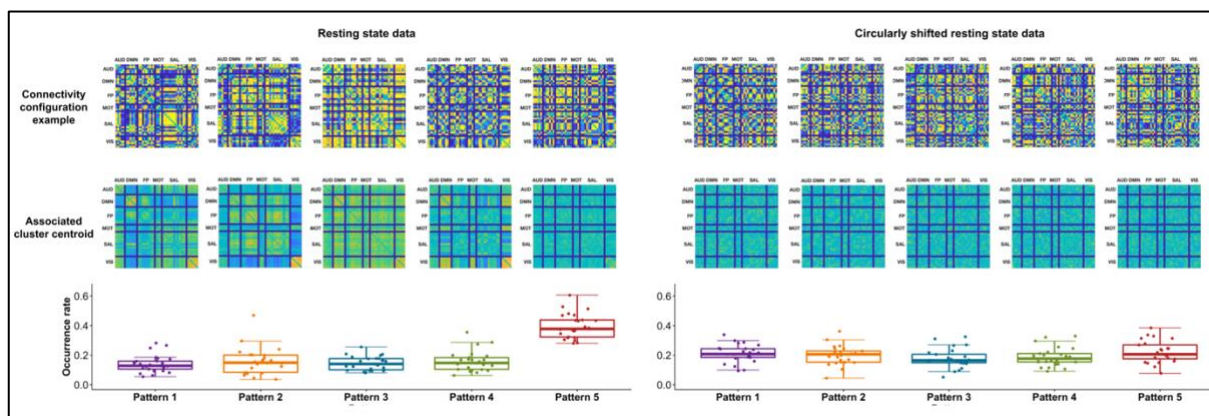


Figure 3.3. Clusters identified in the original and the surrogate data. Examples of resting state (left) and surrogate data (right) coherence matrices (upper panel), their respective cluster centroids (middle panel), and occurrence probabilities of each cluster (lower panel). Each dot represents a participant.

Next, we focused on the task data and hypothesized that the detection rate of the threshold stimuli would vary depending on the connectivity pattern present at the time of presentation. More precisely, we predicted that participants would be more likely to detect the threshold stimuli if they had the connectivity pattern (Pattern 1) which was previously shown to be

associated with conscious states (Demertzi et al., 2019). This would result in a shift of the psychometric curve towards left for the Pattern 1 compared to the other patterns (Figure 3.4A). Moreover, we expected the threshold stimulus to be more easily detected if the previous stimulus was also detected. We tested both hypotheses with a linear mixed model with subject ID as a random effect and pattern ID, SNR and previous stimulus detection status (detected vs. undetected) as fixed effects.

Overall detection rates (all patterns considered) were 0.90 for SNR -7, 0.58 for SNR -9, 0.22 for SNR -11 and 0.002 for catch trials (Figure 3.4B). As hypothesized, we found a significant interaction between the SNR and Pattern ID ($\chi^2(12) = 22.67, p = 0.031$). Detection rates were significantly higher when participants were presenting Pattern 1 (mean = 0.67; median = 0.71) compared to Pattern 2 (mean = 0.55; median = 0.50; $t = 2.69; p = 0.019$, after FDR correction), Pattern 3 (mean = 0.57; median = 0.62; $t = 2.67; p = 0.019$), Pattern 4 (mean = 0.54; median = 0.57; $t = 3.49; p = 0.0042$) and Pattern 5 (mean = 0.57; median = 0.60; $t = 3.34; p = 0.0042$) only for the threshold SNR -9 (Figure 3.4C-D). No significant differences were found in the other SNRs except between Pattern 2 and Pattern 5 at SNR -11 (mean: **0.16 vs. 0.25**; $t = -3.29; p = 0.01$). We also found a main effect of previous detection ($\chi^2(1) = 21.20, p < .0001$), indicating an increased chance of detection if the previous stimulus was also detected, regardless of the pattern ($\chi^2(3) = 6.59, p = 0.086$) and the SNR ($\chi^2(4) = 7.43, p = 0.11$). Then, we assessed whether the reaction time differed depending on the ongoing patterns. Although we did not find any significant differences between patterns, we found a main effect of the SNR ($\chi^2(2) = 276.83, p < .0001$). Not surprisingly, the reaction times were slower for SNR -7 (mean = 1.02s) compared to SNR -9 (mean = 1.10s, $t = -9.43; p < .0001$) and SNR -11 (mean = 1.20s, $t = -13.16; p < .0001$).

To further investigate the dynamic interplay between the ongoing brain patterns and conscious perception, we assessed whether conscious access in turn alters ongoing brain configurations. To do so, we calculated the occurrence probability of each pattern in a 9-second window following the threshold (SNR -9) stimulus presentation and compared the subject-averaged probabilities between detected and undetected trials using Wilcoxon signed-rank test. The occurrence of Pattern 1 increased following detection, with participants being more likely to transition to highly connected patterns after a stimulus detection ($V = 258, p = 0.0088$) (Figure 3.4E). Conversely, we found an increased occurrence of Pattern 4 when participants did not detect the stimuli ($V = 69, p = 0.01$). The occurrence of the other patterns did not differ between

detected (D) and undetected (ND) trials (Pattern 2: $V = 147$, $p = 0.69$, Pattern 3: $V = 138$, $p = 0.52$, Pattern 5: $V = 204$, $p = 0.27$).

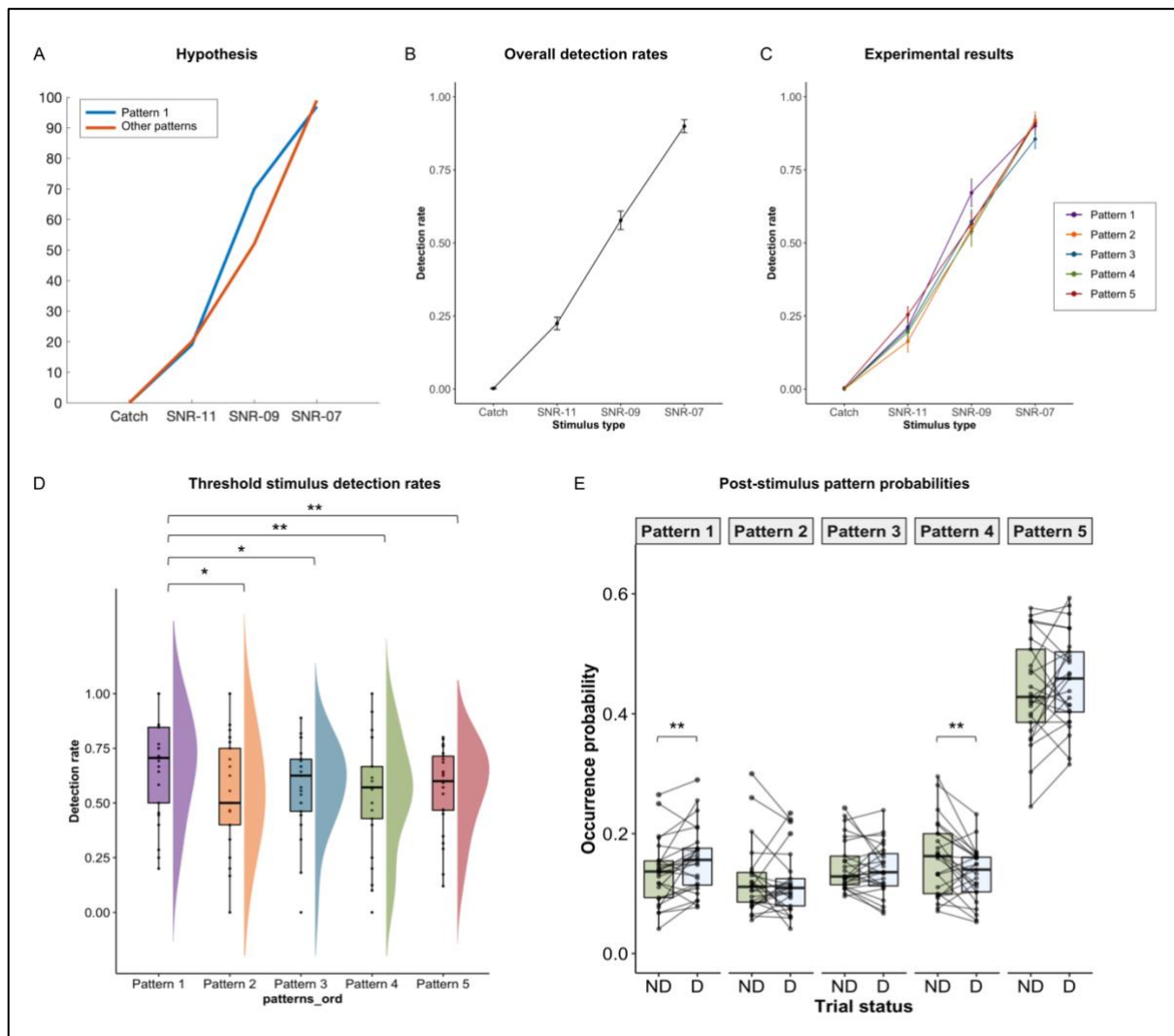


Figure 3.4. Detection rates vary with SNRs and pre-stimulus connectivity configurations. (A) Hypothesis of the experiment. We predicted increased detection rates of the threshold stimulus (SNR - 9) when the highly connected brain pattern (Pattern 1) was present prior to stimulation. (B) Overall detection rates for different SNR. (C) Participant-averaged psychometric curves for each pattern. Error bars indicate the standard error. Participants were more likely to detect the threshold stimulus when displaying Pattern 1 compared to the other patterns. There was no difference in detection rates between the patterns for the other SNRs. (D) Detection rates of the threshold stimulus SNR-09 for different patterns. Pattern 1 was associated with increased detection compared to the other patterns. No difference was found between Patterns 2-5. Each point represents one participant. (E) Subject-averaged pattern probabilities following a detected (D) and undetected (ND) stimulus presentation. The post-stimulus probabilities of Pattern 1 and Pattern 4 varied depending on whether the stimulus was detected or undetected.

Finally, we explored the relationship between these brain patterns and participants' subjective mental states. We asked participants to rate their level of tiredness, success, and attentional focus on a scale of 1-7 after each experimental block. We analyzed the link between participants' ratings and the occurrence probability of each pattern in a given block using Spearman correlations (Figure 3.5). We found a significant correlation between feelings of tiredness and the occurrence of Pattern 4 ($\rho = 0.3$, $p = 0.004$, after FDR correction). Additionally, there was a weaker correlation between tiredness and the occurrence of Pattern 2 ($\rho = 0.2$, $p = 0.048$) and Pattern 5 ($\rho = -0.21$, $p = 0.045$). Moreover, the occurrence probabilities of Pattern 1 ($\rho = 0.21$, $p = 0.045$) and Pattern 3 ($\rho = 0.24$, $p = 0.026$) were positively correlated with the subjective ratings of success and did not vary with changes in tiredness or attentional focus. Interestingly, although we found a significant correlation between subjective success and objective performance (detection rate) in each block ($\rho = 0.29$, $p = 0.00043$), the occurrence probabilities of Pattern 1 and Pattern 3 did not correlate with the overall objective success in the block. However, we observed a weak tendency for Pattern 1 ($\rho = 0.13$, $p = 0.1$).

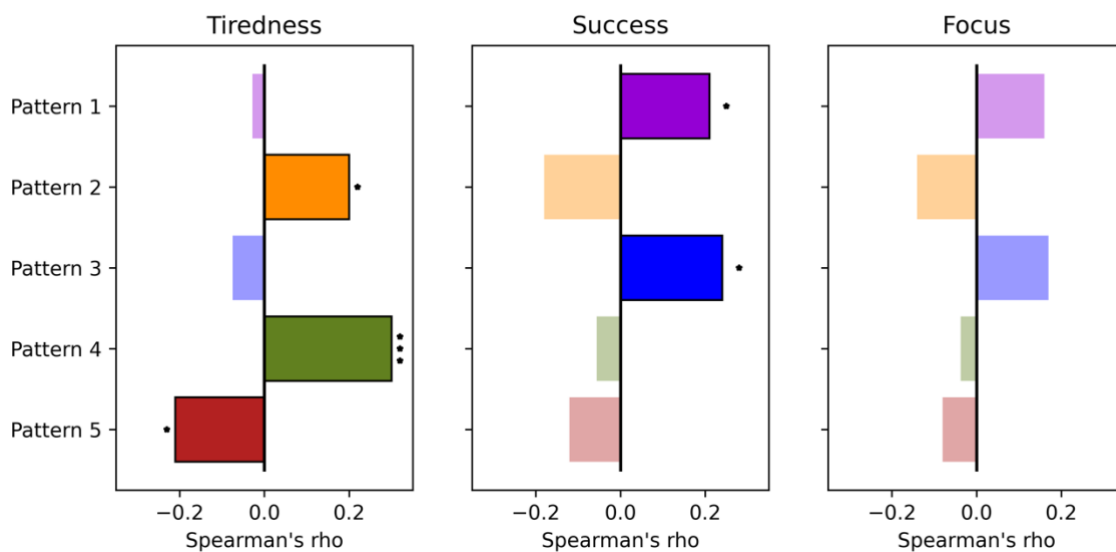


Figure 3.5. Correlations between post-block subjective ratings and pattern occurrence probabilities. Spearman correlation values (x-axis) for subjective ratings of tiredness (left), success (middle), and attentional focus (right). Significant correlations after an FDR correction are marked with stars. Non-significant correlation values are shown as translucent.

Preliminary EEG results

We wanted to further investigate the EEG correlates of these fMRI patterns and to explore how they are modulated with detection of stimuli. Our first step was to ensure that the EEG data we

collected was usable, given that EEG recordings during fMRI scans are often subject to various forms of noise and require cleaning before preprocessing. After visually inspecting the EEG data and examining its power spectrum, we assessed some commonly observed EEG features, such as auditory potentials, the P3 component, and the readiness potential that arise when an auditory stimulus is detected, as well as changes in the time-frequency representation of the data. Observing these effects would verify the quality of the EEG signal and encourage us to conduct more detailed analyses by considering the fMRI patterns.

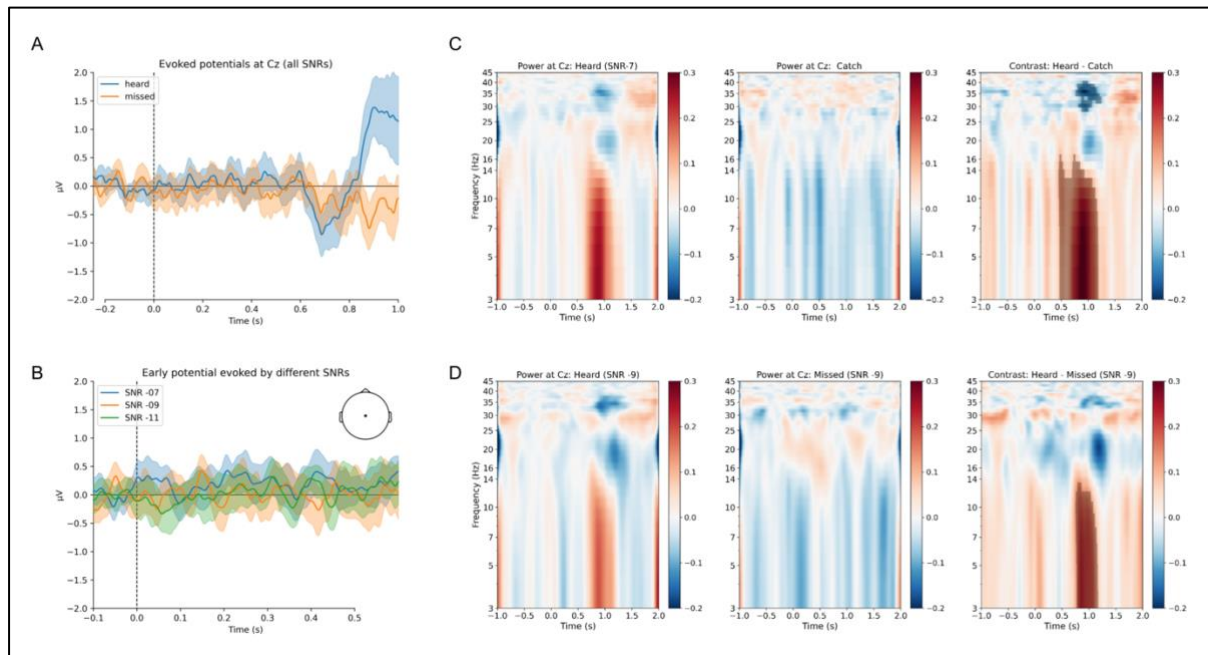


Figure 3.5. Brain responses to auditory stimuli measured from the EEG recordings. (A) Potentials at the Cz electrode evoked by the stimulus in detected (heard, in blue) and undetected (missed, in red) trials. ERPs were computed at the subject level with all stimuli (SNR -7, SNR -9 and SNR -11) combined. Shades represent the 95% confidence intervals. (B) Potentials at the Cz electrode evoked by the stimuli with different SNRs (SNR -7 in blue, SNR -9 in red, and SNR -11 in green), regardless of the detection status of the trials. (C) Time-frequency decomposition of power at the Cz electrode for detected trials at SNR -7 (left), for catch trials (middle) and their contrast (right). Statistical significance is marked with darker shade. (D) Time-frequency decomposition of power at the Cz electrode for detected trials at SNR -9 (left), undetected trials at SNR -9 (middle) and their contrast (right). Statistical significance is indicated by darker shade.

To begin, we computed stimulus-locked potentials evoked by detected and undetected trials, regardless of the signal-to-noise ratio (SNR) and ongoing fMRI patterns (Figure 3.5A). Although we observed a clear response related potential, we did not find any early auditory or P3 components. To further examine the possible changes in the early ERP components, we computed potentials evoked by stimuli with different SNRs, regardless of detection status or

ongoing fMRI patterns (Figure 3.5B). We expected to see a gradient of potentials increasing with the detectability of the stimulus, but surprisingly, we did not observe any differences in the ERPs caused by stimuli with different SNRs. Finally, we explored the time-frequency representation of the detected and undetected trials. Figure 3.5C shows the time-frequency decomposition of power at the Cz electrode for detected trials (SNR -7) and catch trials, and Figure 3.5D shows the contrast between detected and undetected trials for the threshold SNR - 9. In both cases, we found an increase in power for low frequencies (delta, theta and alpha) and a decrease in power in the higher frequencies (beta and gamma) in the detected trials, starting from 600ms after stimulus presentation. These power changes were most likely linked to the motor preparation. We did not observe any earlier changes in the EEG power. The lack of early EPRs and power changes are discussed in the following section.

3.5. Discussion

Our study provides compelling evidence that our ability to process external information is influenced by our ongoing brain connectivity pattern. Participants were more successful in detecting threshold auditory stimuli when they exhibited brain patterns associated with conscious states (Demertzi et al., 2019) before the stimulation. It's worth noting that this increase in performance was only observed for threshold stimuli; the detection rates for supra- and sub-threshold stimuli were not affected by the preceding brain pattern. This may be because sub-threshold stimuli do not provide enough bottom-up information to trigger ignition (Dehaene et al., 2006) and supra-threshold stimuli are strong enough to provoke ignition regardless of the ongoing brain pattern. Therefore, threshold stimuli provide a sweet spot where changes in brain connectivity can impact the processing of stimuli and give rise to conscious access when the brain state is favorable.

In previous studies, threshold stimuli were used to examine the impact of baseline brain activity on conscious perception (Busch et al., 2009; Hesselmann, Kell, Eger, et al., 2008; Hesselmann, Kell, & Kleinschmidt, 2008; Ploner et al., 2010; Wyart & Tallon-Baudry, 2009). However, all of these studies focused on the variations in the local activity within task-related regions. While these localized activities can provide information on the excitability of the task-related regions, their connection to consciousness is difficult to establish. Most current theories of consciousness suggest that perceptual awareness arises from long-range interactions between different brain regions (Dehaene & Changeux, 2011b; Brown et al., 2019; Mashour et al., 2020; Pennartz, 2022). In order to test the predictions of these current theories, it is essential to

investigate how the coordination of different brain networks affects conscious perception. Our results align with the global theories of consciousness, as opposed to local theories of consciousness (Lamme, 2006, 2010), by demonstrating that some long-range connectivity configurations are more favorable for conscious perception.

Our findings not only demonstrate the influence of ongoing brain patterns on conscious perception but also reveal that conscious perception, in turn, can impact ongoing brain patterns. Specifically, participants were more likely to transition to highly connected patterns following the detection of the threshold stimulus. It has been recently shown that the processing of high-level stimuli, such as audio-visual movies, can impact ongoing brain connectivity dynamics (Türker et al., 2023). Taken together, these results highlight the complex interplay between ongoing brain dynamics and conscious perception, in which they mutually influence each other.

Another interesting finding was the fact that Pattern 4 occurred more frequently following undetected trials. In other words, participants were less likely to exhibit Pattern 4 if they had detected the threshold stimulus. This result is consistent with the subjective ratings of tiredness, as we found a significant correlation between the occurrence probability of Pattern 4 and how tired participants felt in a block. If this brain pattern is indeed associated with tiredness, it would explain the increased occurrence of the pattern when participants were unable to detect the threshold stimulus, potentially due to fatigue. However, we did not observe a predictive effect of this pattern on subsequent detection, meaning that displaying such a pattern did not decrease detection rates. Additional research is necessary to clarify this point. On the other hand, several other results provided a more coherent and convincing picture, indicating a strong link between Pattern 1 and the capacity for conscious perception: the enhanced performance following Pattern 1, the correlation between the occurrence of Pattern 1 and subjective success in the task, and finally the increased occurrence of Pattern 1 following detection.

In a recent study, Mortaheb and colleagues investigated the relationship between ongoing brain connectivity and participants' ongoing mentation (Mortaheb et al., 2022). The authors found that mind blanking - a wake state without any mental content, was associated with brain patterns exhibiting positive connectivity among different brain regions, a pattern also observed in our study (Pattern 3) and in a prior study (Demertzi et al., 2019). Previous research has linked mind blanking to sluggish responses in sustained attention tasks (Unsworth & Robison, 2016; Andriillon et al., 2021). In light of this literature, we would have expected to observe longer

reaction times when participants exhibited this positively connected pattern, indicating potential mind-blanking. However, we did not find such an effect in our study. It is important to note some important differences between Mortaheb et al.'s study and ours. Unlike Mortaheb's study, our study wasn't specifically designed to explore mind blanking. We didn't include any direct probes about mind blanking, but rather only asked participants about their mind wandering at the end of each block. Moreover, while reaction times can serve as an indirect measure of mind blanking, subjective reports offer more direct evidence. In the future, combining both our and Mortaheb's paradigms could offer a more comprehensive understanding of how ongoing brain and mental states interact with the ability to perceive the external world.

Our study takes a distinct approach from prior research in this field. While previous studies typically compared pre-stimulus brain activity in detected versus undetected trials (Ergenoglu et al., 2004; Boly et al., 2007; Hesselmann, Kell, & Kleinschmidt, 2008; Hesselmann, Kell, Eger, et al., 2008; Monto et al., 2008; Busch et al., 2009; Wyart & Tallon-Baudry, 2009; Sadaghiani et al., 2009; Ploner et al., 2010; Pincham & Szűcs, 2012; Sadaghiani et al., 2015; Baria et al., 2017), we opted for a hypothesis-driven approach by independently labeling brain patterns, regardless of the trial outcome. Rather than looking for differences in brain activity between detected and undetected trials, we predicted and showed that certain pre-defined brain activity configurations can enhance conscious perception. By doing so, we were able to demonstrate that specific brain patterns are relevant for both conscious access and conscious states, unifying these two areas of research that are often investigated separately.

Our study also replicated the brain connectivity patterns observed during rest in prior publication (Demertzi et al., 2019; Türker et al., 2023). Despite using different MRI scanners and scanning different populations, our findings were consistent with the prior study, suggesting that our method is capable of producing reliable results despite variations in experimental conditions. Some may argue that the similarity between the two studies could be attributed to an inherent feature of our method, rather than experimental data. To rule out this possibility, we tested our clustering method on surrogate data that shared the same features as our original data set. This control analysis yielded completely different connectivity patterns from the original ones, lacking all types of connectivity, as expected. Therefore, we can confidently state that we successfully replicated previous results using a different experimental setup.

It is reasonable to question why Pattern 5, which has been associated with unconscious states in Demertzi et al., did not affect conscious perception. One might expect a decrease in perceptual abilities when participants exhibited this connectivity pattern. We speculate that pattern could be the centroid of a "default cluster," where connectivity patterns are assigned if they don't belong to other clusters, rather than a cluster reflecting unconsciousness. This would explain why this pattern occurs so frequently (around 40%) in healthy controls in both the current and previous research. However, it's possible that unconscious patients do also show brain activity lacking inter-areal connectivity, which would increase the frequency of this pattern (around 55% in minimally conscious patients and 70% in vegetative state patients in Demertzi et al., 2019). A more detailed study of the patterns assigned to this cluster can help us understand why they're attributed (whether they truly lack coherence or are assigned by default because they don't fit into any other cluster) and shed light on what this cluster really represents.

To conduct our study, we had to overcome several technical obstacles. One significant challenge was the presentation of auditory threshold stimuli during fMRI scans due to the scanner noise. To address this, we used a staircase procedure to identify a personalized threshold for each participant that resulted in ~50% detection for stimuli with SNR -9. This procedure was conducted prior to the task while fMRI data was being acquired. For those interested in implementing a staircase procedure in the scanner environment, our custom script can be accessed [here](#). Additionally, acquiring simultaneous fMRI and EEG data is demanding due to the cardio-ballistic and gradient artifacts on the EEG. Although there are methods to correct for these artifacts (Allen et al., 2000), residual artifacts may still exist. Therefore, it is essential to find ways to minimize artifacts during data acquisition. During our pilot acquisitions, we tested various strategies and discovered that turning off the helium pump and fMRI ventilation helped minimize these artifacts. Consequently, we advise researchers who plan to perform simultaneous fMRI-EEG acquisitions to consider implementing these strategies if possible.

Our preliminary EEG results showed clear changes in the ERPs and time-frequency analysis due to motor response preparation. However, contrary to our initial hypothesis, we did not observe any effects in the earlier time-window associated with auditory processes or conscious access, such as P3 (Sergent et al., 2005; Del Cul et al., 2007; Bekinschtein et al., 2009). It is possible that the small changes induced by weak stimuli were not detectable in our EEG data,

as the auditory system was continuously stimulated by the scanner and background noise. Additionally, the target stimuli were relatively weak, and the EEG acquisitions were conducted inside the fMRI scanner, which may have made it challenging to detect target-induced weak brain responses due to the noise in the EEG signal.

There are several steps we plan to take in order to further our research. Firstly, we aim to develop better methods for denoising the EEG data, which will allow us to observe classical EEG effects and investigate how ongoing fMRI patterns influence EEG responses evoked by stimulation. Additionally, we will conduct further EEG analyses, such as inter-trial phase coherence, as they may be detectable in the absence of ERP or power effects (Andrillon et al., 2015). We also intend to explore EEG correlates of ongoing connectivity patterns using resting-state data. Specifically, we will assess how different spectral, complexity, and connectivity measures, which have previously distinguished between conscious and unconscious states (King et al., 2013; Sitt et al., 2014), vary with fMRI patterns. Since EEG is a low-cost, portable, and easy-to-use tool for clinical evaluation of patients with disorders of consciousness, identifying electrophysiological correlates of fMRI patterns would facilitate the translation of our research to a medical context. Furthermore, our study has opened up possibilities for other exciting research projects that examine how fluctuations in the ability to perceive external information from different modalities occur. Given the significance of these brain configurations for both conscious access and conscious states, we believe that the observed results are not limited to the auditory domain alone. We anticipate that future studies will demonstrate that perception of stimuli from other modalities, such as visual or somatosensory, would be similarly affected by these ongoing patterns.

The results of our study indicate that ongoing patterns of brain connectivity, which are associated with conscious states, may play a functional role in shaping conscious experience by altering the capacity to perceive external information. In the future, identifying these periods of high-connectivity patterns in individuals with consciousness disorders could enable us to identify periods of increased sensitivity to the external world, paving the way for personalized patient-care protocols.

CHAPTER IV

BRAIN AND BEHAVIORAL DYNAMICS IN SLEEP

“We had been talking with Emma about the extent to which sensory stimuli could be integrated into a dream. She was much more optimistic than I was, but my opinion changed one summer night in Turkey. I was at my aunt's summer house when I fell asleep, directly into a lucid dream. This was not unusual for me as I was used to having lucid dreams at the sleep onset. As usual, I got out of the bed and started walking around, exploring the room, touching the objects around me to see how they felt in the dream. Suddenly, I realized that a strange cloud with a zebra pattern was floating in front of my eyes. It was impossible to escape it, as it followed my head movements and was always in front of me wherever I looked. I tried to touch it but I couldn't. My hand passed through it: not because it was a cloud, but because it was not there. Although I could still see it, it felt like it was not part of the environment, as if it existed in another reality. It was a strange feeling. I felt a little overwhelmed and decided to wake up. The moment I woke up I realized that my pillowcase had that zebra pattern, and that I had slept with my eyes half open. I had not noticed the pillowcase before falling asleep and it was a real surprise to realize that it had somehow been integrated into my dream. I called Emma the next morning to tell her that her intuition was right, as it usually is.”

**BEHAVIORAL AND BRAIN RESPONSES TO VERBAL STIMULI
REVEAL TRANSIENT PERIODS OF COGNITIVE INTEGRATION OF
EXTERNAL WORLD DURING SLEEP**

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4.1. Abstract

Sleep has long been considered as a state of behavioral disconnection from the environment, without reactivity to external stimuli. Here, we questioned this sleep disconnection dogma by directly investigating behavioral responsiveness in 49 napping subjects (27 with narcolepsy and 22 healthy volunteers) engaged in a lexical decision task. Participants were instructed to frown or smile depending on the stimulus type. We found accurate behavioral responses, visible via contractions of the corrugator or zygomatic muscles, in most sleep stages in both groups (except slow-wave sleep for healthy volunteers). Across all sleep stages, responses occurred more frequently when stimuli were presented during high-cognitive states than during low-cognitive states, as indexed by EEG before the stimulus. Our findings suggest that transient windows of reactivity to external stimuli exist during bona-fide sleep, even in healthy individuals. Such windows of reactivity could pave the way for real-time communication with sleepers across all sleep stages to probe sleep-related mental and cognitive processes.

4.2. Introduction

Sleep has classically been considered as a time when we cannot react to external stimuli. However, congruent evidence from event-related potentials (Bastuji & García-Larrea, 1999; Ruby et al., 2008; Strauss et al., 2015), fMRI (Issa & Wang, 2011), or intracranial recordings (Nir et al., 2015) have shown that at least low-level sensory processing is preserved across sleep stages. Further studies indicated that sleepers can even process symbolic stimuli at different cognitive levels of representation, including semantic and decisional stages (Kouider et al., 2014; Andrillon et al., 2016; Andrillon & Kouider, 2020; Xia et al., 2023). Moreover, learning-related sensory cues presented during sleep positively impact subsequent recall of cue-related material upon awakening (Oudiette & Paller, 2013; Rasch et al., 2007; Rudoy et al., 2009) and can even influence participants' behavior (e.g. smoking reduction) a week later (Arzi et al., 2012, 2014). Recent studies suggest that word association learning during sleep is possible (Ruch et al., 2022; Züst et al., 2019) and could generalize into wakefulness in a cross-modal manner (Koroma et al., 2022). While all these examples of sensory processing during sleep are thought to occur automatically and unconsciously, some studies have shown an incorporation of sensory stimuli into reported dream content (Konkoly et al., 2021; Solomonova & Carr, 2019), suggesting that, at least sometimes, external stimuli could be processed up to conscious level during sleep. However, the lack of single trial evidence of stimulus integration during sleep complicates the exploration of the neurophysiological basis of this complex and variable phenomenon. Obtaining behavioral responses that serve as real-time indicators of subjective reports could allow us to analyze brain dynamics associated with sensory and cognitive integration in a trial-by-trial manner.

Because behavioral responses have long been assumed to be possible only during wakefulness, they are either rejected from the analysis (Andrillon et al., 2016; Comsa et al., 2019) or not collected at all in sleep studies. The rare studies which measure behavioral responses in sleeping participants discovered manual behavioral responses during N1 sleep (Canales-Johnson et al., 2020; Jagannathan et al., 2022; Ogilvie, 2001; Strauss et al., 2015, 2022), but not in deeper sleep stages. However, the loss of limb muscle tone could mask behavioral responses during consolidated sleep. Facial muscles, which are less affected by muscle atonia than the limbs (Rivera-García et al., 2011), could be more suited for assessing behavioral responsiveness. For example, eye movements persist during REM sleep and can be used to signal lucidity in people who are aware of dreaming while asleep (Konkoly et al., 2021; LaBerge et al., 1981) (i.e.: lucid dreamers). Combining eye movements and

zygomatic/corrugator contractions, we showed that lucid dreamers could respond to queries sent during their dreams in polysomnography-verified REM sleep (Konkoly et al., 2021).

In the present work, we capitalized on this research strategy to further question the behavioral disconnection dogma in sleep and explore stimuli integration at the behavioral and neurophysiological levels. Based on our previous results (Konkoly et al., 2021), we reckoned that such responsiveness would most likely occur during lucid dreaming. We aimed to first assess behavioral responses during lucid REM sleep, then test whether these results could extend in non-lucid REM sleep and other sleep stages. We recruited 27 participants with narcolepsy, - who present excessive daytime sleepiness, a short REM sleep latency, and a high frequency of lucid dreams (Dodet et al., 2015), making them an ideal population to collect multiple lucid dreams in the lab (Oudiette et al., 2018). We additionally recruited 21 healthy participants (non-lucid dreamers). Participants were explicitly instructed to perform an auditory lexical decision task while napping by frowning or smiling three times depending on the stimulus type (word versus pseudo-word). Facial EMG on corrugator and zygomatic muscles was recorded in addition to usual polysomnography signals.

We discovered that behavioral responses were possible across most sleep stages including N2 sleep and non-lucid REM sleep, both in participants with and without narcolepsy. Regardless of the group or sleep/wake stages, responsiveness was associated with previously validated electrophysiological markers of higher cognitive states. Finally, we found electrophysiological and subjective (post-nap reports) evidence for a conscious processing of external stimuli during lucid REM sleep. Our findings demonstrate that sleepers can transiently process external stimuli at a high-cognitive level and behaviorally respond to them across most sleep stages.

4.3. Material and methods

4.3.1. Participants

Participants with narcolepsy. Thirty participants with narcolepsy were recruited for this study (14 women, mean age: 35 ± 11 years) from the patients followed in the National Reference Center for Narcolepsy in the Pitié-Salpêtrière Hospital. Twenty-four of them (80%) were frequent lucid dreamers who reported more than 3 lucid dreams per week on average (others reported less than 1 lucid dream per year). Participants met the international criteria for narcolepsy, including (i) excessive daytime sleepiness occurring daily for at least 3 months; (ii) a mean sleep latency lower than or equal to 8 min and two or more sleep onset REM sleep

periods on the multiple sleep latency tests (5 tests performed at 08:00, 10:00, 12:00, 14:00, and 16:00; and (iii) no other better cause for these findings, including sleep apnea syndrome, insufficient sleep, delayed sleep phase disorder, depression, and the effect of medication or substances or their withdrawal. They were required to pause their medication for the day of the experiment to facilitate sleep onset. We recruited patients with narcolepsy type 1 ($n = 17$, with clear cataplexy or hypocretin deficiency) and type 2 ($n = 13$, no cataplexy or hypocretin deficiency). Among the 30 participants, 3 (2 women) were discarded from the analyses because of technical issues affecting the recordings. In total, data from 27 participants with narcolepsy (21 frequent lucid dreamers) were analyzed in this study.

Healthy participants. Twenty-two healthy participants (all non-lucid dreamers) were recruited for this study (10 women, mean age: 24 ± 4 years). They had no or little experience with lucid dreaming (less than two lucid dreams in their lives). They had no sleep disorder and were in good shape, as assessed by a sleep clinician. To further facilitate sleep onset, we asked participants to sleep about 30% less than usual during the night preceding the experiment (either by going to bed later or waking up earlier) and to avoid stimulants on the day of the experiment. Fourteen went through the experiment in the morning and eight of them went through the experiment in the afternoon. One participant was discarded from the analysis because of technical issues affecting the recordings.

All participants were native French speakers and gave written consent to participate in the study. The protocol had been approved by the local ethics committee (CPP Ile-de-France 8). Participants with and without narcolepsy were paid €200 and €70 respectively, as compensation for their participation in the study (participants with narcolepsy also took part to an unrelated experiment the following day; the results of this second study are not described here).

4.3.2. Experimental design

In this study, we tested participants' ability to perceive, discriminate, and respond to auditory stimuli while asleep. Participants lied in a bed in a sound attenuated room in the sleep unit. They were asked to perform a lexical decision task in which words and pseudo-words were verbally presented in a pseudo-randomized fashion. Participants with narcolepsy went through five 20-min naps, with an 80-min break between each nap (Figure 4.1). Before the experiment, participants underwent a short training (10 min) to familiarize themselves with the type of

stimuli and the task (10 repetitions). Stimulus presentation volume was 48 dB on average and adjusted for each participant during the training period. Each nap session contained ten “ON” stimulation periods during which 6 stimuli (3 words and 3 pseudo-words) were presented every 9 to 11 seconds on top of continuous white noise presented throughout the nap. Each stimulus was presented only once in the entire experiment. The “ON” stimulation periods were separated by 1 min non-stimulation periods (OFF periods) during which only white noise was presented. Following a previously validated response paradigm during sleep (Konkoly et al., 2021), participants were instructed to decide whether the stimulus was a word or a pseudo-word and indicate their response by making three, brief, successive contractions of either the corrugator (frowning) or the zygomatic (smiling) muscles, depending on the stimulus type (e.g., contracting the corrugator if they heard a pseudo-word and the zygomatic if they heard a word). The muscle-stimulus association was counterbalanced across participants. Importantly, the stimulation started when the subjects were still awake, but participants were explicitly authorized to fall asleep while performing the task. They were asked to perform the task before falling asleep, if they woke up during a nap, and if they heard the stimuli in their sleep. If participants were lucid dreaming but did not hear any stimuli (word or pseudo-words), they were instructed to communicate their lucidity with a "mixed" signal, alternating a single corrugator muscle and a single zygomatic muscle contraction. Note that we chose not to use the gold-standard method to signal lucidity here (Left-Right-Left-Right ocular code) for three reasons: i) the ocular code ‘pollutes’ the EOG channel, which might lead to bias when scoring REM sleep, ii) several lucid dreamers with narcolepsy explicitly told us that facial codes were easier to perform, less disturbing of the ongoing dream, and less awakening than the ocular code, and iii) our experiment required three different codes (one for each stimulus type and one for signaling lucidity if no sounds were heard). After each nap, participants were awakened by an alarm that rang until they pressed a button. They were asked to report ‘what was going through their mind’ before the alarm and indicate whether i) they had a lucid dream, ii) they communicated their lucidity with the mixed-signal, iii) they heard the stimuli during the nap, iv) they responded to the stimuli, and v) they remember any stimuli (word or pseudo-word) from the nap (free recall). Finally, participants performed an old-new recognition task, during which they were presented with stimuli they heard during the preceding nap and new stimuli that were never presented during the experiment. Participants had to indicate whether they had heard the stimuli during the preceding session with one of the following responses: 1: I heard it from the dream (for example, a person from their dream saying the word), 2: I heard it from the outside world (pronounced by the computer), 3: I am not sure I heard it, 4: I am sure I did

not hear it. They responded by pressing the corresponding button without any time pressure. The four options were explained to the participants during training, prior to the first session.

Healthy participants went through the same procedure except that the 5 naps were combined into a single, longer, 100-min daytime nap.

4.3.3. Stimuli

Stimuli were French words and pseudo-words pronounced by a female voice, taken from the MEGALEX database (Ferrand et al., 2018). All stimuli were controlled for their duration (690ms) and the words were controlled for their frequency and valence. Five distinct lists (one for each nap session) of sixty stimuli (thirty words and thirty pseudo-words) were created for each participant in a randomized fashion. Participants heard each stimulus only once during the day. Stimuli were presented through speakers using the Psychtoolbox extension (Brainard, 1997) for MATLAB (The MathWorks). Stimuli were played every 9–11 s (random uniform jitter) after a 60 second OFF period (without stimuli). Button-press responses in the old-new recognition task were collected through a regular keypad.

4.3.4. Electrophysiological recording

Electroencephalography (EEG, 10 channels: Fp1, Fp2, Cz, C3, C4, Pz, P3, P4, O1, O2, referenced to the right mastoid (A2 electrode); 10–20 montage), electrooculography (EOG, 2 channels, positioned above the right superior canthus and the left inferior canthus), electromyography (EMG, 1 channel on chin muscle for sleep staging, 1 channel on zygomatic and 1 channel on corrugator muscles for recording participants' behavioral responses) and electrocardiography (ECG, 1 channel) were continuously recorded during the nap sessions. All signals were recorded simultaneously at a 2048 Hz sampling rate. EEG data were amplified through a Grael 4K PSG:EEG amplifier (Medical Data Technology, Compumedics Ltd, Australia).

4.3.5. Sleep scoring and identification of muscular responses

Sleep scoring. Sleep stages were scored offline by a certified sleep expert according to established guidelines (Berry et al., 2017) using Profusion software (COMPUMEDICS, Medical Data Technology). For scoring, the EEG and EOG signals were filtered between 0.3 Hz and 15 Hz, the EMG and ECG signals were filtered between 10Hz-100Hz and 0.3Hz-70Hz, respectively. A 50 Hz notch filter was applied on all channels. Sleep scoring was visually

performed on 30-second time epochs, each scored as wakefulness, N1, N2, N3, or REM sleep, according to the AASM international rules. Detailed information on the sleep characteristics can be found in Table S12. Micro-arousals were scored when alpha rhythm was present during more than 3 sec and less than 15 sec (if longer, the epoch was scored as wake) and, in REM sleep, when there was an increase in chin muscle tone in addition to the alpha rhythm. Trials containing micro-arousals were excluded from further analyses. A nap was considered lucid based on the subjective report (if the participant reported having a lucid dream during the nap). In this case, all REM sleep epochs of this nap were then considered as lucid REM sleep. Note that healthy participants never reported having a lucid dream.

Identification of muscular responses. The recording of the nap was divided into 120 mini-epochs of 10 seconds. The sleep stage for each mini-epoch was defined by the sleep score of the corresponding 30-second epoch. Mini-epochs containing a micro-arousal were discarded from the analyses. The presence of zygomatic or corrugator muscle contractions was assessed visually, looking offline at the EMG signal for each mini-epoch. Importantly, the scorer was blind to the sleep stage and to whether a stimulus was presented during the mini-epoch (corresponding to an ON period) or not (corresponding to an OFF period). Muscle contractions were considered as a response if they contained at least two consecutive contractions. Single contractions were considered as a twitch and scored as a no-response. To ensure the quality of the scoring, 10% of the data was later re-evaluated by another blind scorer who showed 84% consistency with the first scorer.

4.3.6. EEG preprocessing and analysis

Only the EEG segments corresponding to the “ON periods” were analyzed.

4.3.6.1. Preprocessing

Raw files were set to a right mastoid reference (A2 electrode).

Following previous work (Sitt et al., 2014), raw EEG files were band-pass filtered between 0.1 and 45Hz, with 50Hz and 100 Hz notch filters. Data was down-sampled to 250Hz. Trials were then segmented in the following way:

- from -1000 ms to 8000 ms relative to stimulus-onset for raw spectral analyses (power spectral densities in the pre- and post-stimulus periods)

- from -1000 ms to 4000 ms relative to stimulus-onset for event related potentials (ERPs) and time-frequency analyses.
- from -350 ms to 1700 ms for temporal generalization decoding against baseline analysis.
- from -1000 ms to 0 ms relative to stimulus-onset for computation of electrophysiological markers of higher cognitive states and related machine learning analyses.

The obtained epochs were cleaned, based on their voltage maximum peak-to-peak amplitude, using a fully automatic procedure via autoreject algorithm (Jas et al., 2017). The Python (Van Rossum & Drake, 2009) implementation of the autoreject algorithm allows for the automatic calculation of an optimal global rejection threshold for a set of epochs, using a cross-validated machine learning algorithm. For each wake/sleep stage in our data (Wake, N1, N2, N3, and REM sleep), we calculated a separate global rejection threshold (the same for all participants in each group for a given sleep/wake stage) and we rejected all trials with at least one EEG channel exceeding the given threshold. Note that this drastic rejection method was associated with high rejection rates but ensured the quality of our data. More conservative automatic cleaning methods such as interpolation of bad channels were not applicable to our 10 channels EEG montage. All epochs from two participants with narcolepsy were rejected due to our strict rejection criterion. Therefore, only 25 participants with narcolepsy were included in the EEG analyses.

All trials were labeled as belonging to a particular *sleep/wake stage* (Wake, N1, N2, N3, or REM sleep) according to the sleep scoring described above (corresponding 10s mini-epoch), as being *responsive* or *non-responsive* according to the presence or absence of a valid behavioral response (corrugator or zygomatic muscle contraction), and as *lucid* or *non-lucid* according to the global label of the nap (cf. above).

4.3.6.2. Spectral analyses of pre- and post-stimulus periods.

We computed the power spectral densities (PSDs) in delta (1-4Hz) and alpha (8-12 Hz) frequencies bands using Welch's method. The length of each Welch segment (windowed with a Hamming window) was set to be equal to the length of the FFT (Fast Fourier Transform) and equal to 250 samples (1000ms). The obtained segments were then averaged, in order to obtain a single value per epoch, channel and frequency. To obtain the normalized PSDs in each frequency band of interest (alpha and delta), we: 1) added the raw power of all the frequencies

in each frequency band of interest; 2) computed for each trial and each electrode the normalized PSD by normalizing the raw frequency band PSD by the total power of the given electrode; 3) averaged all the channels to obtain a single PSD value per frequency band per trial.

4.3.6.3. Time-frequency analysis

We computed single-trial stimulus-locked time-frequency representation for each group and each sleep/wake stage using Morlet wavelets. We choose the wavelets frequencies ($n = 30$) on a logarithmic scale with a lower bound of 2 Hz and an upper bound of 30 Hz (frequencies: 2, 2.2, 2.4, 2.6, 2.9, 3.2, 3.5, 3.8, 4.2, 4.6, 5, 5.6, 6.1, 6.7, 7.4, 8.1, 8.9, 9.8, 10.7, 11.8, 12.9, 14.2, 15.6, 17.1, 18.8, 20.6, 22.7, 24.9, 27.3, 30 Hz). The number of cycles was adapted to each frequency ($n_{\text{cycles}} = \text{frequency}/2$). For computational reasons, we applied a decimation factor of 2 before conducting this analysis. We obtained a time-frequency power matrix for each trial and each electrode. We then applied a log-ratio baseline correction relative to the -1000 to 0ms time-period. For statistical analysis on predefined frequency-bands (delta: 2-4Hz, alpha: 8-12 Hz, and beta: 12-30 Hz), we extracted the total power in the given frequency band for each time sample and conducted a mass-univariate analysis over the time dimension for each electrode (see statistical analysis).

For response-locked time-frequency analysis, we realigned the baseline-corrected time-frequency matrices relative to the behavioral response onset. The new realigned trials spanned from -1500ms to 1000ms relative to response onset (we dropped for further analysis all trials with insufficient time-points either before or after response onset).

4.3.6.4. Response-locked event related potentials

After baseline correction (-1000 to 0ms relative to stimulus onset), we realigned time-domain signals of responsive trials relative to the behavioral response onset. We then averaged trials to obtain event related potentials, independently for each group and each sleep/wake stage. For visualization purposes, we applied a low-pass filter of 10Hz before plotting the obtained response-locked event related potentials.

4.3.6.5. Electroencephalographic markers tracking cognitive modifications

Previous work has shown that cognitive and consciousness state modifications can be tracked using different spectral, connectivity, or complexity measures derived from the scalp or intracranial electroencephalographic recordings. By combining these markers, it is possible to

distinguish conscious participants, patients in a minimally conscious state, and patients with unresponsive wakefulness syndrome (King et al., 2013; Sitt et al., 2014). These measures can also differentiate sleep stages (REM sleep and wakefulness *versus* N3) (Bourdillon et al., 2020) and track cognitive and consciousness modifications related to psychedelics or meditation (Martínez Vivot et al., 2020).

In our study, we selected 3 types of measures among those markers:

- Spectral measures: we computed the normalized power spectral densities (PSD) in delta (1-4 Hz), theta (4-8 Hz), alpha (8-12 Hz), beta (12-30 Hz), and gamma (30-45) frequency bands using the same methods described above.
- Connectivity measures: we computed the weighted symbolic mutual information (wSMI), a functional connectivity measure capturing linear and non-linear coupling between sensors, which relies on the symbolic transformation of the EEG signal. We computed the wSMI in the theta band (4-8Hz) (King et al., 2013). The choice of the theta frequency band was based on previously reported results (King et al., 2013; Sitt et al., 2014) , showing that the wSMI calculated on this frequency band was the most efficient in detecting residual consciousness in brain-injured patients with a DoC.
- Complexity measures: we computed three different complexity measures, the Kolmogorov Complexity (KC), the Permutation Entropy in the theta frequency (PE θ), and the Sample Entropy (SE).

See Supplementary material of Sitt et al. (2014) for a detailed description of each measure and its computation. Details regarding the sample entropy can be found in Richman & Moorman, (2000).

Each one of the previously described markers was computed during the 1000ms time window *preceding* the presentation of the stimulus (word or pseudo-word), during the ON-periods, independently for each subject, trial and for every electrode ($n = 10$) or pair of electrodes ($n = 45$) for the wSMI. A wSMI global score for each electrode was computed by calculating the median connectivity of each electrode with all the other electrodes. Finally, for each subject and each trial, each marker was summarized by calculating the mean across channels, resulting in a single scalar per marker per trial.

4.3.6.6. Prediction of responsiveness using a decision tree algorithm

We aimed at predicting, independently for each sleep/wake stage, if a given trial would contain a response or not based on the EEG markers computed during the 1000ms time period preceding the stimulus presentation. We used a Random Forest algorithm, a classification algorithm consisting of many decision trees. This algorithm implements bootstrapping and feature randomness when building each tree, which ensures the construction of an uncorrelated forest of trees. Since the different trees in the forest are uncorrelated, their global prediction by committee is more accurate than that of any individual tree. Random Forest has shown to be among the best currently used machine learning classifiers, in a very wide range of different datasets ($n=112$) from several research fields (Fernandez-Delgado et al., 2014), outperforming other choices as SVM classifiers.

We conducted an independent analysis for each sleep/wake stage. For each trial, the classifier was provided with 10 features, as well as the label (“responsive” versus “non-responsive”) of the trial. The 10 features were the 9 EEG markers described in the previous section and the subject identity. The Random Forest classifier was composed of 100 estimators (trees). Since our data was unbalanced in terms of the number of responsive trials compared to non-responsive ones, the weights of each class were adjusted in an inversely proportional manner to class frequencies.

Two different training/testing strategies were used:

- For the participants with narcolepsy, we used for each stage a standard 10-fold stratified cross-validation procedure. In each fold, data was split into training (9/10 of the trials) and testing (1/10 of the trials) sets, in a manner that preserved class frequencies in each split. Trials of each class were shuffled before splitting in a pseudo-randomized manner. In each fold, the predictions of the classifier for the testing set were used to compute the Balanced Accuracy score and the F1-score of the classifier (see definition and method for calculation of these scores below). We then computed the mean Balanced Accuracy and F1 scores across folds, as well as their confidence interval. F1 scores can be found in Figure S4.16 and Table S4.9.
- For the participants without narcolepsy, since *responsive* trials were scarce in particular during N2 sleep and REM sleep, we decided to train our classifier with the data of the participants with narcolepsy and to test its performance on data from participants without narcolepsy. Specifically, we fitted our classifier with the N2 sleep trials from

participants with narcolepsy, and then tested its predictions on N2 sleep trials from the participants without narcolepsy. As before, we computed balanced accuracy and F1 scores. To obtain a distribution of scores in the absence of cross-validation, we repeated the fitting and testing steps 10 times (note that the random parameters of the Random Forest classifier allowed us to obtain a distribution of -closely related- scores in this manner).

As mentioned above, we computed two scores to measure the performance of our classifier, both measures being well adapted to unbalanced datasets (Kelleher et al., 2015) as ours (with more non-responsive trials than responsive ones during sleep):

The balanced accuracy score corresponds, in binary classification problems, to the mean of the *sensitivity* (Se) – also called *recall* (“How many relevant items are retrieved?”) and the *specificity* (Sp) (“How many non-relevant items are correctly identified”). In terms of true positives (TP), false negatives (FN), true negatives (TN) and false positives (FP) (where, in our case, true positives are responsive trials correctly identified by the classifier, and true negatives non-responsive trials correctly identified by the classifier), the balanced accuracy score can be computed by the following formula:

$$\text{Balanced Accuracy} = \frac{\overbrace{\frac{TP}{TP + FN}}^{\text{Se}} + \overbrace{\frac{TN}{TN + FP}}^{\text{Sp}}}{2}$$

The F1-score corresponds, in binary classification problems, to the harmonic mean of the *precision* (“How many retrieved items are relevant?”) and the *sensitivity*. It can be computed by the following formula:

$$\text{F1 score} = \frac{2}{\underbrace{\left(\frac{TP}{TP + FN}\right)^{-1}}_{\text{Sensitivity}} + \underbrace{\left(\frac{TP}{TP + FP}\right)^{-1}}_{\text{Precision}}}$$

We first run an analysis taking into account all responses (correct and incorrect). Then, we separately studied the prediction accuracy when considering only correct or incorrect responses.

4.3.6.7. Decoding of stimulus-related brain activity

We aimed at assessing brain responses to stimuli in function of participants' sleep/wake stages and of their responsiveness to the task using a multivariate pattern analysis (MPVA) with the temporal generalization decoding method (King & Dehaene, 2014). The idea of this analysis is to test, for a given time-point after stimulus presentation, how different the multivariate pattern of activity across electrodes was at this specific time point compared to the pattern at baseline (before stimulus presentation), for the different conditions.

To reduce computation time, we first down-sampled our data to 100Hz (decimation factor of 2.5). To ensure a correct features/number of trials ratio, we restricted our analysis to 3 centro-parietal electrodes (Cz, Pz, and P3), and, for each condition (sleep stage/responsiveness), we only included in our analysis the participants who had at least 15 trials of the given condition. Given these restrictions, we only had enough participants for statistical analysis for Lucid REM sleep (10 participants for responsive trials, and 9 participants for non-responsive trials) and for Wake (14 participants for responsive trials). Then, for each condition, participant, trial, and channel, we computed the mean voltage during the 350ms baseline period before stimulus presentation and used this value to create dummy "baseline" trials with the same dimensionality as the original trials. Note that after this step, for each condition and each participant, we obtained a balanced set of dummy "baseline trials" (reflecting baseline brain activity before/without stimulus presentation) and actual trials where the stimulus was presented.

Then, independently for each condition and each participant, we trained a linear classifier to decode stimulus-present versus stimulus-absent trials ("baseline" dummy trials versus actual trials), using an L2-regularized ($C=1$) logistic regression, in a 5-fold cross-validation procedure. In each fold, all the trials were shuffled in a pseudo-randomized manner and split into a training set ($\frac{4}{5}$ of the trials) and a testing set ($\frac{1}{5}$ of the trials). The features (channel amplitudes) were standardized across training trials before being provided to the classifier for training. This training procedure was applied at each time step independently. Following the time generalization approach, the model trained at each time step was then tested at all the time steps on the testing set trials, at each cross-validation fold. The classifier performance at each training and testing time was evaluated by the area under the receiver operating curve (AUC) at each cross-validation fold. At the end of the cross-validation procedure, the global performance of the classifier at each training and testing time was obtained by averaging the intermediate values obtained at each fold, for each participant and each experimental condition.

Group-level performance for each condition was finally obtained by averaging across participants, independently for each condition (stage /responsiveness).

4.3.6.8. Statistical analysis

Most statistical analyses were conducted in R (R Core Team, 2021) using the lme4 (Bates et al., 2015), emmeans (Lenth, 2021), BayesFactor (Morey & Rouder, 2013), car (J. Fox & Weisberg, 2019) and DHARMA (Hartig, 2022) packages. For the machine learning analysis, statistics were conducted in Python (Van Rossum & Drake, 2009) using the numpy (Harris et al., 2020), scipy (Virtanen et al., 2020), pingouin (Vallat, 2018) and scikit-learn (Pedregosa et al., 2011) packages. All statistics were corrected for multiple comparisons using the False Discovery Rate (FDR) Benjamini–Hochberg procedure. FDR corrections were applied separately to each group of statistical tests (each panel in the figures). For example, one correction was performed for Figure 3A, combining NP and HP and all sleep stages. Assumptions of the generalized linear models were evaluated using DHARMA (Hartig, 2022) package in R (R Core Team, 2021). For linear mixed models, the distributions of residuals as well as Q-Q plots were visually inspected. Significance of single factors were tested with Wald X-Tests using car (J. Fox & Weisberg, 2019) package. When the statistics were computed at the subject level rather than at the single trial level, the observations were weighted according to the number of trials that each participant had.

Behavior. Linear mixed models with subject ID as a random factor (random intercept) were used for all statistical analyses. We evaluated participants' ability to respond to stimuli in different sleep stages (Figure 4.1 and Figure 4.3). First, we focused on the comparison between the ON and OFF periods separately for each sleep stage. Binomial generalized linear mixed models with stimulation period (ON vs. OFF) as the independent variable and responsiveness (response vs. no response; both contraction types combined) as the dependent variable were used in this analysis. Next, we focused on the ON stimulation periods during which participants were presented with stimuli. The model had sleep stages (wake, N1, N2, N3, REM sleep in healthy participants and wake, N1, N2, N3, non-lucid REM, and lucid REM sleep in participants with narcolepsy) as the independent variable and responsiveness (response vs. no response) as the dependent variable. For accuracy, we computed the percentage of correct responses for each participant at each sleep stage and compared them to the 50% chance level using Wilcoxon signed rank test. Only participants with at least 3 responses were included in this analysis. Finally, the differences in reaction times in different sleep stages were assessed using

a linear mixed model (Figure 4.3C). An inverse transformation was applied to the reaction times ($1/RT$) to better fit the model assumptions.

EEG markers (spectral, connectivity and complexity). In order to investigate how different neural markers differ in trials with a response and without any response, we first z-scored marker values at subject level. We then used a mixed linear model for each EEG marker with subject ID as a random factor, responsiveness as the independent variable, and the EEG marker as the dependent variable. The analysis was conducted at a single-trial level. Since responsiveness and sleep stages were not independent (for example, in wake we observed more responses than in N2 sleep), we could not include sleep stage as an additional independent variable in the models. Thus, we performed the tests separately for each sleep stage, resulting in a test for each marker in each sleep stage. We performed a similar analysis to compare, in REM sleep, lucid and non-lucid trials.

Time-frequency analysis. We conducted a mass-univariate analysis over the time-dimension on preselected frequency bands of interest (delta, alpha, beta), using mixed linear models with responsiveness as the independent explanatory factor and subject ID as a random factor (the power in each time-sample being the dependent variable). This analysis was conducted independently for each group, sleep/wake stage and electrode. A correction for multiple comparisons was applied using the False Discovery Rate (FDR) procedure.

Prediction of responsiveness at a trial level using a Random Forest Classifier. We scored classifier performance at each sleep/wake stage and for each group using the Balanced Accuracy score and the F1-score (cf. above). To assess how different these scores were from chance level, we performed, independently for each score, a 500-permutation procedure. At each permutation, trial labels (responsive versus non-responsive) were randomly shuffled, and the entire 10-fold cross-validation procedure was performed, allowing us to obtain a distribution of chance-level scores.

Decoding of stimulus-related brain activity using temporal generalization decoding. For each experimental condition (sleep stage/responsiveness), classification performance at each training and testing time was tested against 0.5 (chance) using a two-sided non-parametric sign test across subjects, and these statistics were then corrected for multiple comparisons using the False Discovery Rate (FDR) Benjamini–Hochberg procedure. In Figure 6B, significant time points ($p < 0.05$ FDR corrected) with an $AUC > 0.5$ are outlined in black.

4.4. Results

Participants can behaviorally respond to auditory stimuli across most sleep stages.

In this study, we tested participants' ability to behaviorally respond to auditory verbal stimuli across different sleep stages. We included both participants with narcolepsy (NP, $n = 27$) and healthy participants (HP, $n = 21$). Their sleep/wake stage was continuously monitored by polysomnography (EEG, EOG, EMG). Words and pseudo-words were verbally presented in a pseudo-randomized order during daytime naps; 1-min periods of stimulation (ON periods) alternated with 1-min periods without stimuli (OFF periods) (Figure 4.1). Participants were instructed to perform a lexical decision task by frowning or smiling three times according to the stimulus type (behavior-stimulus matching counterbalanced across participants) every time they heard a stimulus, whether they were awake or asleep.

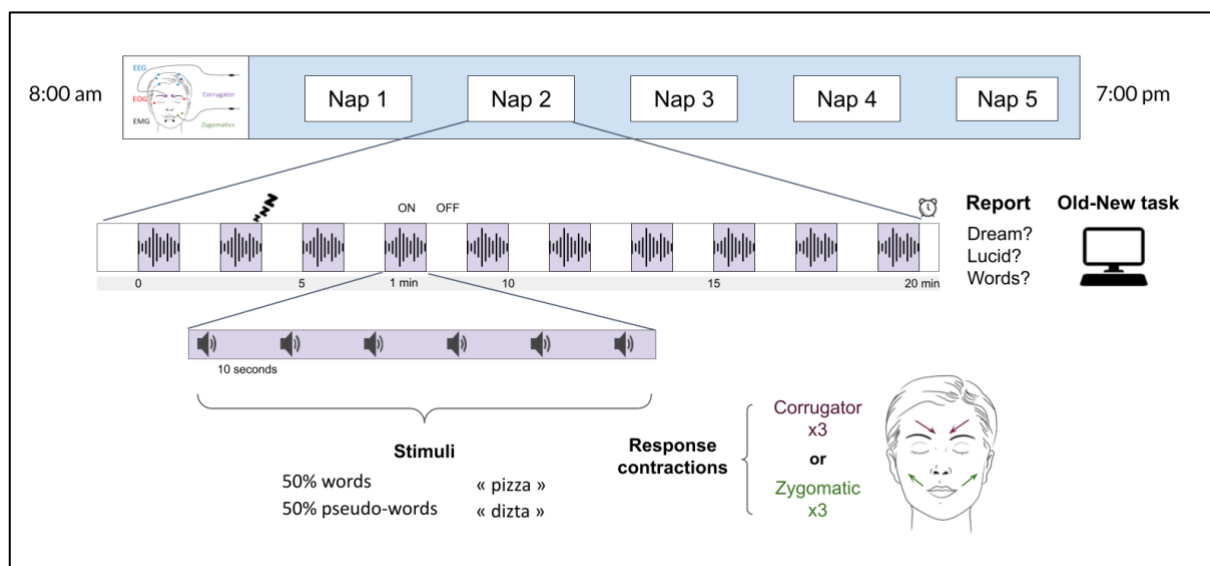


Figure 4.1. Experimental design. Participants with narcolepsy went through five 20-minute naps during the same day. In each nap, periods with stimulation (ON) alternated, every minute, with periods when no stimulus was presented (OFF). During the ON periods, participants were presented with words and pseudo-words and asked to either frown (corrugator muscle contractions) or smile three times (zygomatic muscle contractions) in response to the stimuli. Stimuli were presented every 10 seconds (± 1 second). Following each nap, participants were asked to report whether: (i) they had any dream; (ii) they were lucid; and (iii) they recalled any words presented during the nap. Immediately after this debriefing, participants performed a forced-choice 'old/new' recognition task. Healthy participants went through the exact same procedure except that they had a single 100-min nap.

As we previously showed (Konkoly et al., 2021), such behavioral responses are visible on surface EMG sensors measuring corrugator (frowning) and zygomatic (smiling) isometric contractions (see Figure 4.2, Figure S4.2, Figure S4.3 and Figure S4.4 for examples). At the end of each nap, participants reported: i) their mental content during the nap, (ii) whether they had a lucid dream, and (iii) whether they recalled having actively performed the lexical task while sleeping. Each nap was labeled as lucid or non-lucid in function of participants' post-nap subjective report, with all REM sleep trials from this nap labeled as lucid or non-lucid accordingly. Participants were also instructed to signal their lucidity (if any) with a “mixed-code”, by frowning then smiling once. These objective dream lucidity signals typically matched participants' subjective reports upon awakening (Supplementary Results).

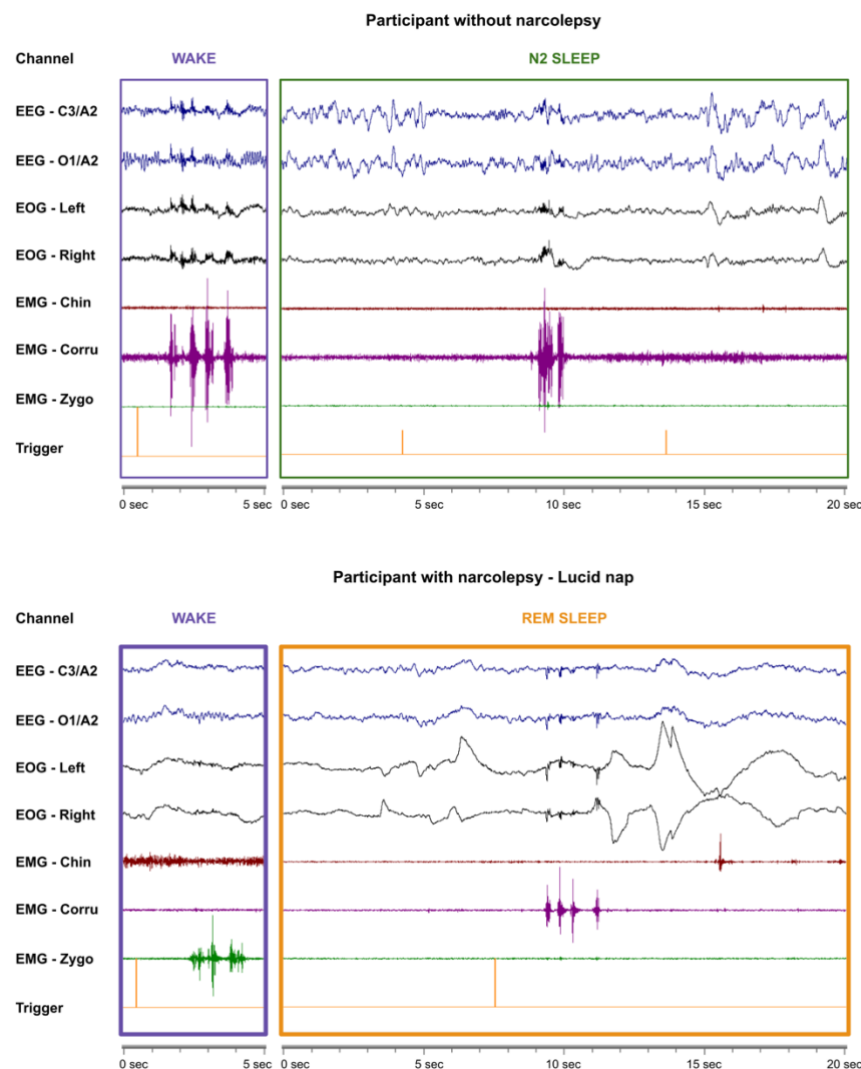


Figure 4.2. Examples of behavioral responses during N2 sleep in healthy participants (upper panel), and during lucid REM sleep in participants with narcolepsy (lower panel). Wake periods corresponding to the same participants are shown on the left side of the figures as a comparison. The

orange vertical line on the last channel indicates the stimulus onset. In these examples, we observed the typical markers of N2 sleep: spindles (EEG); and REM sleep: low chin tone (EMG), rapid eye movements (EOG), and theta rhythm (EEG).

We assessed responsiveness to task-stimuli across sleep stages in the two groups, by visually inspecting the corrugator and zygomatic EMG while blind of the sleep stage and the presence/absence of a stimulus. Results from our visual scoring are consistent with the ones provided by an automatic algorithm (Supplemental material). We compared response rates (including both correct and incorrect responses from the two muscles) during *ON* and *OFF* stimulation periods (Figure 4.3A). Importantly, we excluded all responses performed during micro-arousals, keeping only periods when participants were asleep according to the sleep scoring rules (Berry et al., 2017). As expected, we found significantly higher response rates during ON vs. OFF periods, both during Wakefulness (HP: 78.8% vs. 1.5%, $z = 30.02$, $p < .0001$; NP: 86.1% vs. 2.1%, $z = 27.02$, $p < .0001$, after FDR correction) and N1 sleep (HP: 22.2% vs. 1.5%, $z = 10.99$, $p < .0001$; NP: 64.2% vs. 1.7%, $z = 18.29$, $p < .0001$) in both groups. Crucially, we also found, in both HP and NP, significantly higher response rates in ON vs. OFF periods during N2 (HP: 4.7% vs. 1.9%, $z = 4.52$, $p < .0001$; NP: 20.27% vs. 2.2%, $z = 16.57$, $p < .0001$) and (non-lucid) REM sleep (HP: 6.5% vs. 2.2%, $z = 3.59$, $p = .0003$; NP: 34.2% vs. 1.4%, $z = 13.93$, $p < .0001$). Results for N3 sleep are provided in Supplementary Results. Note that the response rates were higher in NP than in HP during ON stimulation periods in all sleep stages (N1: $z = 4.74$, $p < .0001$; N2: $z = 4.44$, $p < .0001$; REM: $z = 4.95$, $p < .0001$). This was not true for OFF stimulation periods, during which the two groups had similar contraction rates ($\chi^2(1) = 0.03$, $p = 0.87$) in all sleep stages (no interaction). Response rates during ON periods decreased significantly from Wake to N1 sleep, REM sleep, then N2 sleep (in order) in both HP and NP. (Figure 4.3A and Table S4.1). Participants could therefore provide behavioral motor codes during most sleep stages, but response frequency decreased in function of sleep depth. Interestingly, only NP reported having performed the task during sleep upon awakening.

To verify that participants actually performed a lexical decision while asleep, we next computed subject-level accuracy scores (Figure 4.3B and Figure S4.5). Note that we did not have enough responsive trials per participant to perform this analysis in REM sleep in HP. Both HP and NP performed the task significantly more accurately than chance level in all tested sleep stages, with median accuracy above 71% (HP: Wake 94.2%, $p < .0001$; N1 83.3%, $p = .0003$; N2 84.5%, $p = 0.01$. NP: Wake 87.9%, $p < .0001$; N1 84.1%, $p < .0001$; N2 71.8%, $p = .0001$; non-lucid REM sleep 73.37%, $p = 0.003$). We observed a significant main effect of the

sleep stages on accuracy in both HP ($\chi^2(2) = 11.01$, $p = 0.004$) and NP ($\chi^2(4) = 38.23$, $p < .0001$), indicating a decrease in performance from Wake to deeper sleep stages. Moreover, accuracy was higher in HP than in NP ($\chi^2(1) = 13.65$; $p = .0002$) in all tested sleep stages.

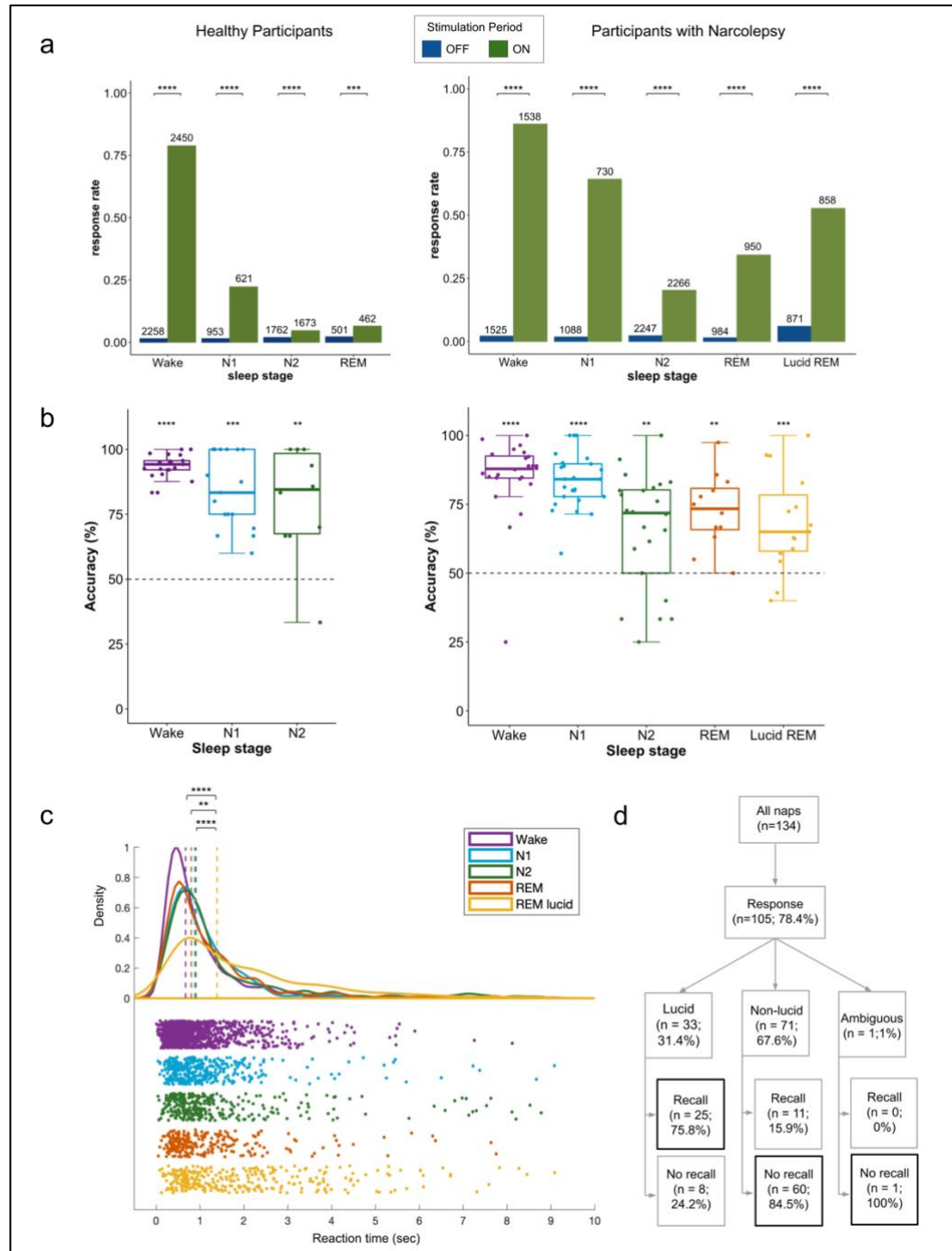


Figure 3. Behavioral results. (a) The overall response rate across different sleep stages during OFF (blue) and ON (green) stimulation periods in participants without (left) and with (right) narcolepsy. The response rate was computed by combining both response types (zygomatic and corrugator muscle contractions), whether the response was correct or not. The total number of trials in a given condition is indicated on top of the bars. We used binomial generalized mixed-linear models with participants as

a random factor for statistical analysis. Significant differences between ON and OFF periods are indicated for each sleep stage. Response rates were significantly larger in ON than in OFF periods in all sleep stages. (b) Accuracy computed over responsive trials in the lexical decision task for participants without narcolepsy -HP (left) and with narcolepsy -NP (right). Only participants with at least 3 responses were included in this analysis. Each dot represents a participant and dashed lines indicate the 50% chance level. Both HP and NP were significantly more accurate than chance in all sleep stages. (c) Distribution of reaction times from stimulus onset to response in correct trials (words and pseudo-words) in NP across sleep stages. Dashed lines indicate medians. A mixed-linear model with subject as a random factor revealed slower reaction times in lucid REM sleep. (d) Flowchart detailing the repartition of naps in participants with narcolepsy: the percentage of naps with at least one behavioral response is indicated and the responsive naps are further divided depending on whether participants reported a lucid dream upon awakening and whether they explicitly recalled responding during the nap. Please note that, after the naps in which participants with narcolepsy responded to stimuli, the majority of participants who were lucid remembered performing the task while those who were not lucid did not. **** : $p < 0.0001$, ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, all p values are corrected for multiple comparisons using Benjamini–Hochberg procedure.

We then wondered if one behavioral hallmark of lexical decision task during wakefulness, defined by slower response times (RTs) for pseudo-words than for words (Perea et al., 2016), persisted in our sleeping participants. Only correct responses were included in this analysis. For both NP and HP, we found a main effect of both sleep stage (HP: $\chi^2(2) = 25.47$, $p < .0001$; NP: $\chi^2(4) = 82.5$, $p < .0001$) and stimulus type (HP: $\chi^2(1) = 45.59$, $p < .0001$; NP: $\chi^2(1) = 36.9$, $p < .0001$) on RTs; crucially, there was no significant interaction effect between these two factors (HP: $\chi^2(2) = 2.7$, $p = 0.25$; NP: $\chi^2(4) = 7.3$, $p = 0.1$), suggesting that the effect was not modulated by sleep stage. (Figure S4.6). Responses to pseudo-words were on average 100 ms slower than responses to words in HP (median for words: 1.29s), and 130ms slower in NP (median for words: 1.42s). This was also the case for each sleep stage independently. In NP, responses were faster during wakefulness than during sleep (median RT: Wake, 1.36s vs. N1 sleep 1.56s, $p = 0.034$; N2 sleep 1.59s, $p = .0001$; non-lucid REM, 1.49s, $p = .0001$), whereas no significant differences were found between sleep stages (Figure 4.3C). A similar pattern was observed for HP, including significantly shorter reaction times in Wakefulness and N1 than in N2 sleep (Wake vs. N2 sleep: $t = 4.6$, $p < .0001$; N1 vs. N2 sleep: $t = 2.64$, $p = 0.008$). Moreover, we found significantly shorter reaction times in accurate trials compared to inaccurate ones in Wake ($t = -6.91$, $p < .0001$), N1 sleep ($t = -2.31$, $p = 0.021$) and N2 sleep ($t = -3.82$, $p = .0001$) in HP and in Wake ($t = -5.56$, $p < .0001$), N1 sleep ($t = -2.24$, $p = 0.025$) and REM sleep ($t = -5.275$, $p < .0001$) in NP.

We finally assessed whether lucid and non-lucid REM sleep differed on the behavioral and subjective level. Only NP reported lucid dreams upon awakening, in 33/134 naps (24.6%). Like in non-lucid REM sleep, response rates were higher during ON *vs.* OFF periods in lucid REM sleep (52.7% *vs.* 6%, $z = 18.04$, $p < .0001$). Accuracy was also better than chance (65% *vs.* chance level at 50%, $p = 0.001$) and not statistically different than in non-lucid REM sleep ($t = 1.24$, $p = 0.3$). Reaction times were significantly shorter in accurate trials compared to inaccurate ones ($t = -2.61$ $p < .009$). Importantly, lucidity significantly increased the response rate in REM sleep ($z = 7.97$, $p < .0001$) to a level similar to the one observed in N1 sleep (Figure 4.3A and Table S4.1). Interestingly, RT were significantly longer during lucid REM sleep than during wakefulness but also than during other sleep stages (median RT: lucid REM sleep, 2.1s *vs.* N1 sleep, 1.56s, $p < 0.0001$; *vs.* N2 sleep, 1.59s, $p = 0.0001$; *vs.* non-lucid REM sleep, 1.49s, $p = 0.002$) (Figure 4.3C). Finally, after naps associated with at least one behavioral response during sleep, participants who reported lucidity recalled more frequently having performed the task during sleep (task recall after 75.8% of lucid naps *vs.* 15.5% of non-lucid naps; $\chi^2(2) = 36.15$, $p < .0001$; Figure 4.3D).

Fine-grained electrophysiological analyses confirm polysomnographic scoring and reveal local brain activations in the sleeping brain during responsive trials.

Sleep/wake stages were scored according to established guidelines (Berry et al., 2017) by a certified sleep expert blind to the responses (corrugator and zygomatic EMG channels were removed for sleep scoring). Figure 4.2 and Figures S4.2-4 show 15 examples of responses during bona-fide sleep for both HP (in N2 and REM sleep) and NP (in N2, REM and N3 sleep). Given the novelty and importance of this result, we performed additional analyses confirming that these responsive trials did occur during sleep periods.

First, we performed spectral analyses during both the baseline period (-1000 to 0 ms relative to stimulus presentation) and the post-stimulus period (0 to 8000 ms) (Figure 4.4A). For both time-windows, and for all sleep stages in both HP and NP, power spectral densities in responsive trials reflected the expected profile of the given sleep/wake stage. Compared to wake trials, all responsive trials were associated with lower alpha and higher delta spectral power (see Figure 4.4A and Table S4.4 for the statistical comparisons). Additional analyses quantifying classical sleep graphoelements (spindles and slow waves) in responsive and non-responsive NREM sleep are provided in Supplemental Results. Overall, our results are in line

with the manual sleep scoring and confirm that the background brain activity in responsive sleep trials presents the typical signatures of sleep.

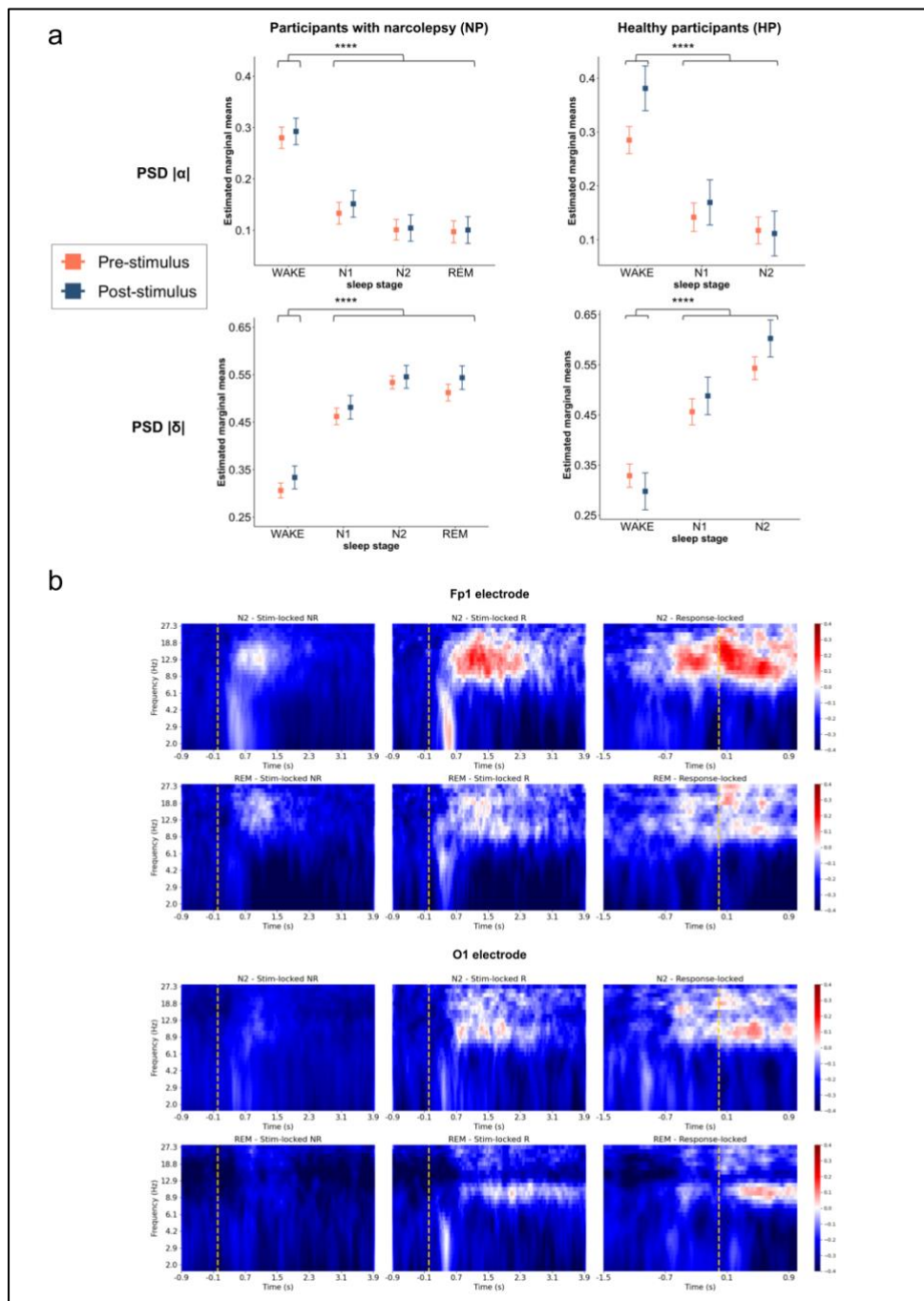


Figure 4.4. Participants exhibit sleep activity in responsive trials, with local brain activations associated with responsiveness. (a) Normalized PSD values in alpha (PSD $|\alpha|$) and delta (PSD $|\delta|$) frequencies in responsive trials across different sleep stages in pre- and post-stimulus periods. Pre-stimulus marker values are computed over 1s-period prior to the stimulation whereas post-stimulus marker values are calculated in the 8s-period following the stimulation. Please note that marker values in different sleep stages were never at wake level, indicating that participants were indeed asleep while

they were responding. (b) Time-frequency analysis (TFA) performed on the Fp1 (upper panel) and the O1 (lower panel) electrodes in N2 and REM sleep of NP. The left and middle panels are stimulus-locked TFA in non-responsive (NR) and responsive (R) trials, respectively. The right panels show response-locked TFA. Transient and spatially localized increases in alpha and beta frequencies were associated with behavioral responsiveness to the task.

We next wondered what differences in brain processing could account for the presence or absence of behavioral responses during sleep. We performed a mass-univariate stimulus-locked time-frequency analysis independently for each group and each sleep stage. We applied a log-ratio baseline correction relative to the -1000 to 0 ms time window to only capture the time-frequency activity induced by stimulus processing. The average time-frequency matrix for responsive and non-responsive trials is presented in Figure 4.4B for NP (N2 and REM sleep), and in Figure S4.10 for HP (N1 and N2 sleep). This analysis revealed: i) the absence of significant delta band modulation by responsiveness; ii) compared to non-responsive trials, a more pronounced and more sustained activation in alpha (8-12 Hz) and beta (12-30 Hz) bands, mostly observed in frontal electrodes, and roughly spanning from 1200 ms to 3800 ms post-stimulus presentation (see Figure S4.11 for the exact time-intervals for each frequency band). To assess whether this alpha and beta band modulation was due to ultra-short arousals (shorter than the usual 3s criteria defining micro-arousals) or to cognitive and motor processes induced by the stimuli, we performed a response-locked time-frequency analysis (Figure 4.4B, right panel), as well as response-locked event related potentials (ERPs) (Figure S4.12). We observed a power increase in alpha and beta frequency bands starting from 700 ms before the behavioral response; this power increase was predominant on frontal sites and during the period following the response. This spatial profile of activity is different from the typical, occipital activation observed during microarousals. Crucially, comparison between the response-locked time-frequency matrix and ERPs revealed that the observed pre-response alpha and beta band activation was concomitant with a motor preparation potential (Bereitschaftspotential), observed mainly on frontal electrodes, in all wake/sleep stages in both NP and HP. This frontal location is consistent with the known physiology of facial muscles motor preparation and execution (Balaban & Weinstein, 1985; Kurtzberg & Vaughan, 1982; Recio et al., 2014).

In sum, our results suggest that participants' responses happened in a global background of sleep brain activity (with a similar stage-specific physiology compared to non-responsive trials), but that they involve local (in time and space) brain activations likely linked to cognitive and motor processing of the stimulus. Taken together with our behavioral results, these results

demonstrate that sleepers can perceive verbal stimuli, make a lexical decision, and perform an adequate motor response while remaining asleep in N1, N2 and REM sleep. The fact that participants' responses were accurate and slower for pseudo-words than for words suggests that stimuli were processed at a high-cognitive level (at least beyond the lexical level). These results overall suggest the existence of transient states that allow responsiveness to external information during sleep, whose frequency and duration depend on sleep stage.

Electrophysiological markers of higher cognitive states predict responsiveness during ordinary sleep.

To explore whether responsiveness during sleep could be explained by an ongoing, richer cognitive state prior to stimulation in non-lucid participants (NP and HP), we computed electrophysiological markers known for distinguishing high versus low cognitive states (Martínez Vivot et al., 2020; Sitt et al., 2014). These markers were previously shown to differentiate patients with unresponsive wakefulness syndrome from patients in a minimally conscious state and healthy participants (King et al., 2013; Sitt et al., 2014; Engemann et al., 2018), as well as wakefulness and REM sleep from N3 sleep (Bourdillon et al., 2020). In addition to classical spectral measures (normalized power spectral densities [PSD] in delta, theta, alpha, beta, and gamma frequency bands), we included one connectivity measure (weighted symbolic mutual information [wSMI] in the theta band), and three complexity measures (the Kolmogorov Complexity [KC], the Permutation Entropy in the theta band [PE θ], and the Sample Entropy [SE]). Crucially, we computed these markers in the 1000ms time window *before* the stimulus presentation; therefore, these markers reflected the “resting-state” brain dynamics of the participants just before the stimulus presentation, and not the evoked activity of the stimulus or the response.

To ensure that these markers would provide meaningful information about the cognitive state of our participants, we first assessed how the markers varied in different sleep stages as a sanity check (NP: Figure S4.14, HP: Figure S4.15). As expected, we found that complexity, connectivity values and high-frequency PSD decreased from wake to N1 sleep, REM sleep, N2 sleep and N3 sleep (in order), this descending profile mirroring the response rates (see tables S3-4 for statistical comparisons between the different sleep stages, for each marker and each group). The reverse was observed for delta PSD. These results demonstrated that our markers can reliably distinguish participants' *sleep/wake stage*.

Next, we assessed how these electrophysiological markers differed in responsive and non-responsive trials, except during REM sleep in HP (not enough remaining responsive trials after EEG preprocessing). Figure 4.5A shows the difference in the estimated marginal means of the z-scored marker values in responsive and non-responsive trials for each sleep stage in non-lucid NP (left panel) and HP (right panel) (see Tables S4.7-8 for detailed comparisons). Positive marker values indicate an increase of the markers in the responsive trials compared to non-responsive trials whereas negative marker values signify a decrease in the responsive trials. Our analysis revealed similar patterns of variations in non-lucid NP and HP, including an increase in the EEG complexity and in the high-frequency PSD, and a decrease in the delta PSD in responsive trials vs. non-responsive trials. Connectivity (wSMI) did not differ in the two conditions.

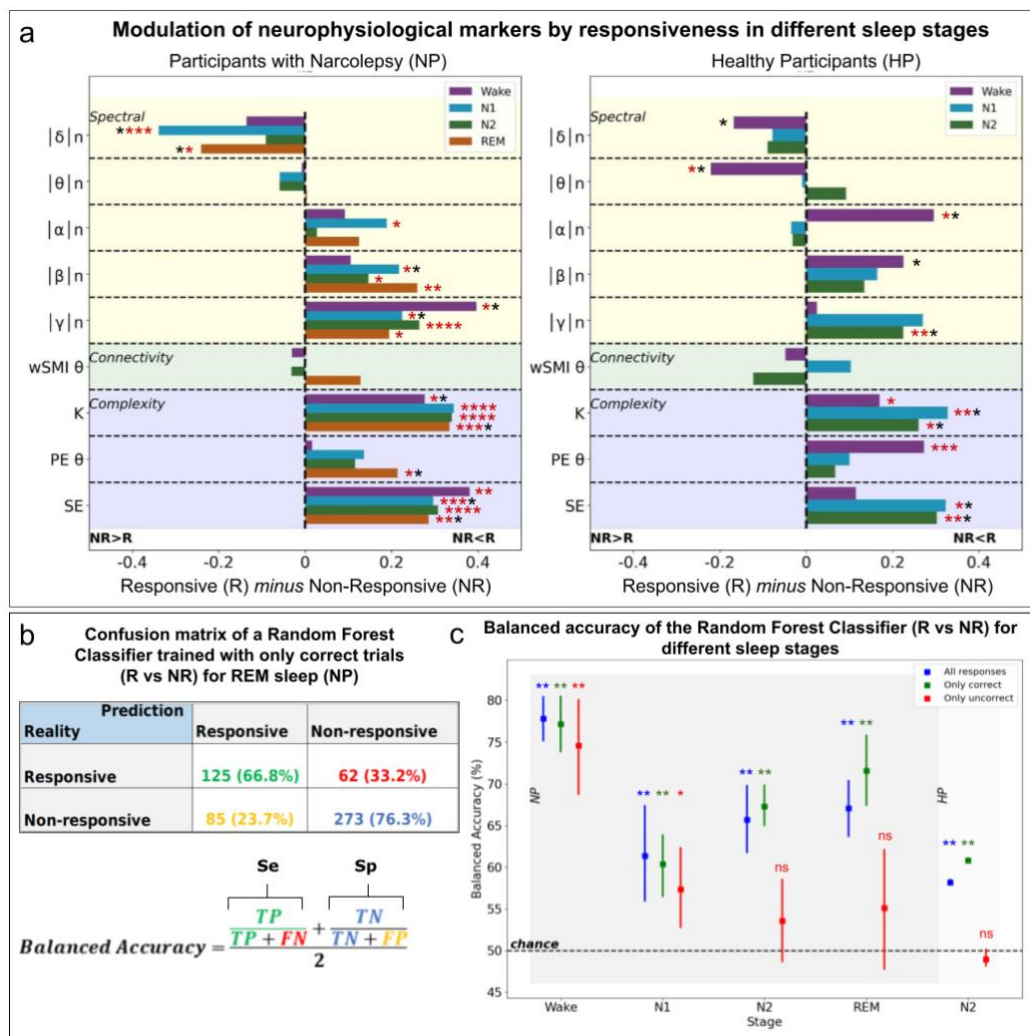


Figure 4.5. EEG markers of high cognitive states computed before stimulus presentation predict responsiveness to stimuli in each non-lucid sleep stage. (a) Univariate analysis; After the z-score transform of marker values, we subtracted the marginal estimated mean of non-responsive trials (NR)

from responsive (R) trials for each marker and each stage. Almost all markers showed a variation in the direction corresponding to increased cognitive states when contrasting responsive trials to non-responsive trials (e.g.: increased EEG complexity and decreased EEG delta power), both in participants with (left) and without narcolepsy (right). Note the similarity with Figure 3 in Sitt et al. (2014) which contrasted conscious to non-conscious states in patients suffering from disorders of consciousness. (b) and (c) Multivariate analysis. We fed a random forest classifier with these 9 EEG markers and trained it to classify R trials versus NR ones using a 10-fold cross-validation method. We conducted this analysis considering all responses (in blue), then separately for both correct (in green) and incorrect responses (in red). A confusion matrix for correct REM sleep trials in non-lucid naps of participants with narcolepsy is shown in (b), with a description of the balanced accuracy measure that we computed to take unbalanced datasets into account. The confusion matrix for each stage and group can be found in Table S4.9. TP: True Positives (responsive trials classified as responsive). TN: True Negatives (non-responsive trials classified as non-responsive). FP: False Positives (NR trials classified as responsive). FN: False Negatives (R trials classified as non-responsive). Balanced accuracy scores are plotted in (c) for different sleep stages, in function of response accuracy, both for participants with narcolepsy (Wake, N1, N2, REM sleep; left) and without narcolepsy (N2, right), with the corresponding statistical significance against chance-level (approximated by 500 permutations). Note that: (i) responsiveness to stimuli could be predicted for each sleep/wake stage in participants with narcolepsy (NP); (ii) the classifier trained with data from participants with narcolepsy could generalize to healthy participants (HP), as shown by significant decoding of responsiveness in N2. ****: $p < 0.0001$, ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, **red stars** indicate significance after FDR correction for 72 comparisons.

To further explore the predictive power of these EEG markers on responsiveness, we trained a random forest classifier using a multivariate combination of these markers collected in non-lucid NP and did so independently for each sleep stage. We then tested whether this classifier could predict responsiveness on a trial-by-trial basis in both NP (using a classical stratified cross-validation procedure) and HP trials (in N2 sleep). The balanced accuracy score was above 60% for all sleep stages in NP non-lucid naps (reaching 67% for REM sleep) and reached 58% for N2 sleep in HP (Figure 4.5C). All balanced accuracy scores were significantly different than the chance level computed by a 500-permutation procedure ($p < 0.002$ for all stages in NP, and $p = 0.006$ for N2 sleep in HP), with a mean balanced accuracy score of permutation trials around 50% for all stages (Table S4.9).

One could argue that these EEG markers measure differences in motor capacities (i.e. more or less motor inhibition) rather than differences in cognitive capacities. To explore this possibility, we tested whether our classifier better predicted responsiveness when including only correct

responses. Prediction performance increased for all sleep stages in both NP and HP (except for N1 in NP where performance slightly decreased while remaining significantly higher than chance) (Figure 4.5C). Balanced accuracy reached 72% for REM sleep in NP and 61% for N2 sleep in HP ($p = 0.002$, 500-permutation procedure). Next, we tested the opposite by including only incorrect responses. Interestingly, prediction performance drastically decreased, falling to chance level for all sleep stages other than N1 sleep in NP (where it also decreased significantly while remaining higher than chance level) (Figure 4.5C). The fact that prediction performance was driven by correct responses is a strong indicator that the differences in brain dynamics measured by the EEG markers reflected differences in cognitive processing between responsive and non-responsive trials, and not mere motor capacities.

In sum, our EEG results suggested that a particular brain state prior to the stimulation, characterized by increased complexity and faster oscillations, allowed responsiveness during sleep. A multivariate combination of these markers predicted the presence/absence of response in a trial-by-trial level. The facts that: i) the markers varied with responsiveness similarly in non-lucid NP and HP, and ii) that the classifier trained with NP data could classify responsive trials in HP better than chance, strongly suggest that the same brain dynamics underlie responsiveness in both participants with and without narcolepsy (in non-lucid sleep). Finally, the finding that the predictive power of those markers was driven by correct trials strongly suggest that behavioral responses were due to a higher cognitive processing of the stimulus.

Evidence of conscious processing of external stimuli in lucid dreaming

To investigate the specificities of lucid REM sleep in NP, we first compared the electrophysiological markers between responsive and non-responsive trials in this condition. Interestingly, none of these markers differentiated responsive from non-responsive trials in lucid REM sleep (all uncorrected $p > 0.05$) (Figure 4.6A and Supplementary Table 4.8). Using a Bayesian analysis, we confirmed a true absence of difference between responsive and non-responsive trials in lucid REM sleep; for each marker, Bayes Factor comparing our full mixed linear model to the one of a “null-model” with only the random effect, ranged from 0.21 to 0.08, indicating moderate (<0.33) to strong (<0.1) evidence for the null model (Lee & Wagenmakers, 2014).

We next investigated how the marker values in lucid REM sleep differed from the ones in non-lucid (ordinary) REM sleep. Lucid trials were associated with higher complexity (sample

entropy), higher normalized PSD of gamma, and lower normalized PSD of delta values compared to non-lucid trials. Statistical analyses (both frequentist and Bayesian) restricted to responsive trials revealed similar values in lucid and non-lucid conditions for all markers, indicating comparable brain activity during responsive trials between non-lucid and lucid REM sleep (Figure 4.6A and Table S4.11).

In sum, lucid REM sleep was characterized by a systematic increase in EEG markers of higher cognitive states, irrespective of behavioral responsiveness to the task, with a pattern of markers similar to the one observed in non-lucid/responsive trials (i.e. faster oscillations and higher complexity compared to non-lucid/non-responsive REM trials). This suggests a ceiling effect for marker values in lucid REM sleep, indicating a sustained high-cognitive state during this condition.

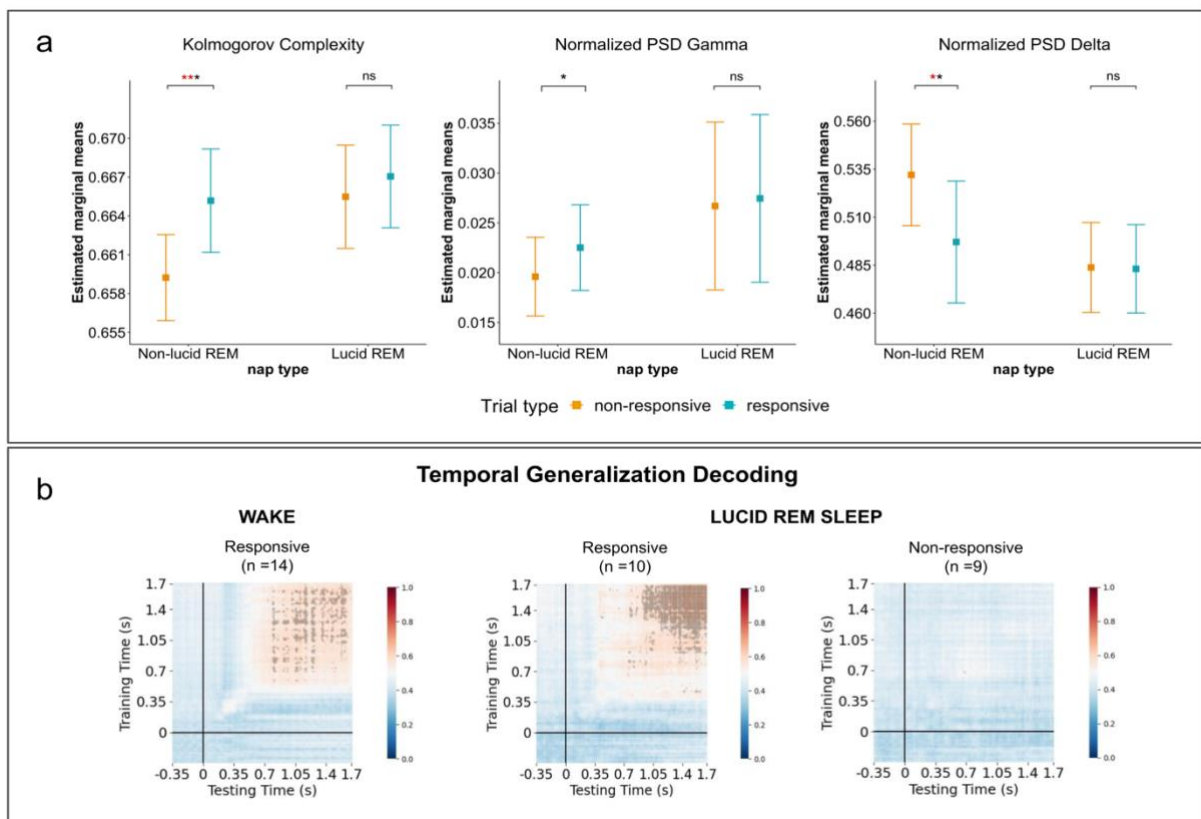


Figure 4.6. Effect of lucidity on EEG markers and response to stimuli in participants with narcolepsy. (a) The top panel shows Kolmogorov complexity (left), normalized gamma PSD - *norm-gamma* (middle), and normalized delta PSD - *norm-delta* (right) prior to stimuli onset as a function of whether the stimulus will be followed by a behavioral response (in blue) or not (in orange), for lucid and non-lucid REM sleep in participants with narcolepsy. Kolmogorov complexity and *norm-gamma* were significantly higher for responsive trials compared to non-responsive trials in non-lucid naps for all participants. Conversely, the *norm-delta* was significantly lower in responsive trials in non-lucid

naps. No such differences were observed in lucid naps, suggesting a ceiling-effect for markers of high cognitive states in lucid naps (see Table S4.10 for statistical details). Overall, Kolmogorov complexity and norm-gamma were higher, and norm-delta was lower in lucid naps compared to non-lucid naps irrespectively of the responsiveness. (b) Time-generalization decoding of stimulus-related brain activity compared to baseline brain activity, in trials with (top) and without (bottom) response, in Wake (left) and Lucid REM sleep (right). The logistic regression classifier was trained on each time point and then tested on all the time points to obtain a generalization pattern. Each intersection point of a training time and a testing time shows the AUC (Area under the receiver operator curve) of the classifier. Time points with an $AUC > 0.5$ and that are statistically significant are outlined in black (two-sided non-parametric sign test across subjects with FDR correction for 41 616 comparisons, $p < 0.05$). Note that in trials with a behavioral response, we observed for both Wake and Lucid REM sleep short diagonal pattern suggestive of a ballistic transient chain of distinct processing stages, followed by a squared-shape pattern revealing a late, stable, and sustained stage of processing which has been previously associated with conscious access. ****: $p < 0.0001$, ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, ns: non-significant, **red stars** indicate significance after FDR correction for 15 comparisons.

This neurophysiological profile combined with the subjective report of having performed the task during sleep (see behavioral results) suggest that NP *consciously* processed the stimuli *when* in lucid REM sleep. Several signatures of conscious processing have been described in the literature, including the late P3b component in evoked related potentials (Bekinschtein et al., 2009; Del Cul et al., 2007; Sergent et al., 2005) or the square-like shape pattern in the temporal generalization method (King & Dehaene, 2014; Sanchez et al., 2020). Such a pattern reflects a late, stable, and sustained processing stage and that has been previously related to conscious access (King & Dehaene, 2014; Sanchez et al., 2020; Sergent et al., 2021). Given our unbalanced dataset, we primarily used the temporal generalization approach to explore consciousness of external stimuli in lucid REM sleep (see Figure S4.13 for stimulus-locked ERPs). Briefly, this analysis tests how stimulus-induced brain activity differs from baseline activity; it consists in training a linear classifier at each time-point to differentiate stimulus-present versus stimulus-absent epochs and testing its performance for all the other time-points (for example, training the classifier at $t=2$ and testing its ability to correctly classify at $t=1,2,3,4,5,\dots$, obtaining thus a whole matrix of performance for each training time point/testing time point). We found that responsive trials during lucid REM sleep were associated with the expected square-like shape pattern starting from 350ms post-stimulus presentation (Figure 4.6B). This pattern was similar to the one observed in responsive Wake trials, indirectly supporting our hypothesis that NP are conscious of the stimuli presented

during responsive trials in lucid REM sleep. In contrast, we did not find any discernible decoding pattern for non-responsive trials in lucid REM sleep, suggesting that NP are not conscious of external stimuli when they do not respond. This result might seem at odds with our previous observation that marker values computed *prior* to the stimulation were similarly high in responsive and non-responsive trials (Figure 4. 6A) in lucid NP. It suggests that high marker values are indicative of a rich cognitive state, which is permissive (but not necessarily sufficient) for responsiveness during sleep.

Lucid REM sleep trials were therefore associated with: (i) a subjective report of having performed the task while sleeping; (ii) a systematic increase in EEG markers of higher cognitive states; (iii) an electrophysiological signature of conscious processing of external stimuli in responsive trials (temporal generalization pattern), and (iv) longer reaction times, suggesting that participants were engaged in a dual task during which external information (outside world, including verbal stimuli) and internal information (ongoing dream) competed for attention (Andrillon & Kouider, 2020). All these findings hint that lucid participants could consciously integrate and respond to external stimuli during sleep.

4.5. Discussion

Our results provide compelling evidence that sleeping humans present *transient windows* of sensory connection with the outside world during which they process external information at a high-cognitive level and can physically respond. Until now, behavioral responsiveness had only been demonstrated during the sleep onset period (Ogilvie, 2001; Strauss et al., 2015, 2022) or in the unique case of lucid REM sleep (Konkoly et al., 2021). Our findings go further by demonstrating the possibility for behavioral responsiveness to external stimuli in bona-fide sleep in a large group of participants. Responses were associated with temporally and spatially localized activations in the sleeping brain. While remaining rare in healthy participants, we argue that the existence of these transient windows of behavioral reactivity provides a much more complex picture of sleep/wake phenomena than previously considered. Furthermore, we show that these transient windows of cognitive and behavioral connection are associated with specific brain dynamics (faster oscillatory activity and higher signal complexity), which predict responsiveness on a trial-by-trial basis. Finally, for the particular case of lucid REM sleep, we provide strong arguments in favor of a *conscious* processing of *external* information, including the presence of a neural signature of conscious access (King & Dehaene, 2014) in responsive trials and explicit recall of having performed the task during sleep.

Our study presents several limitations. First, we primarily chose to assess behavioral responses using a visual inspection of the corrugator and zygomatic muscle activity on EMG channels. We favored this method to an automated algorithm, which requires choosing an arbitrary threshold and would need to be validated against a gold-standard (which does not exist). Note however that our visual scoring was consistent with an automatic detection of responses based on EMG signal variance. Second, we only investigated responsiveness during daytime naps, thus preventing us to fully assess behavioral responsiveness during N3 sleep (not enough trials) and more generally during night-time sleep. Third, our 10-electrodes montage with a mastoid reference was not ideal to compute the wSMI connectivity measure (Chella et al., 2016), making the results of this analysis difficult to interpret. Fourth, we used post-nap subjective reports to determine lucidity instead of the gold-standard, objective signal of lucidity (LaBerge et al., 1981; Oudiette et al., 2018; Voss et al., 2009). Nevertheless, we also collected an objective lucidity signal (successive corrugator and zygomatic contractions) that substantially matched participants' subjective reports upon awakening, confirming the reliability of subjective reports in determining participants' lucidity. Finally, we only obtained lucid naps in patients with narcolepsy. Therefore, our results for lucid REM sleep need confirmation in lucid healthy participants.

Although the response rate was minimal during OFF periods (compared to ON periods), it was still greater than zero, which might appear surprising in the absence of stimuli. This can be due to several factors: (i) participants might have had spontaneous contractions, (ii) they might have dreamt about the task and contracted their muscles in response to a dreamt auditory stimulation, or (iii) we might have over-estimated the contraction rates. Spontaneous single contractions called 'twitches' are common during REM sleep. However, we only considered two or more successive contractions as responses, eliminating all twitches. Moreover, behavioral responses were assessed while blind to the sleep stage and to the stimulation period (ON vs. OFF), ensuring that any putative false detection bias is uniformly distributed in all sleep stages and stimulation periods. Therefore, any differences in the response rates between ON and OFF periods reflect a genuine effect.

One might argue that the behavioral responses we observed during sleep occurred during brief episodes of wakefulness. Yet, all trials containing a micro-arousal (before and/or after the stimulation) were excluded from all analyses to ensure that participants were indeed asleep while responding, at least according to the well-accepted sleep scoring rules (Berry et al.,

2017). Moreover, EEG spectral measures in responsive sleep trials reflected the expected sleep stage variations, with significantly higher delta power and significantly lower alpha power compared to Wake trials. Finally, post-stimulus analyses revealed an increase in alpha and beta power in responsive trials. However, given the frontal localization of these modifications and the timing relative to the motor preparation potentials, we argue that they reflect cognitive and motor processes rather than micro-arousals, at least in the classical sense. Recent studies suggest that the discrete frontiers between wake and sleep might be fuzzier than the international sleep criteria would allow (Berry et al., 2017). For example, local sleep-like phenomena can be observed during wake, and influence cognitive capacities and behavior (Andrillon et al., 2019, 2021). In the same way, it is possible that our participants had ‘local wake events’ (local in space and/or time) allowing them to respond to external stimuli while sleeping. Our current gold-standard sleep scoring guidelines are not suited to detect such subtle variations in brain dynamics. By calling into a question the assumption that behavioral and coarse physiological measures of sleep always align, our study could precipitate the development of finer-grained sleep scoring which better captures cognitive capacities including behavioral responsiveness in the wake-sleep continuum. Such endeavor may be clinically relevant. For example sleepwalking could be interpreted as extreme forms of these local wake events, still happening on a global background of sleep brain activity (Arnulf, 2018; Idir et al., 2022).

While both participants with and without narcolepsy displayed responses during sleep, those with narcolepsy responded more. Since both groups had similar contraction rates during OFF periods, patients’ increased responsiveness is not due to an overall decrease in the detection criterion. Enhanced responsiveness in patients could be due to: i) an acquired capacity to remain connected with their surroundings while sleeping as an adaptation to their tendency to fall asleep in unconventional situations, ii) a reduced muscle atonia compared to healthy controls (Dauvilliers et al., 2007), iii) a higher proneness to experience “local wake events” due to narcolepsy-related sleep-wake instability (Dauvilliers et al., 2007). Even though participants with narcolepsy responded more frequently during sleep, both populations shared common EEG marker modifications in responsive trials. Crucially, the performance of a classifier trained with data from participants with narcolepsy generalized to healthy participants. These two findings strongly suggest that the existence of these transient windows of behavioral reactivity is a general feature of sleep, of which narcoleptic participants present an exacerbated profile.

Our results enhance our understanding of the lucid dream phenomenon and of its neural correlates (Dresler et al., 2012; Voss et al., 2009). We found modifications in spectral power (increase in normalized PSD of gamma and decrease in normalized PSD of delta) as well as an increase in signal complexity (Sample Entropy) during lucid REM sleep, compared to non-lucid REM sleep, supporting the findings from a recent study (Baird et al., 2022). Importantly, we provide strong evidence that lucid participants perceived stimuli in a conscious manner. This evidence included subjective report (the gold standard for assessing conscious access) and the presence of neural responses previously shown to reflect conscious perception (a stable and sustained brain activity in response to stimuli) (King & Dehaene, 2014; Sanchez et al., 2020; Sergent et al., 2021). These results show that lucid dreaming is not only characterized by a reemergence of metacognitive and volitional capacities (Dresler et al., 2014; Filevich et al., 2015), but also by a capacity to consciously process external information.

To what extent were non-lucid sleepers conscious when responding to stimuli remains an open question. Indeed, contrarily to lucid dreamers, non-lucid dreamers typically could not recall having performed the task during sleep and we could not perform temporal generalization decoding due to the insufficient number of trials in these participants. Either way, our findings have major consequences for consciousness research. If non-lucid sleepers unconsciously processed stimuli, the fact that they could make a lexical decision associated with a behavioral response would push further the boundaries of what is considered possible for an unconscious process. On the other hand, if non-lucid sleepers were actually conscious when responding, our experimental design could help probing the minimal core of cortical activity required for conscious processing. In our opinion, several lines of evidence favor conscious processing in N2 and non-lucid REM sleep. First, neurophysiological markers computed before the stimulation in responsive trials were similar to the ones in lucid participants, suggesting that the neural state associated with responsiveness was comparable in both cases. Furthermore, the unconventionality of the response modality (corrugator or zygomatic muscle contractions) makes the automatization of the task difficult. Finally, reaction times to stimuli largely exceeded the one classically observed for automatic and unconscious processing (typically around 200ms vs. several seconds in our task) (Rossetti, 1998). One may wonder why participants would fail to report having done the task if they had consciously performed it. We hypothesize that the rich neural states presumably allowing responsiveness need to be sustained over a certain time to be encoded. These rich states might have been less stable in non-lucid participants, as suggested by the difference in neurophysiological markers between responsive

and non-responsive trials, (not found in lucid participants), preventing episodic memory encoding and thus subjective reports.

The standard view of sleep/wake states assumes that we would be either awake or asleep. Overall, our findings suggest that this view does not account for the richness and high variability within each of these states. This intuition goes along with a recent theory in the memory domain (Helfrich et al., 2021), arguing that the high prevalence of aperiodic brain activity during sleep (up to 50% of brain activity without prominent oscillations, even in N3 sleep) could play a central role in processing internal stimuli (i.e. imprinting memories into existing networks). Our results supplement this view by showing that access to external information might fluctuate even in traditionally defined states of consciousness (e.g. a given sleep stage) depending on the ongoing brain activity. We could imagine sleep and wake as a continuum of stages whose physiology is more (e.g. wake) or less (e.g. N3 sleep) favorable for the emergence of the rich neural states that enable conscious access and behavioral response to external stimuli (Naccache, 2018).

Our study opens the way for many exciting studies investigating sleepers' cognitive capacities and their associated phenomenology. By implementing a second probe about a participant's current mental state, we could assess metacognition during responsive moments (e.g., do sleepers know that stimuli come from the outside, or do they integrate them in their dream?). We could also test the extent to which the sleeping brain is able to acquire new information, hence fueling the debate on whether sleep learning is limited to conditioning (Arzi et al., 2012) and implicit memory processes (Züst et al., 2019) or could extend to the formation of an explicit memory trace. By tracking how the neurophysiological markers indexing a rich cognitive state fluctuate in real time and by sending stimuli depending on their values, we could test the causal relationship between the neural state and responsiveness. Moreover, we could target these brief windows of reactivity in sleep to attempt real-time communication with individuals across different sleep stages, which would open the exciting possibility to inquire about any sleepers' mental states beyond the particular case of lucid dream (Konkoly et al., 2021). Our findings also raise questions relevant for clinical practice: are responsive periods during sleep less recuperative than unresponsive periods? Our methods could be used to investigate "sleep depth" in patients suffering from excessive daytime sleepiness or for bringing mechanistic insights into the puzzling mismatch between subjective wake perception and classical sleep markers in paradoxical insomnia. By demonstrating the existence of windows of behavioral

responsiveness across most sleep stages, our study provides a new tool for unlocking the mystery of what happens in sleepers' minds.

4.6. Supplementary methods

Automatic response detection algorithm

In addition to our visual evaluation of response contractions, we also detected behavioral responses using an objective, automatized method. To do so, we created a response detection algorithm based on voltage variance in our two EMG channels of interest (corrugator and zygomatic muscles). This algorithm computed the signal variance in the 1 second pre-stimulus baseline period and compared it to the post-stimulus variance using sliding-windows. Our algorithm had two predefined parameters: (1) the length of the sliding window and (2) a constant k . If the variance in a given sliding window exceeded k *baseline variance, the algorithm labeled the trial as responsive; otherwise, the trial was labeled as unresponsive. We ran the algorithm with different combinations of parameters. We used 1 and 2 second time windows (parameter 1), based on the observation that a unique muscle contraction took approximately 300ms. The second parameter k was either 5, 7, or 10. Examples of muscle contractions and corresponding variance modulations are shown in Figure S4.8.

Automatized detection of spindles and slow-waves

Raw EEG files were band-pass filtered between 0.1 and 45Hz, with 50Hz and 100 Hz notch filters. Data was down-sampled to 250Hz. Trials were then segmented from -1000 ms to 8000 ms relative to stimulus-onset. We analyzed N2 trials of healthy participants using a previously validated automatized sleep scoring algorithm (YASA, Vallat & Walker, 2021). For each trial (from -1000 to 8000ms relative to stimulus onset) we assessed whether at least one spindle or slow wave (independently for each one of these two sleep graphoelements) was present during the duration of the trial, in at least two different channels. We then computed for each sleep graphoelement, each participant, and each condition (responsive vs non-responsive trials), the proportion of trials containing graphoelements (spindles or slow waves). We studied the effect of *responsiveness* (responsive vs non-responsive) and sleep/wake stage (N2 sleep vs Wake), as well as their interaction, over the proportion of trials containing at least one spindle or slow wave (independently for these two sleep graphoelements), using repeated measures ANOVA. We corrected p-values for lack of sphericity using a Greenhouse-Geisser correction.

Stimulus locked event related potentials

For each group (HP and NP) and for each sleep/wake stage, we averaged stimulus-locked trials to obtain event-related potentials (ERPs) (after baseline correction relative to the -1000ms to 0 ms time period). We then conducted a mass univariate analysis on time dimension, independently for each EEG channel, using mixed linear models with responsiveness as the explanatory factor, and subject ID as a random effect. We corrected p-values for multiple comparisons using an FDR procedure. Results are presented in Supplementary Figure S4.9. For visualization purposes, we applied a low-pass filter of 10Hz.

4.7. Supplementary results

Responses in N3 sleep

We did not find a significant difference between ON and OFF periods in healthy participants during N3 sleep (0.2% vs. 0.9%, $z = -1.23$, $p = 0.22$), but we found significantly more responses during ON than OFF periods in N3 sleep in participants with narcolepsy (5.7% vs. 2.4%, $z = 3.31$, $p = .0009$). The response rates were higher in NP than in HP during ON stimulation periods in N3 sleep ($z = 3.66$, $p = .0002$).

Performance of the automatic response detection algorithm

We performed two analyses based on the response scoring of the automatic algorithm. First, we compared the concordance of our manual scoring to the one of the algorithm in different sleep stages using different performance metrics (accuracy, recall, and precision). Recall (or sensitivity) corresponds, in the context of our task, to the number of correctly labeled responsive trials divided by the total number of responsive trials (True Positives/[True Positives + False Negatives]). Precision, on the other hand, corresponds to the number of correctly labeled responsive trials divided by the total number of trials labeled as responsive (True Positives/[True Positives + False Positives]). We then tested the significance of these metrics against chance-level using a 500-permutations procedure. We found, for all metrics and all tested sleep stages, a significant match between the two scoring methods, with accuracy ranging from 0.75 to 0.91. The detail of the results can be found in Table S4.2 (for healthy participants) and in Table S4.3 (for participants with narcolepsy).

We then compared the response rate, as scored by the algorithm (blind to the visual scoring), in ON versus OFF stimulation periods. We found significant more responses during ON vs.

OFF periods in all sleep stages in both populations (except in N3 for healthy subjects), replicating the results from our manual scoring. The details of the results based on different parameter combinations can be found in Figure S4.9. Since the two scoring methods were largely congruent and because we do not have a gold-standard to validate the objective performance of our algorithm (besides our visual scoring), we chose to keep our visual scoring for the rest of the analyses.

Mixed contractions to signal lucidity

In this experiment, participants were instructed to perform a lexical decision task in their sleep by contracting three times their corrugator or zygomatic muscles (according to the stimulus). In case they were lucid dreaming but were not hearing any stimuli, they were asked to signal their lucidity with a “mixed contraction” by alternating one corrugator and one zygomatic muscle contraction. We did not observe any mixed contractions in participants without narcolepsy (HP). On the other hand, we observed a total of 117 mixed contractions from 12 participants with narcolepsy (NP) in 19 different naps. Importantly, all 19 naps contained responses to the stimuli during N2 and/or REM sleep. Among the 117 mixed contractions, 93 were observed in REM sleep, 92 being in naps that were reported (upon awakening) to be lucid (Figure S4.7). Moreover, 18 contractions were observed in N2 sleep (12 being in lucid naps) and 6 contractions were observed in N1 sleep (5 being in lucid naps). These results indicate that (i) facial muscle contractions can be used to signal lucidity, validating our previously published results (Konkoly et al., 2021); (ii) participants remember most of the signaled lucidity episodes, especially in REM sleep; and (iii) signaled lucidity episodes are associated with higher responsiveness to the external stimuli.

Similar latencies of zygomatic and corrugator muscles' contractions

We examined the response latencies of the two response types (zygomatic and corrugator contractions) in order to ensure that they had the same level of difficulty. We found similar response latencies for the two muscles in all sleep stages (no interactions were found with the sleep stage) for both participants with ($t = 1.38, p = 0.18$) and without narcolepsy ($t = 0.88, p = 0.38$).

Increased responsiveness is associated with increased accuracy

Since a negative correlation between accuracy and response rate could be a sign of false detection, we tested the relationship between these two behavioral measures. The relationship between the response rate and accuracy was evaluated at the participant level for each sleep stage and group using Pearson's correlation. Only participants with at least three trials were included in this analysis. Our analyses revealed that response rate was positively correlated with accuracy in participants with narcolepsy during Wake ($R = 0.4$, $p = 0.04$), N2 sleep ($R = 0.49$, $p = 0.015$), REM sleep ($R = 0.6$, $p = 0.038$) and lucid REM sleep ($R = 0.64$, $p = 0.001$). We also observed a similar tendency in healthy participants during Wake ($R = 0.38$, $p = 0.094$) and N1 sleep ($R = 0.46$, $p = 0.062$).

Old/New recognition task upon awakening

After each nap, participants performed an old-new recognition task, during which they were presented with stimuli they heard during the preceding nap and new stimuli that were never presented during the experiment. Participants had to indicate whether they had heard the stimuli during the preceding session with one of the following responses: 1: I heard it from the dream (for example, a person from their dream saying the word), 2: I heard it from outside (pronounced by the computer), 3: I am not sure I heard it, 4: I am sure I did not hear it. They responded by pressing the corresponding button without any time pressure. The four options were explained to the participants during training, prior to the first session. We assessed whether participants were able to correctly recognize the stimuli upon awakening. We focused on participants with narcolepsy (NP) since they went through 5 short naps, which should make the recognition of stimuli easier than in healthy participants who had a longer, 100 min nap. First, we computed, for each nap, the percentage of false recognition of new stimuli. A stimulus was considered "recognized" if participants reported either (1) hearing it in their dreams or (2) hearing it from outside of their dreams while asleep. On average 8.46% of new stimuli were falsely recognized. Then, we assessed the correct recognition of stimuli that were previously presented in different sleep stages. The percentage of correct recognition was 21.9% in Wake, 15.71% in N1, 8.6% in N2, 9.3% in REM, and 9.43% in lucid REM sleep. This percentage of correct recognition was significantly different than false recognition only in Wake ($p < 0.0001$, $z = 4.16$) and N1 sleep ($p < 0.002$, $z = 3.7$). Low recognition rates (even in Wake and lucid REM sleep trials) can be due to several factors. First, participants had no explicit instruction to remember the stimuli; they were simply asked to perform a lexical decision task. Moreover,

each nap included a high number of stimuli (60 in each nap for the NP and 300 in the nap for the HP). Recalling such a high number of stimuli would already be an intense challenge for fully awake participants who would actively try to encode the stimuli. All stimuli were only played once throughout the experiment (no repetition of the same stimulus) and half of the stimuli were pseudo-words (harder to encode than words). And finally, the memory test was performed at the end of a nap, so in most cases long after the stimuli were played. For all these reasons, we believe that the explicit recognition task was far too difficult. It is possible that an implicit test would have been more suited to detect evidence of learning during sleep (Züst et al., 2019) than an explicit one.

Classical sleep graphoelements

We quantified the occurrence of classical sleep graphoelements (spindles and slow-waves) in non-responsive and responsive NREM sleep trials. Given that a manual quantification could be considered redundant with the polysomnographic scoring, we decided to use a previously validated automatized detection algorithm (Vallat & Walker, 2021). Since this algorithm has not been validated in patients with narcolepsy, we only analyzed data from HP, and more precisely N2 sleep trials (responsive and non-responsive), as well as Wake trials as a comparison. For each condition and each participant, we computed the proportion of trials including at least one spindle or one slow wave (independently for these two NREM sleep hallmarks), in the -1000 to 8000 ms time-window relative to stimulus-onset. While both spindle and slow wave occurrence (as detected by the algorithm) were modulated by sleep stage (Spindles: Wake 15% (+/-21%) vs. N2 37% (+/-30%), $F(1,12) = 5.7, p = 0.03$; Slow-waves: Wake 0.02% (+/-0.05%) vs. N2 22.4% (+/-21%), $F(1,12) = 14.3, p = 0.003$), we did not find a significant main effect of responsiveness (Spindles: responsive 25% (+/-31%) vs. non-responsive 26.8% (+/-24.5%), $F(1,12) = 0.47, p = 0.5$; Slow waves: responsive 0.07% (+/-0.18%) vs. non-responsive 0.17% (+/-0.17%), $F(1,12) = 2.7, p = 0.13$) nor an interaction with the sleep stage (Spindles: $F(1,12) = 0.06, p = 0.8$; Slow-waves: $F(1,12) = 1.5, p = 0.24$). In sum, we did not find evidence for a reduced occurrence of classical sleep graphoelements in responsive sleep trials, compared to non-responsive ones in HP.

Random Forest classification

All balanced accuracy scores were significantly different than the chance level computed by a 500-permutation procedure ($p = .002$ for all stages in NP, and $p = .004$ for N2 sleep in HP),

with a mean balanced accuracy score of permutation trials very close to 50% for all stages. Similarly, f1 scores were significantly different than chance level ($p = 0.002$) for Wake, N2, and REM sleep in NP (with a statistical trend for N1, $p = 0.06$), and for N2 in HP (see Figure S4.16).

4.8. Supplementary figures and tables

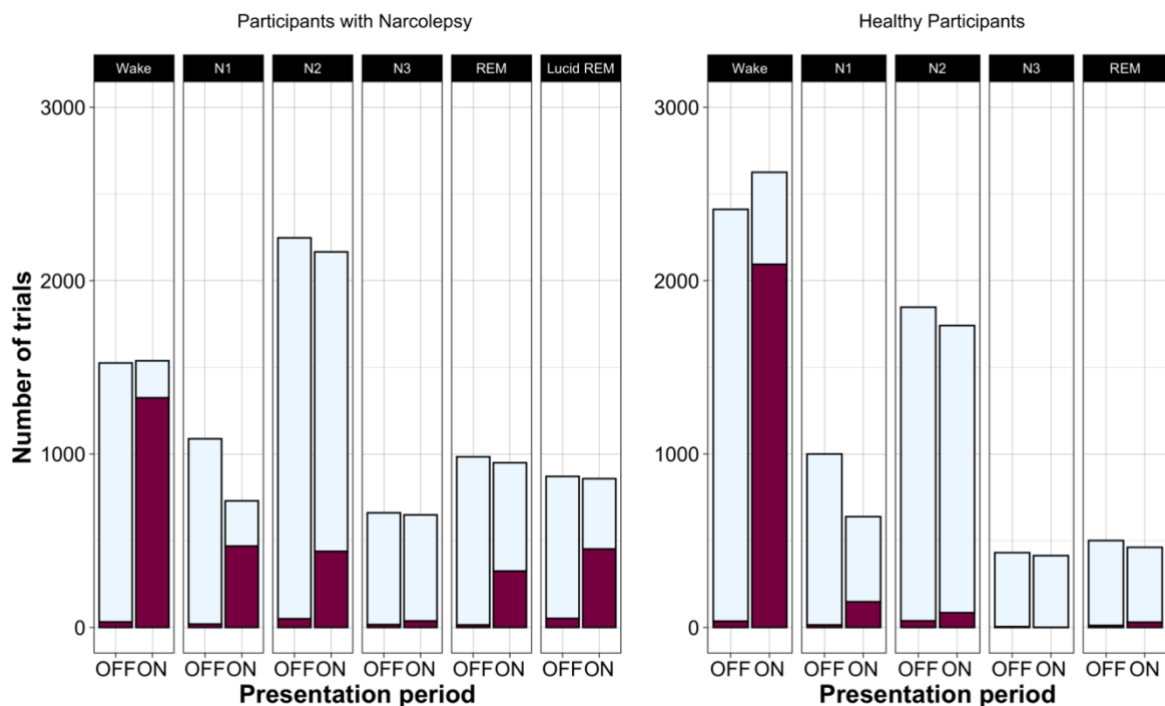


Figure S4.1. Number of trials during ON and OFF stimulation periods in different sleep stages in participants with (left) and without (right) narcolepsy. The partition of trials containing a response is filled with dark red color in both stimulation periods.

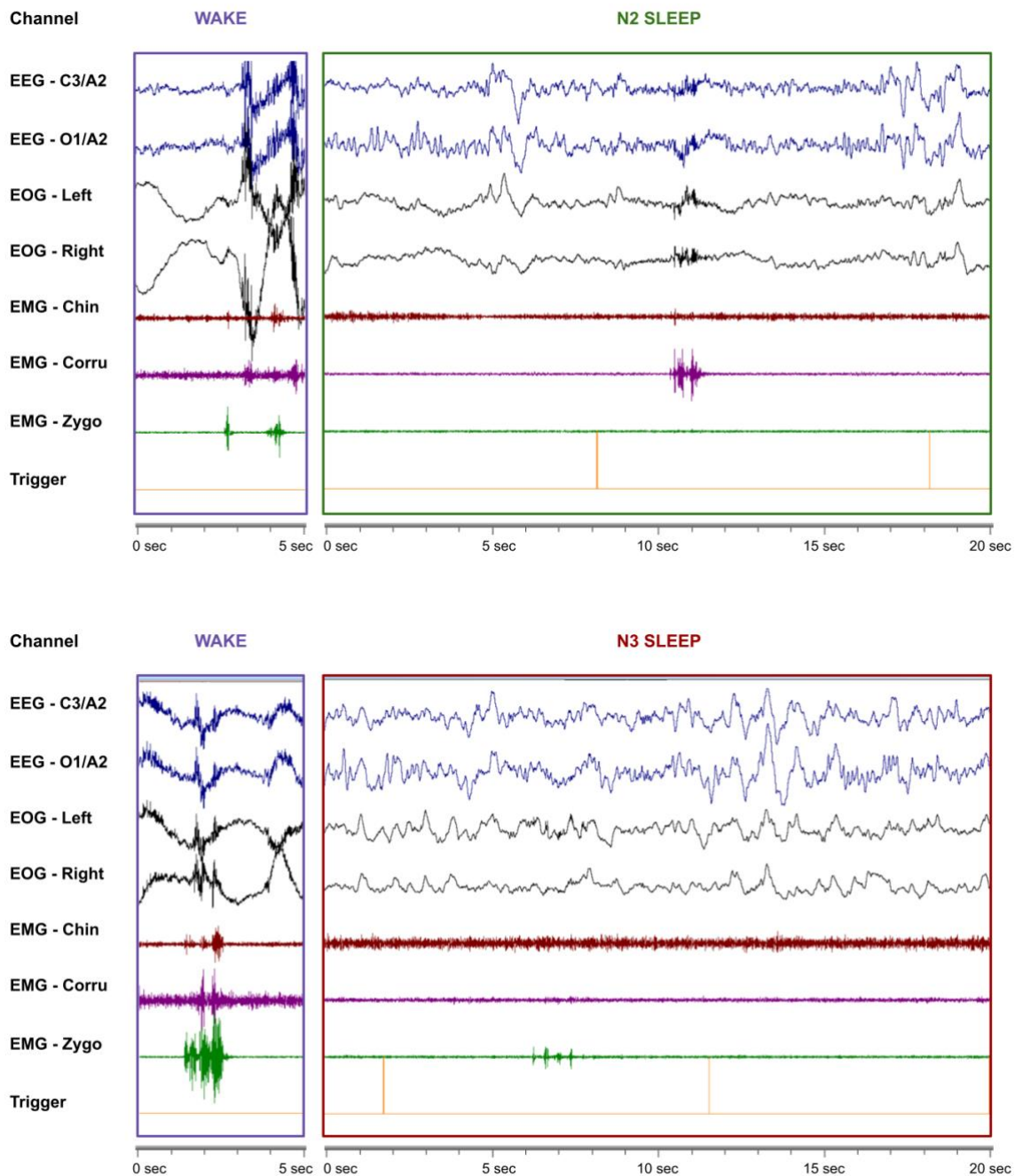
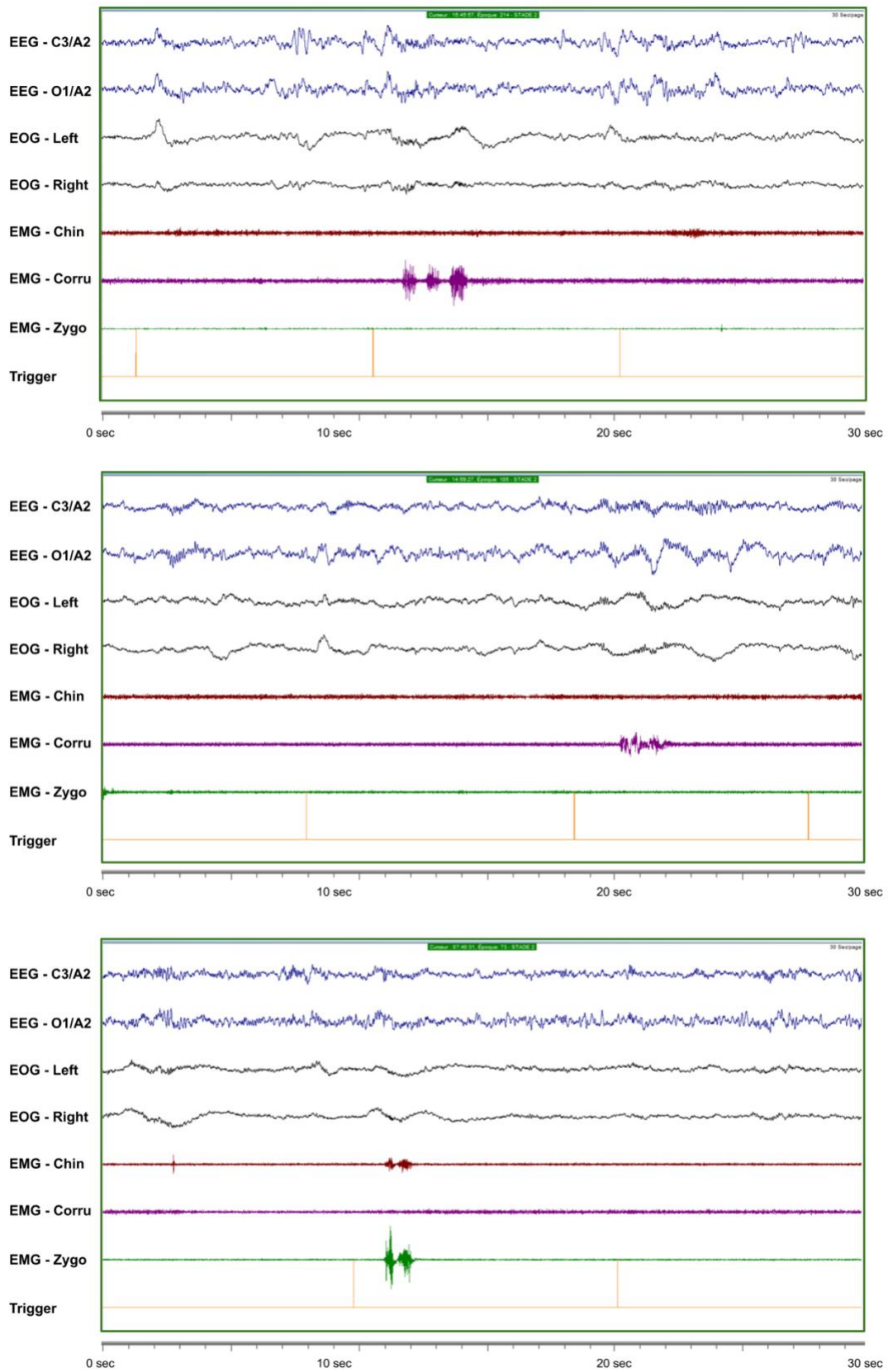


Figure S4.2. Examples of response during N2 (upper panel) and during N3 (lower panel) sleep in participants with narcolepsy. Wake periods corresponding to the same participants are shown on the left side of the figures. The orange vertical line on the last channel indicates the stimulus onset. Responses to stimuli corresponded to contractions of the zygomatic or corrugator muscles.

Figure S4.3. Five examples of responses from different healthy participants during N2 sleep.

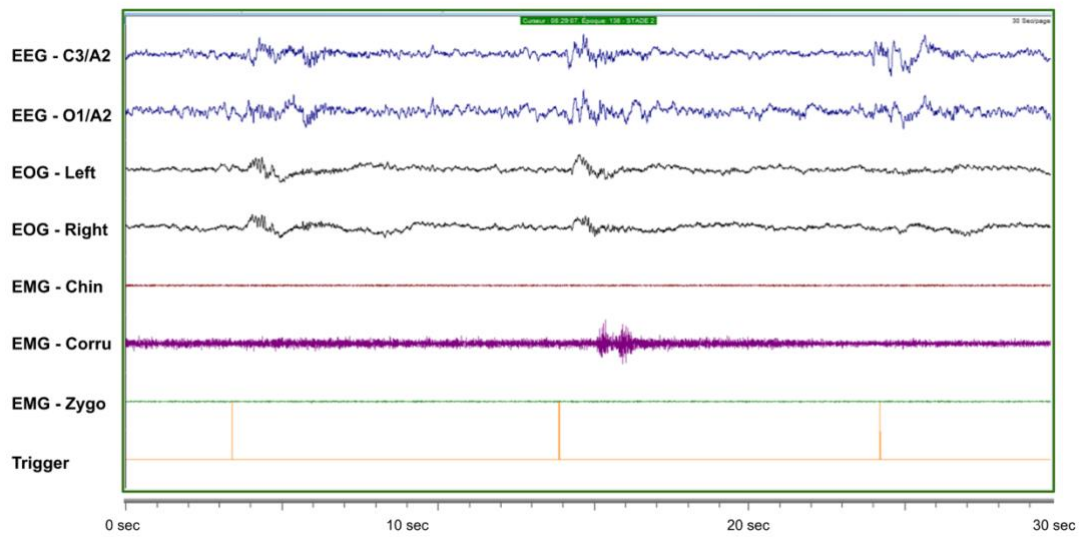
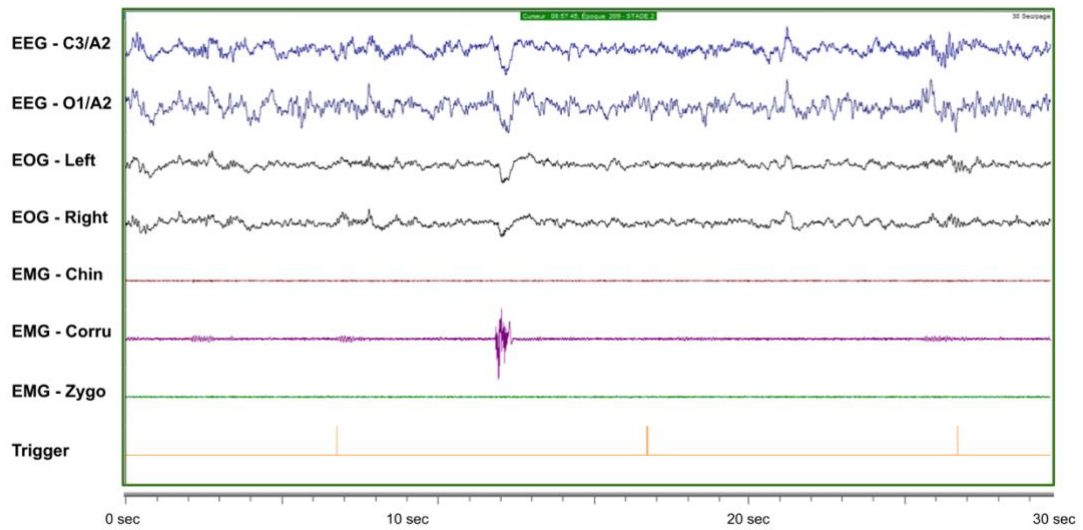
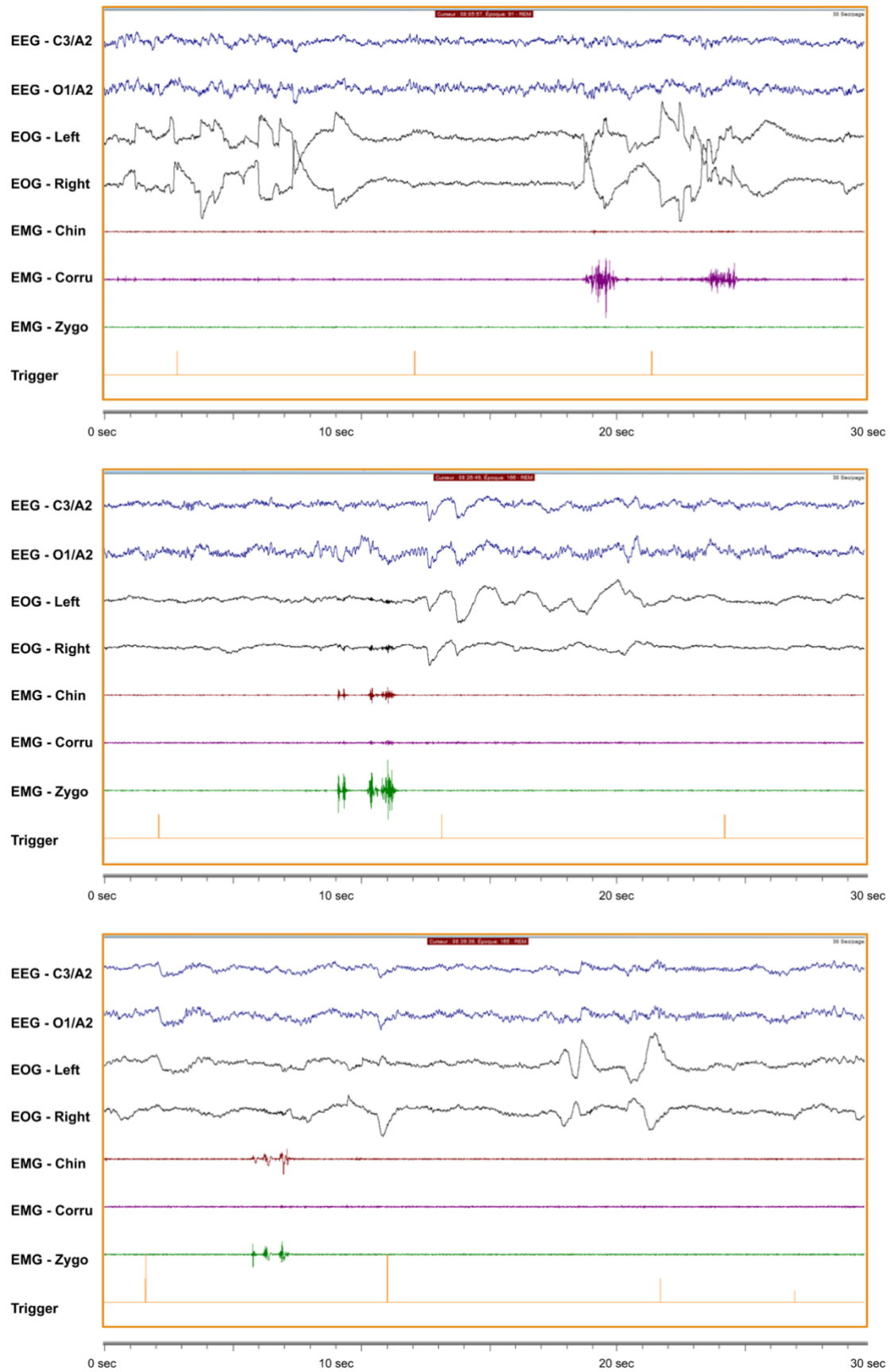
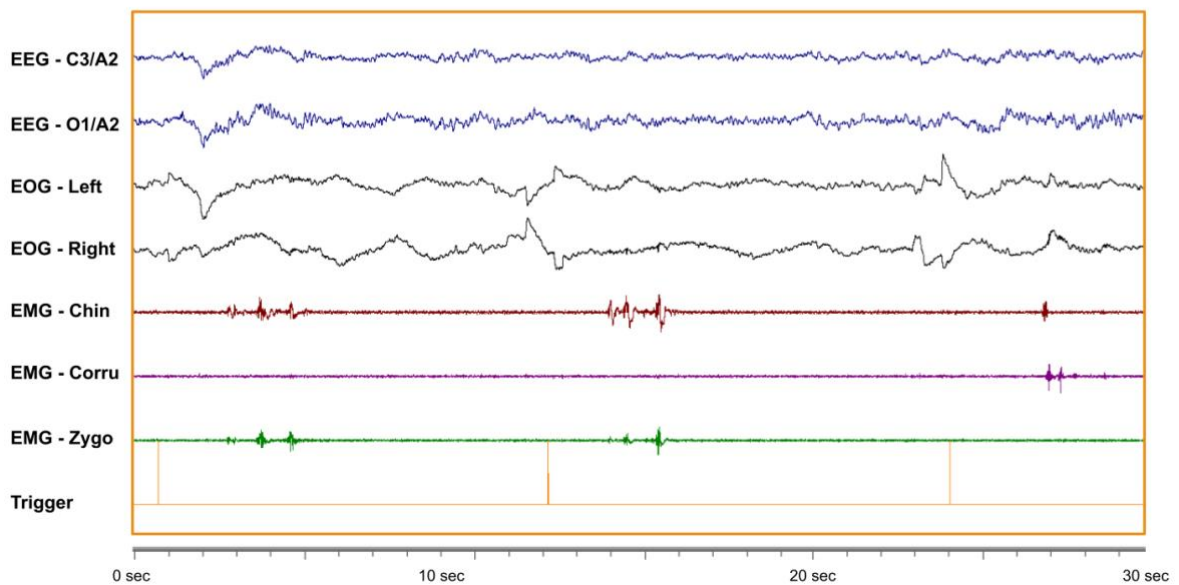
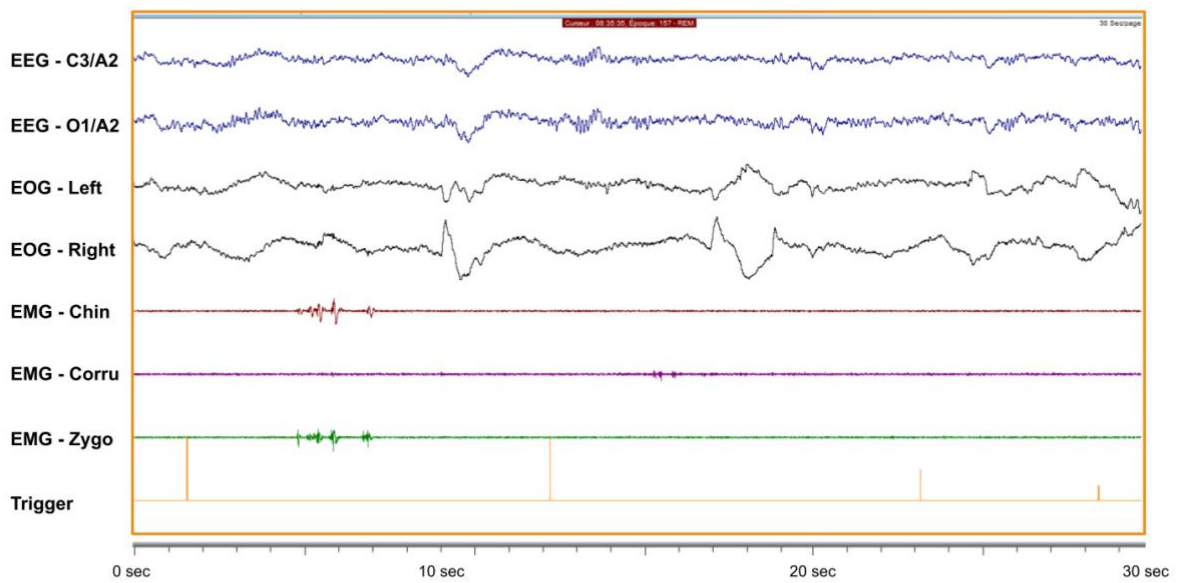
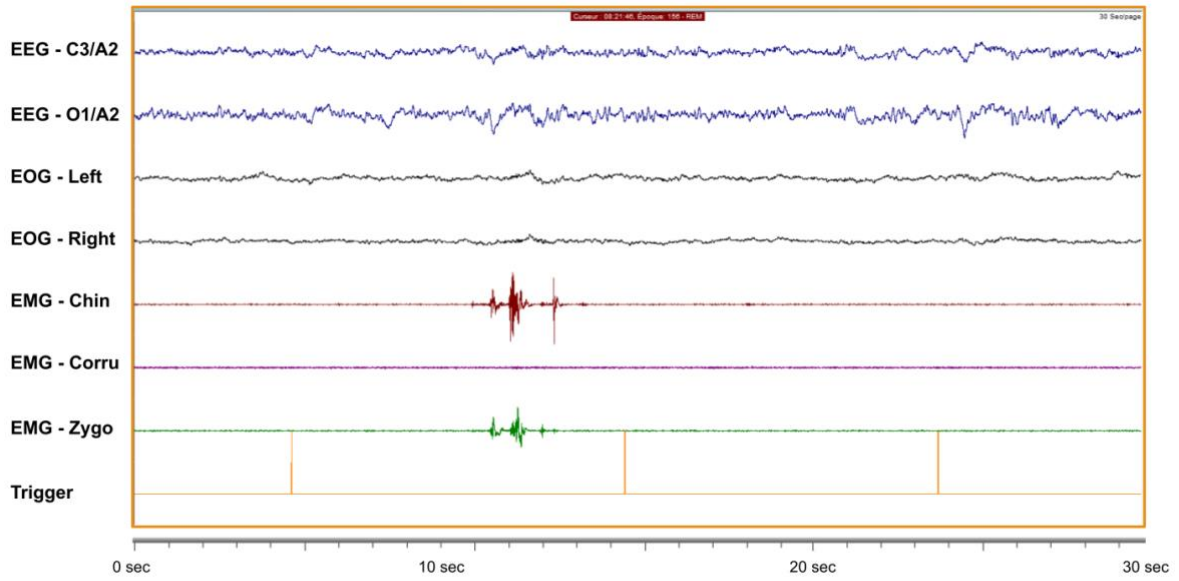


Figure S4.4. Six examples of responses from different healthy participants during REM sleep





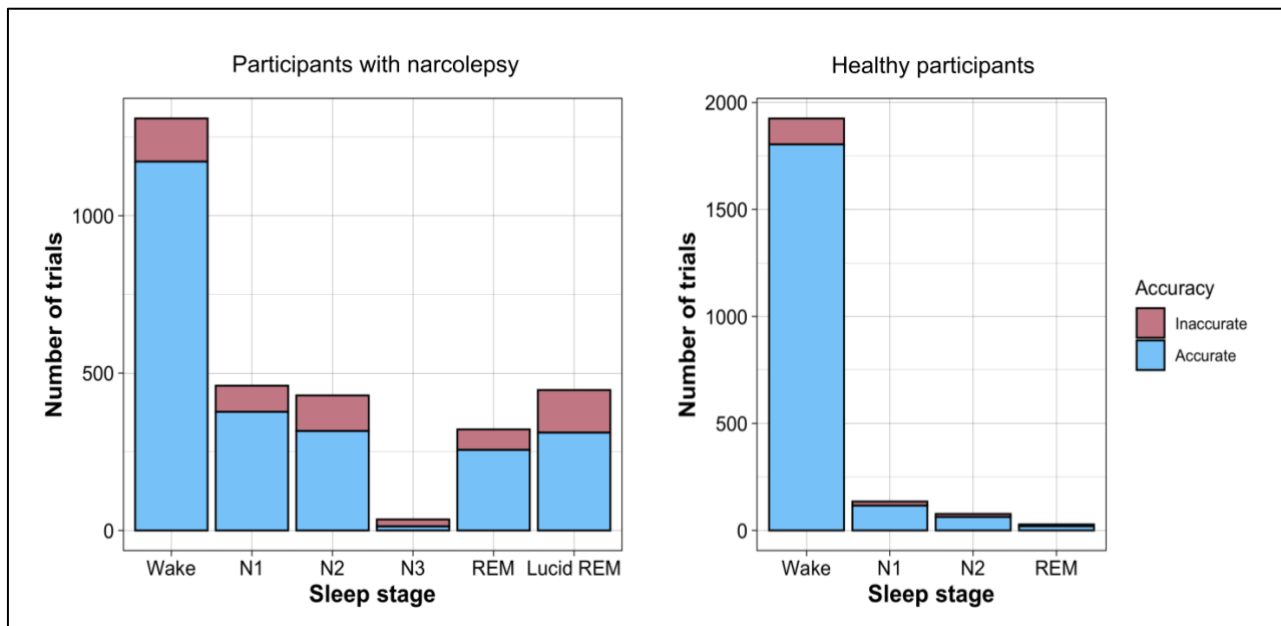


Figure S4.5. Total number of correct and incorrect responses in different sleep stages.

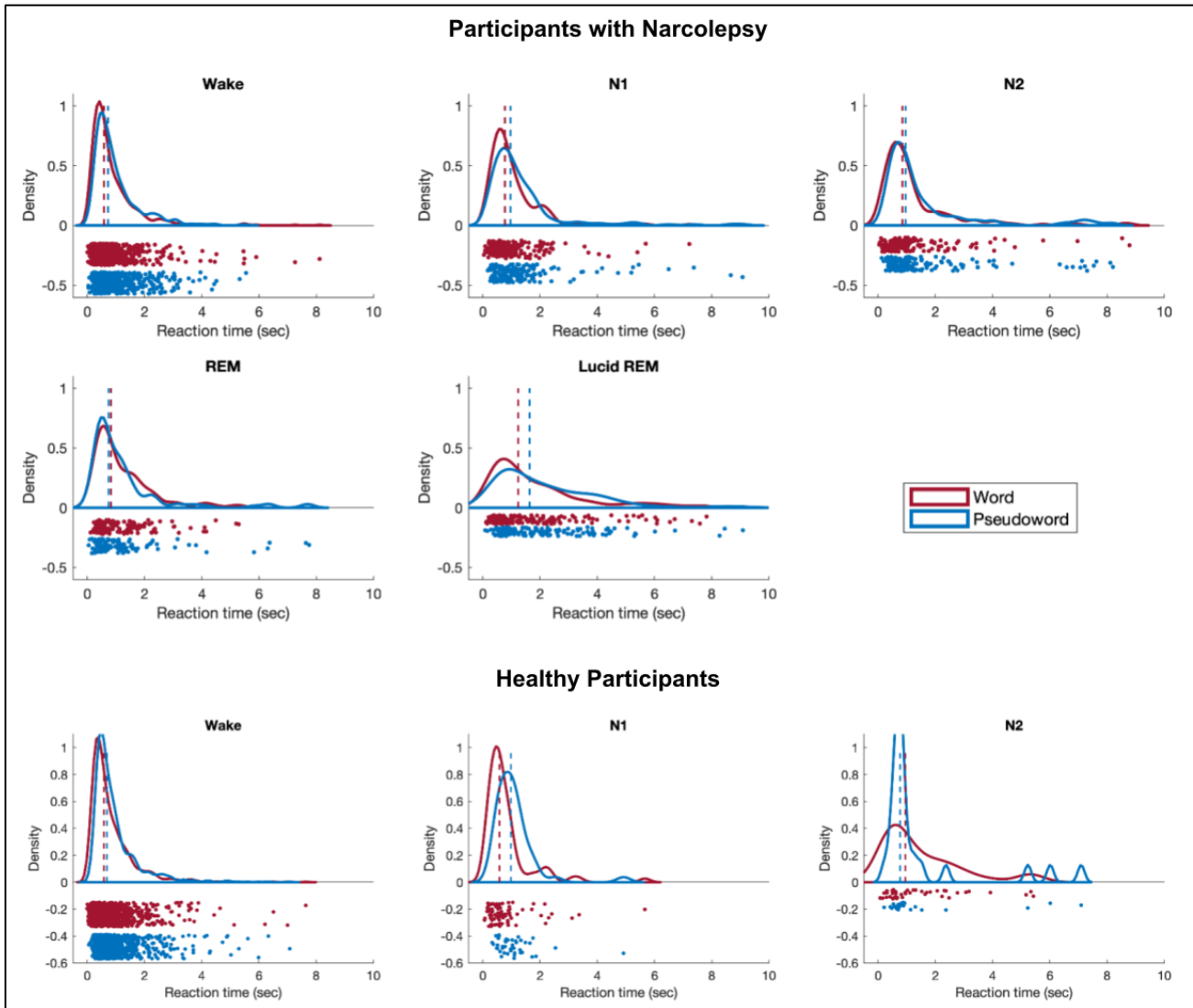


Figure S4.6. Reaction times for words and pseudowords in different sleep stages in participants with narcolepsy and healthy participants.

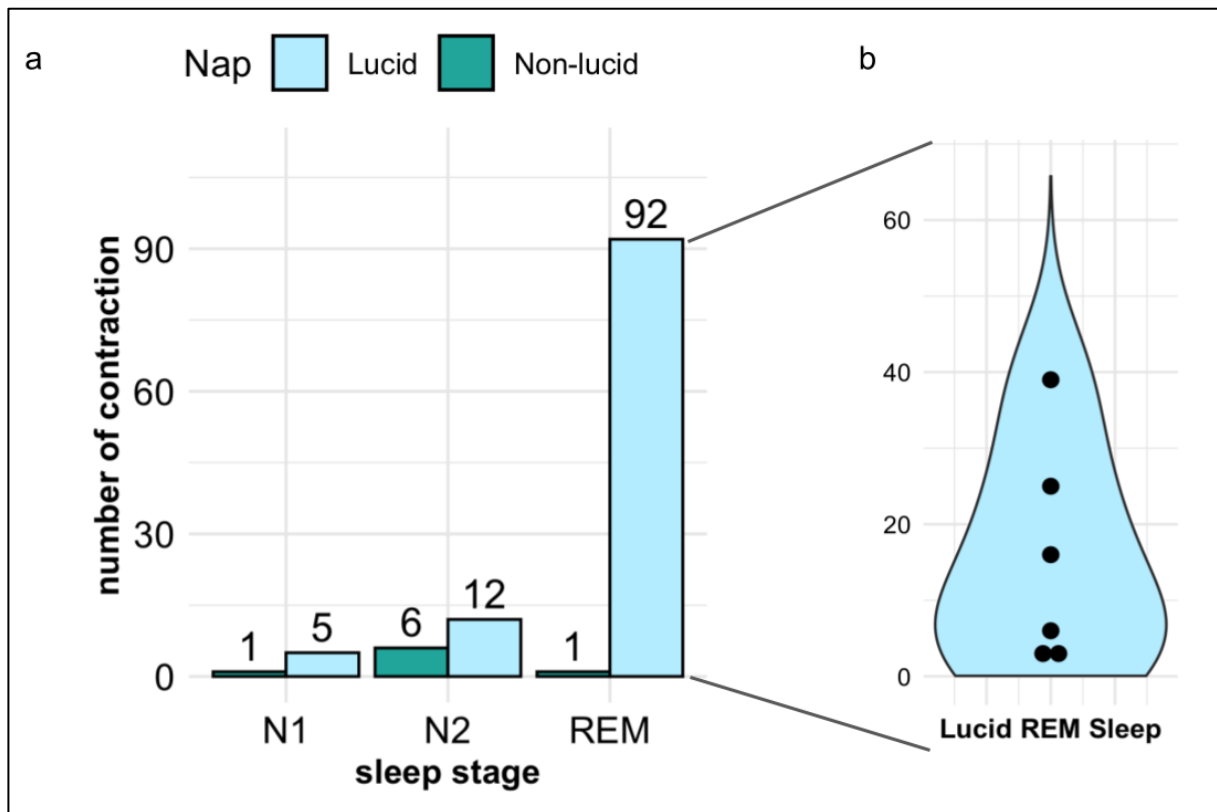


Figure S4.7. (a) Number of mixed contractions (objective lucidity code) in different sleep stages during naps that participants reported to be lucid (sky blue) or non-lucid (green). The relative number of lucidity codes can be found on top of the bars. (b) Number of lucidity codes exhibited by each participant in lucid REM sleep.

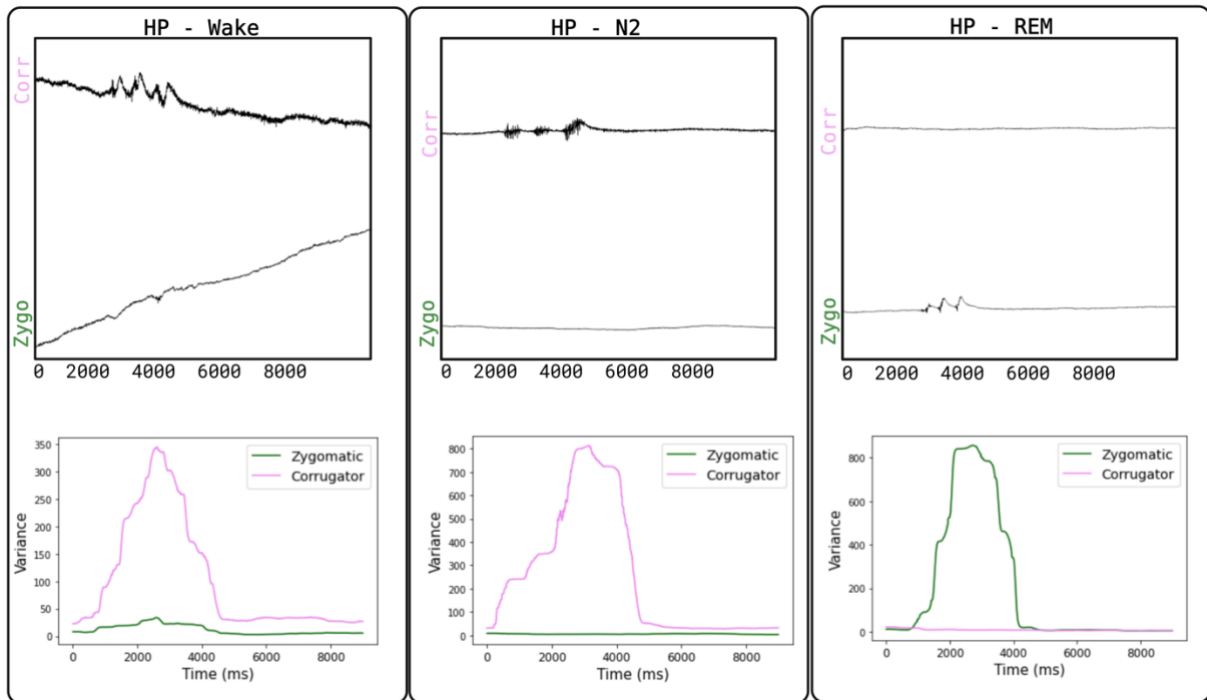


Figure S4.8. Upper panel: Examples of EMG traces showing corrugator (pink) and zygomatic (green) muscles contractions in Wake, N2 and REM sleep in healthy participants (HP). Lower panel: EMG variance modulations computed by the response detection algorithm in the corresponding trials. EMG variance drastically increases in the very time when contractions are visible on the EMG signal and only for the contracted muscle. Note that this method is robust to the slow drifts in the EMG signal (as shown in Wake, left panel) and only detects sudden modulations in the signal such as muscle contractions.

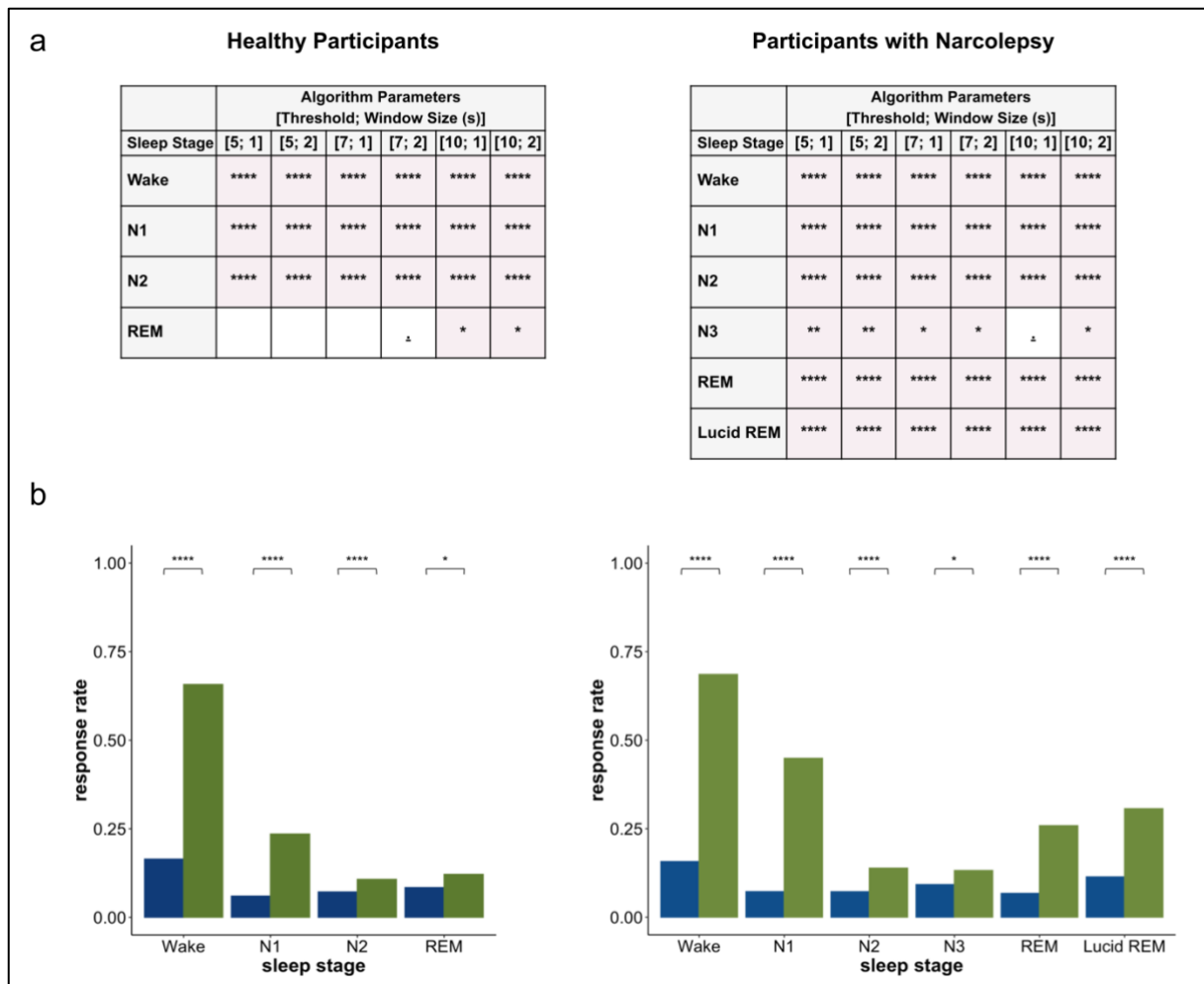


Figure S4.9. Automatic response detection algorithm detects significantly more contractions during ON stimulation periods compared to OFF stimulation periods in different sleep stages and mirrors the manual scoring. (a) Statistical significance of differences in contraction rates between ON and OFF stimulation periods in healthy participants (left) and participants with narcolepsy (right) found by the algorithm using different parameter combinations [Threshold k : 5, 7, 10; Window size: 1 or 2 seconds]. Significant differences after an FDR correction are shaded in red. ****: $p < 0.0001$, ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, dot: $p < 0.1$. (b) Response rates in ON and OFF stimulation periods found by the algorithm using the strictest parameter combination: threshold $k = 10$ and window size = 2 seconds. The algorithm labeled a trial as responsive if the variance of a 2 second window exceeded 10 times the baseline variance. Please note the similarity between this figure and Figure 3a, indicating that response rates found by the algorithm followed the same trend as the manual scoring.

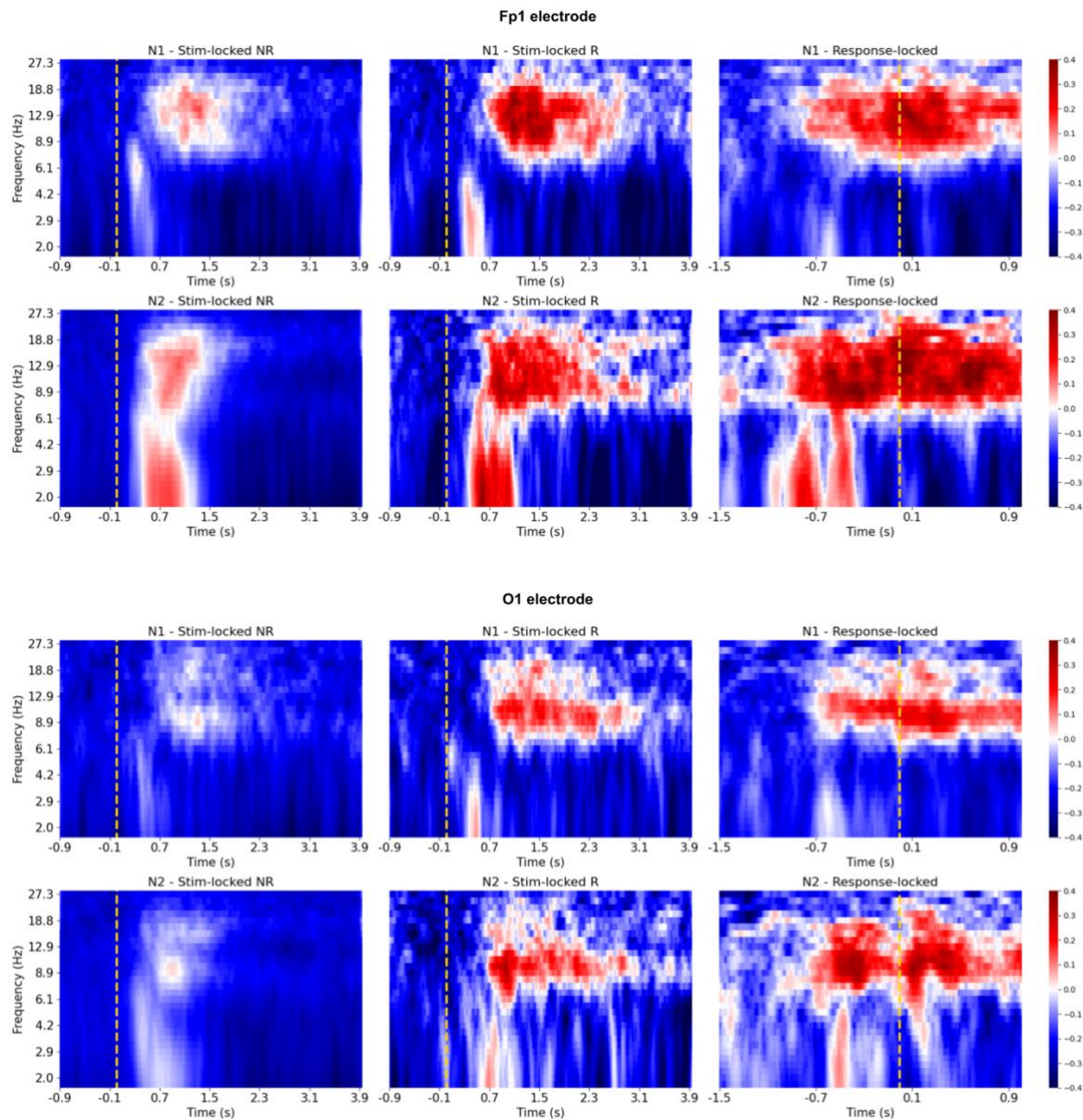


Figure S4.10. Time-frequency analysis (TFA) performed on the Fp1 (upper panel) and the O1 (bottom panel) electrodes in N1 and N2 sleep of HP. The Left and middle panels are stimulus-locked TFA in non-responsive and responsive trials respectively. The right panels show response-locked TFA.

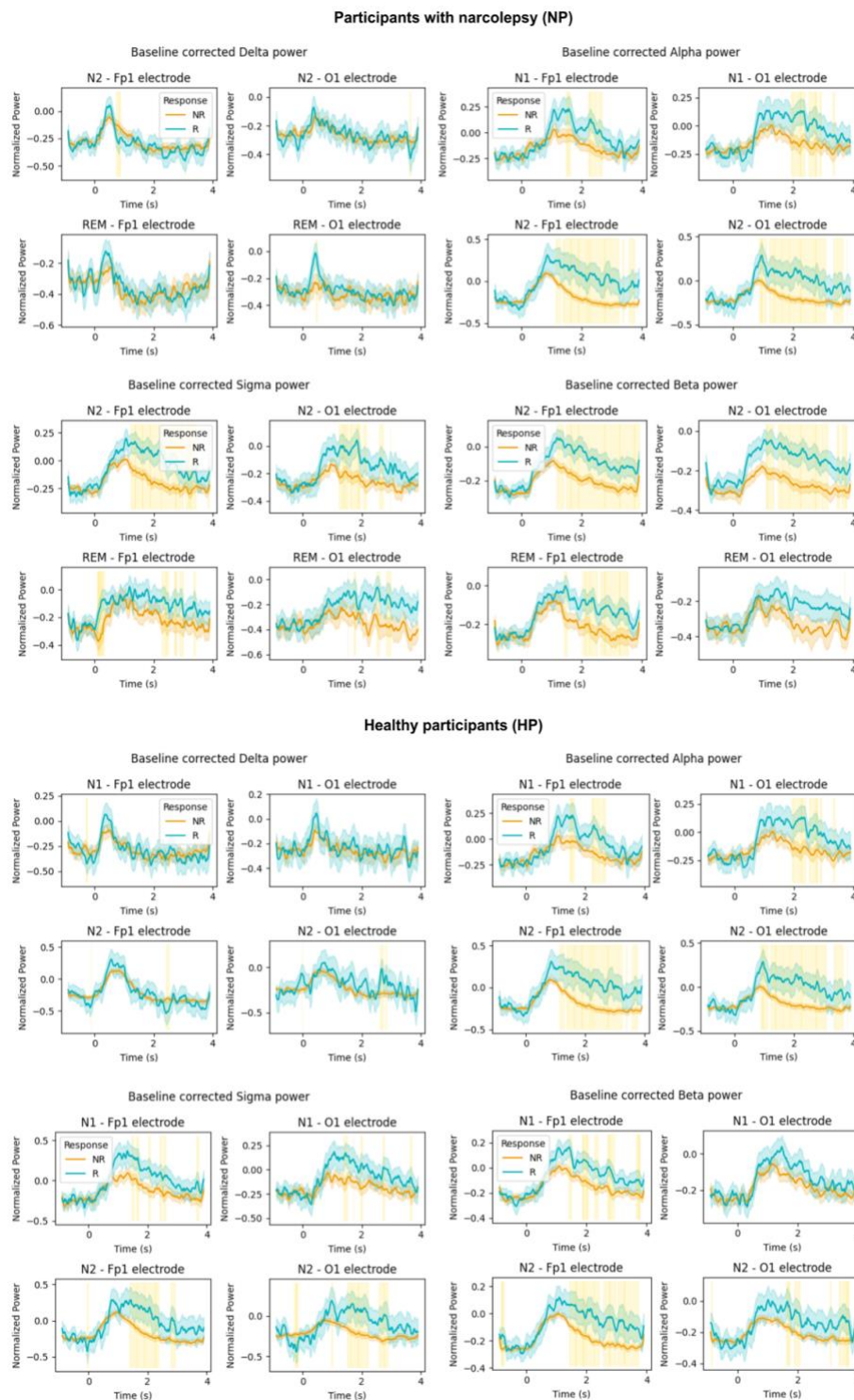


Figure S4.11. Differences in power across time in delta, alpha, low beta/sigma and high beta bands, in responsive (R) and unresponsive (NR) trials during N2 and REM sleep in participants with narcolepsy (upper panel) and during N1 and N2 sleep in healthy participants (lower panel). Significant differences are indicated by yellow shade (FDR corrected p -value < 0.05 , mass univariate analysis on time dimension using mixed linear models with responsiveness as the explanatory factor and subject ID as a random effect)

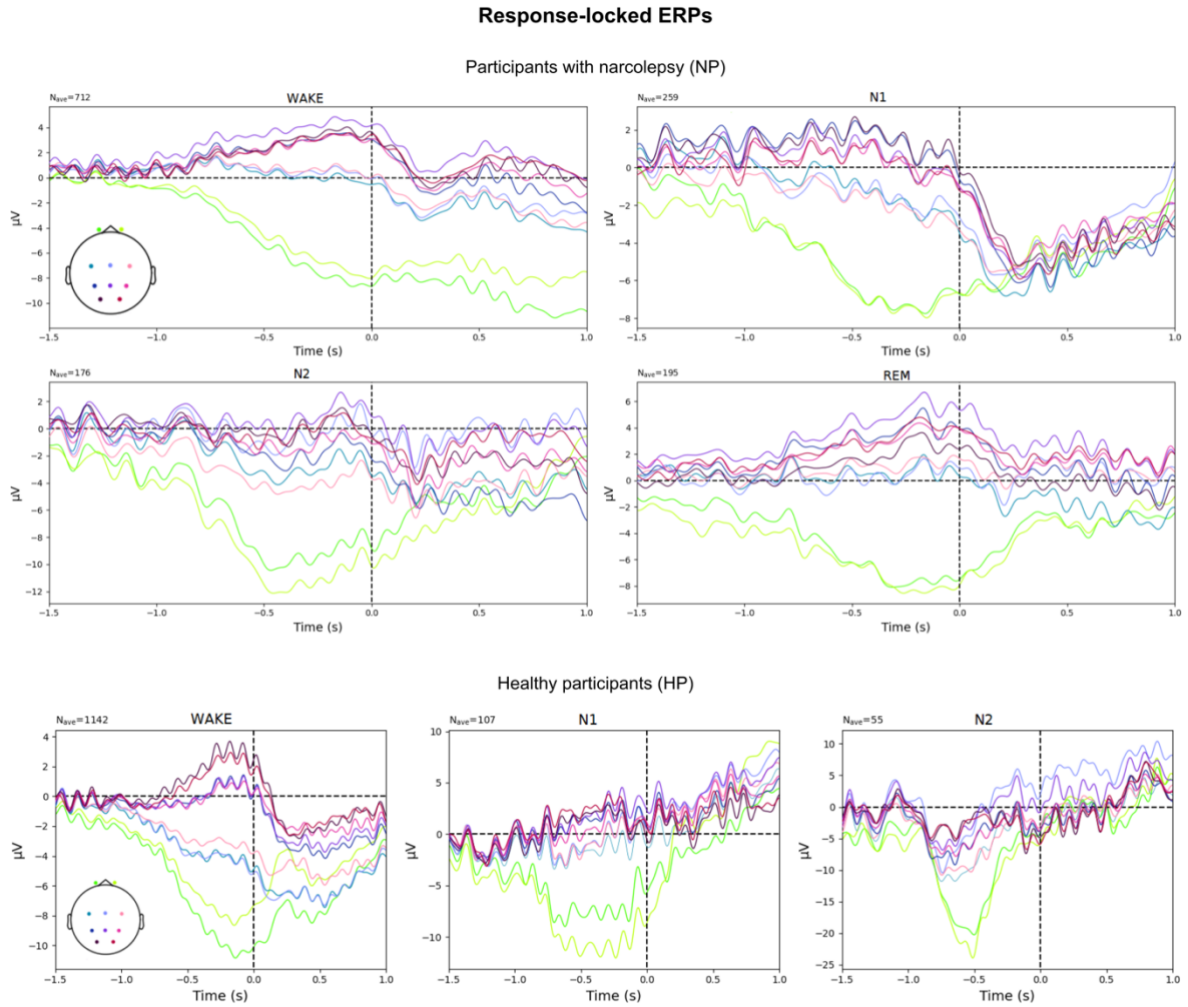


Figure S4.12. Response-locked ERP analysis in participants with narcolepsy (upper panel) and healthy participants (bottom panel). Dashed vertical lines indicate response start. Please note the motor preparation potential over frontal electrodes in all tested sleep stages.



Figure S4.13. Stimulus-locked ERP analysis in participants with narcolepsy. Dashed vertical lines indicate stimulus onset. Significant differences are indicated by yellow shade (FDR corrected p -value < 0.05 , mass univariate analysis on time dimension using mixed linear models with responsiveness as the explanatory factor and subject ID as a random effect)

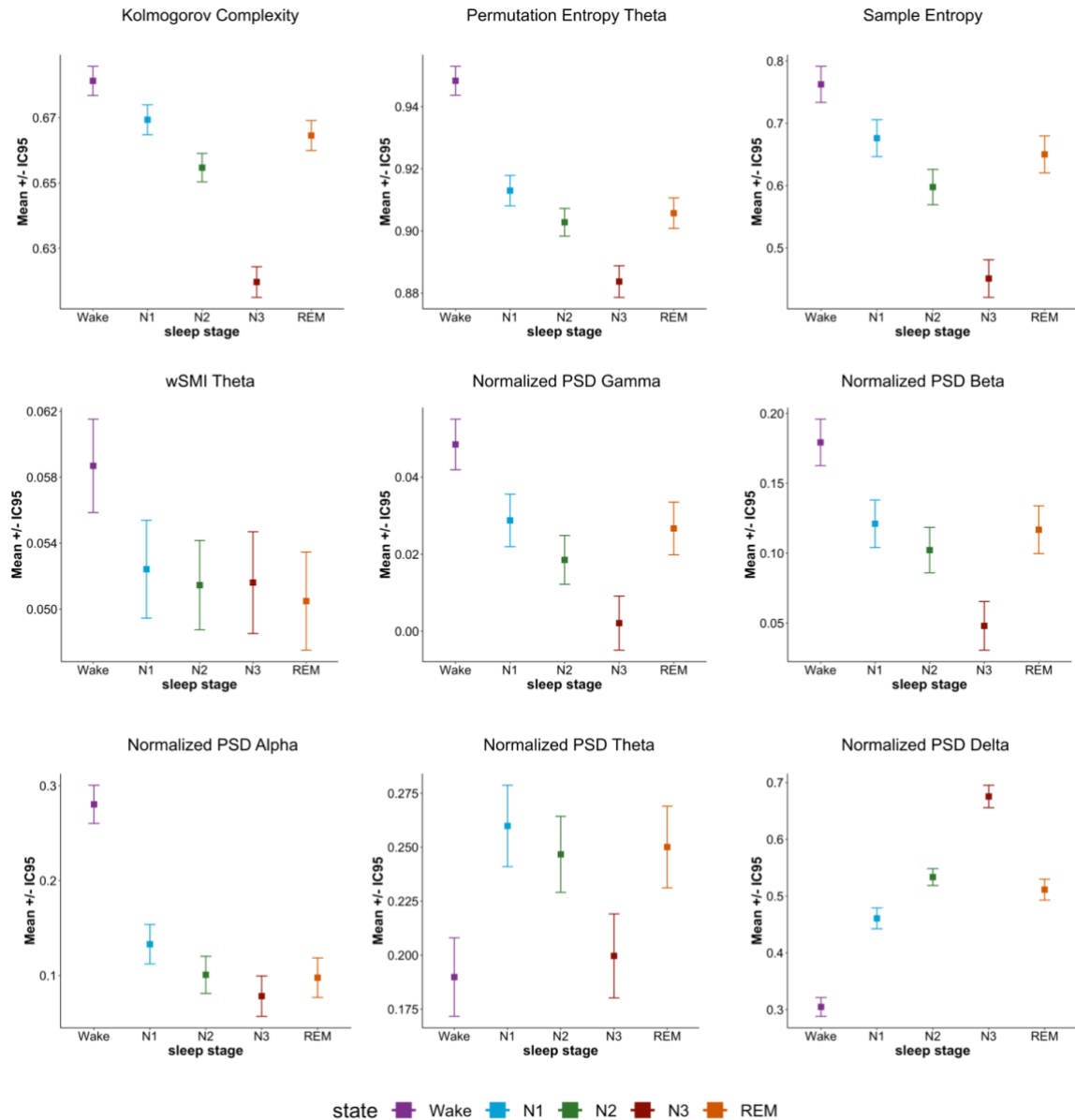


Figure S4.14. Evolution of electrophysiological markers across sleep stages in participants with narcolepsy (NP). Three complexity measures (the Kolmogorov Complexity -KC, the Permutation Entropy -PE, and the Sample Entropy -SE), one connectivity measure (weighted symbolic mutual information (wSMI) in the theta band), and five spectral measures (normalized power spectral densities (PSD) of delta, theta, alpha, beta and gamma frequency bands) were computed separately for the wake, N1, N2, N3, and REM sleep stages in participants with narcolepsy. The results in healthy participants can be found in Figure S3. Each dot indicates marginal means estimated by a mixed-linear model including sleep stage as an independent variable, EEG marker as the dependent variable, and participant ID as a random variable. Error bars depict 95% confidence intervals. Complexity and high-frequency PSD decreased in sleep compared to wake (wake > N1 > REM sleep > N2 > N3), whereas delta PSD increased with sleep (N3 > N2 > REM sleep > N1 > wake). Details of the statistical comparisons can be found in Table S5.

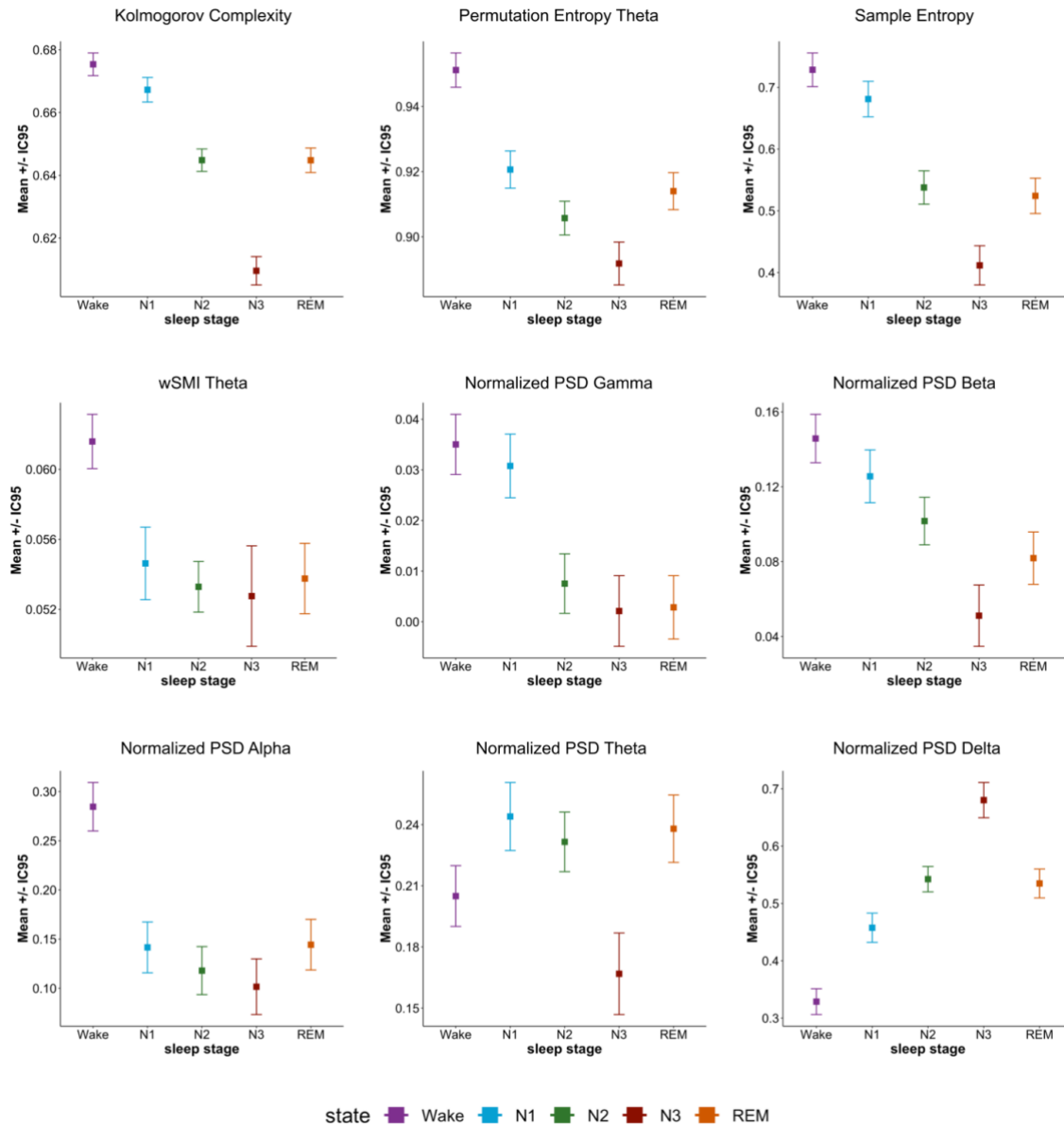


Figure S4.15. Evolution of electrophysiological markers across sleep stages in healthy participants (HP). Three complexity measures (the Kolmogorov Complexity -KC, the Permutation Entropy -PE, and the Sample Entropy -SE), one connectivity measure (weighted symbolic mutual information (wSMI) in the theta band), and five spectral measures (normalized power spectral densities (PSD) of delta, theta, alpha, beta, and gamma frequency bands) were computed separately for the wake, N1, N2, N3, and REM sleep stages in HP. Each dot indicates marginal means estimated by a mixed-linear model including sleep stage as an independent variable, marker as the dependent variable, and participant ID as a random variable. Error bars denote 95% confidence intervals. Complexity and high-frequency PSD decreased in sleep compared to wake (wake > N1 > N2 \approx REM > N3), whereas delta PSD increased with sleep (N3 > N2 \approx REM > N1 > wake). Theta PSD was higher in N1 and lower in N3 sleep. Details of the statistical comparisons can be found in Table S6.

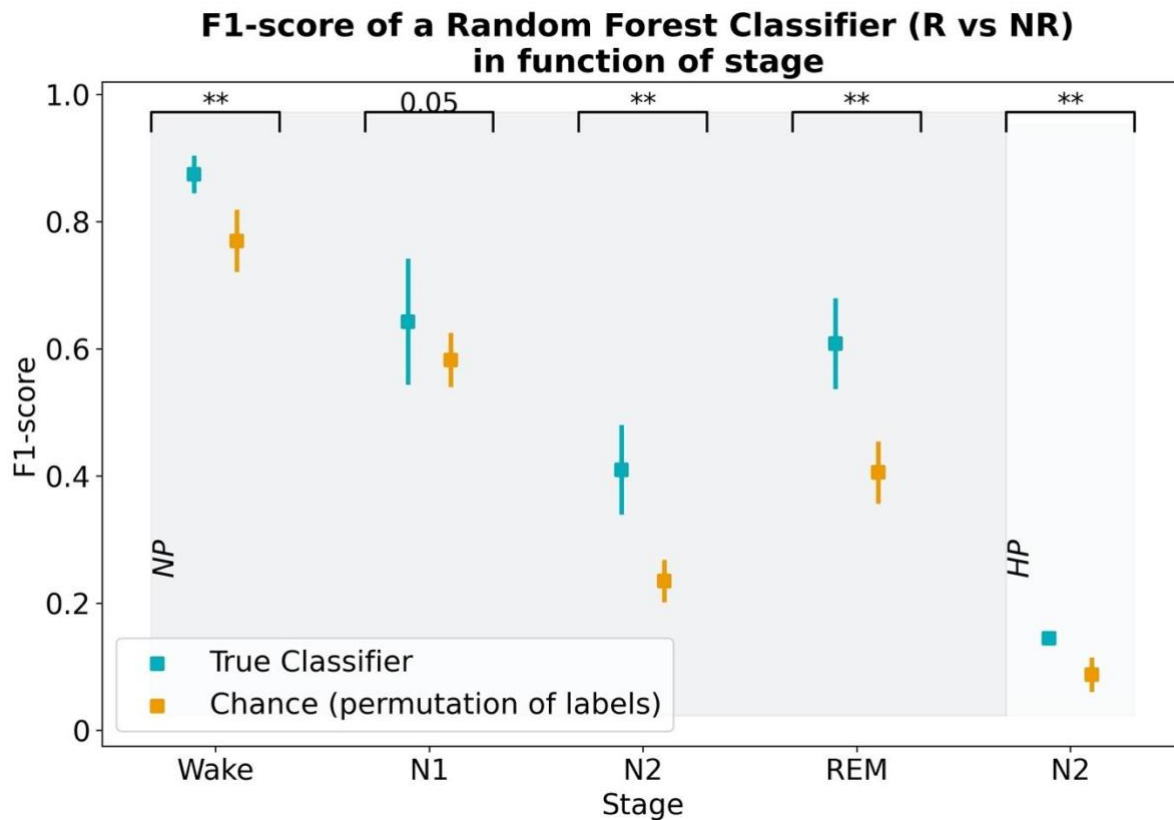


Figure S4.16. F1-score of the Random Forest classifiers trained with the neurophysiological markers to classify between responsive vs non-responsive trials, in different sleep stages, for participants with narcolepsy (NP) and healthy participants (HP). Blue (true classifier): true performance of the classifier (mean F1 score and 95IC across folds). Orange (Chance): chance-level performance computed with 500 random permutations of the data labels (mean F1 score and 95IC across permutations). Both correct and incorrect trials were included in the analysis. Statistical difference between true performance and chance is showed for each sleep stage. **: $p < 0.01$.

COMPARISON	Healthy Participants (HP)		Participants with Narcolepsy (NP)	
	<i>z</i>	FDR corrected <i>p</i> -value	<i>z</i>	FDR corrected <i>p</i> -value
Wake - N1	21.02	< 0.0001	13.47	< 0.0001
Wake - N2	31.81	< 0.0001	31.26	< 0.0001
Wake - N3	8.25	< 0.0001	18.20	< 0.0001
Wake - REM	19.27	< 0.0001	21.89	< 0.0001
Wake - Lucid REM	-	-	15.27	< 0.0001
N1 - N2	11.96	< 0.0001	19.51	< 0.0001
N1 - N3	5.39	< 0.0001	12.08	< 0.0001
N1 - REM	6.31	< 0.0001	9.57	< 0.0001
N1 - Lucid REM	-	-	2.15	0.03
N2 - N3	3.39	0.0008	4.36	< 0.0001
N2 - REM	-2.39	0.017	-8.54	< 0.0001
N2 - Lucid REM	-	-	-18.11	< 0.0001
N3 - REM	-3.91	0.0001	-7.55	< 0.0001
N3 - Lucid REM	-	-	-11.11	< 0.0001
REM - Lucid REM	-	-	-7.87	< 0.0001

Table S4.1. Details of the multiple comparisons of the response rates during ON periods in different sleep stages.

Parameters	Stage	Chance			Chance			Chance		
		Accuracy	Accuracy	P-value	Recall	Recall	P-value	Precision	Precision	P-value
W: 1s , Th: 5	Wake	0.79	0.49	0.002	0.93	0.57	0.002	0.69	0.42	0.002
	N1	0.81	0.70	0.002	0.83	0.25	0.002	0.32	0.09	0.002
	N2	0.75	0.73	0.002	0.60	0.26	0.002	0.08	0.03	0.002
	REM	0.76	0.71	0.002	0.77	0.27	0.002	0.14	0.05	0.002
W: 1s, Th: 7	Wake	0.82	0.50	0.002	0.90	0.52	0.002	0.73	0.42	0.002
	N1	0.86	0.74	0.002	0.79	0.19	0.002	0.40	0.09	0.002
	N2	0.81	0.79	0.002	0.56	0.19	0.002	0.10	0.03	0.002
	REM	0.82	0.78	0.002	0.68	0.19	0.002	0.17	0.05	0.002
W: 1s, Th: 10	Wake	0.83	0.50	0.002	0.87	0.48	0.002	0.76	0.42	0.002
	N1	0.89	0.77	0.002	0.75	0.16	0.002	0.46	0.09	0.002
	N2	0.87	0.84	0.002	0.50	0.13	0.002	0.13	0.05	0.002
	REM	0.86	0.81	0.002	0.68	0.15	0.002	0.22	0.05	0.002
W: 2s , Th: 5	Wake	0.820	0.50	0.002	0.90	0.51	0.002	0.74	0.42	0.002
	N1	0.86	0.74	0.002	0.8	0.20	0.002	0.4	0.09	0.002
	N2	0.83	0.79	0.002	0.58	0.18	0.002	0.11	0.03	0.002
	REM	0.82	0.78	0.002	0.68	0.19	0.002	0.17	0.04	0.002
W: 2s, Th: 7	Wake	0.83	0.50	0.002	0.86	0.48	0.002	0.77	0.42	0.002
	N1	0.89	0.77	0.002	0.75	0.16	0.002	0.46	0.09	0.002
	N2	0.87	0.85	0.002	0.50	0.13	0.002	0.14	0.04	0.002
	REM	0.88	0.83	0.002	0.68	0.14	0.002	0.24	0.05	0.002
W: 2s, Th: 10	Wake	0.83	0.51	0.002	0.81	0.43	0.002	0.79	0.42	0.002
	N1	0.91	0.79	0.002	0.71	0.13	0.002	0.54	0.10	0.002
	N2	0.91	0.88	0.002	0.45	0.09	0.002	0.18	0.04	0.002
	REM	0.91	0.86	0.002	0.57	0.10	0.002	0.28	0.05	0.002

Table S4.2. Different performance metrics (accuracy, recall and precision) measuring the concordance between automatic and manual scoring of responses in Wake, N1, N2 and REM sleep in healthy participants for each parameter combination [Window (W) = 1 or 2 seconds. Threshold k (Th) = 5, 7, 10]. Significance level of each metric against their chance-level performance computed via a 500-permutations procedure are also shown. Note that chance-level accuracy was not 0.5 in sleep due to the imbalance between responsive and unresponsive trials. Importantly, the smallest obtainable p-value with a 500-permutations procedure is 0.002 (1/N permutations).

Parameters	Stage	Chance			Chance			Chance		
		Accuracy	Accuracy	P-value	Recall	Recall	P-value	Precision	Precision	P-value
W: 1s , Th: 5	Wake	0.79	0.49	0.002	0.90	0.56	0.002	0.71	0.44	0.002
	N1	0.85	0.58	0.002	0.88	0.34	0.002	0.65	0.25	0.002
	N2	0.80	0.70	0.002	0.72	0.24	0.002	0.3	0.1	0.002
	N3	0.67	0.65	0.002	0.54	0.33	0.002	0.08	0.05	0.002
	REM	0.79	0.64	0.002	0.72	0.28	0.002	0.43	0.17	0.002
	REML	0.75	0.55	0.002	0.74	0.38	0.002	0.53	0.27	0.002
W: 1s, Th: 7	Wake	0.81	0.49	0.002	0.86	0.51	0.002	0.74	0.44	0.002
	N1	0.87	0.6	0.002	0.83	0.30	0.002	0.69	0.25	0.002
	N2	0.84	0.75	0.002	0.63	0.18	0.002	0.35	0.10	0.002
	N3	0.75	0.73	0.004	0.44	0.25	0.004	0.08	0.05	0.004
	REM	0.82	0.67	0.002	0.65	0.23	0.002	0.48	0.17	0.002
	REML	0.78	0.58	0.002	0.68	0.31	0.002	0.59	0.27	0.002
W: 1s, Th: 10	Wake	0.80	0.50	0.002	0.80	0.46	0.002	0.76	0.44	0.002
	N1	0.88	0.62	0.002	0.77	0.26	0.002	0.75	0.25	0.002
	N2	0.87	0.78	0.002	0.55	0.14	0.002	0.40	0.10	0.002
	N3	0.81	0.79	0.002	0.44	0.2	0.002	0.11	0.04	0.002
	REM	0.84	0.70	0.002	0.60	0.20	0.002	0.53	0.17	0.002
	REML	0.79	0.60	0.002	0.60	0.26	0.002	0.63	0.27	0.002
W: 2s , Th: 5	Wake	0.80	0.50	0.002	0.86	0.51	0.002	0.74	0.44	0.002
	N1	0.87	0.60	0.002	0.83	0.29	0.002	0.70	0.25	0.002
	N2	0.85	0.76	0.002	0.62	0.18	0.002	0.35	0.10	0.002
	N3	0.75	0.73	0.002	0.44	0.24	0.002	0.09	0.05	0.002
	REM	0.82	0.68	0.002	0.62	0.22	0.002	0.48	0.17	0.002
	REML	0.78	0.58	0.002	0.65	0.30	0.002	0.59	0.27	0.002
W: 2s, Th: 7	Wake	0.81	0.50	0.002	0.81	0.46	0.002	0.77	0.44	0.002
	N1	0.87	0.78	0.002	0.54	0.14	0.002	0.40	0.10	0.002
	N2	0.87	0.79	0.002	0.54	0.14	0.002	0.40	0.10	0.002
	N3	0.83	0.79	0.002	0.44	0.17	0.002	0.12	0.05	0.002
	REM	0.84	0.70	0.002	0.6	0.2	0.002	0.54	0.17	0.002
	REML	0.79	0.61	0.002	0.59	0.25	0.002	0.63	0.27	0.002
W: 2s, Th: 10	Wake	0.81	0.51	0.002	0.76	0.42	0.002	0.79	0.44	0.002
	N1	0.88	0.63	0.002	0.71	0.23	0.002	0.78	0.25	0.002
	N2	0.89	0.82	0.002	0.47	0.10	0.002	0.45	0.10	0.002
	N3	0.87	0.85	0.002	0.33	0.11	0.002	0.14	0.05	0.002
	REM	0.86	0.72	0.002	0.57	0.16	0.002	0.61	0.17	0.002
	REML	0.80	0.63	0.002	0.52	0.21	0.002	0.67	0.27	0.002

Table S4.3. Different performance metrics (accuracy, recall and precision) measuring the concordance between automatic and manual scoring of response in Wake, N1, N2, N3, REM and Lucid REM (REML) sleep in participants with narcolepsy for each parameter combinations [Window (W) = 1 or 2 seconds. Threshold k (Th) = 5, 7, 10]. Significance level of each metric against their chance-level performance computed via 500-permutations procedure are also shown. Note that chance-level accuracy was not 0.5 in sleep due to the imbalance between responsive and unresponsive trials. Importantly, the smallest obtainable p-value with a 500-permutations procedure is 0.002 (1/N permutations).

	Participants with Narcolepsy (NP)				Participants without Narcolepsy (HP)			
	PSD $ \delta $		PSD $ \alpha $		PSD $ \delta $		PSD $ \alpha $	
	Pre-stim	Post-stim	Pre-stim	Post-stim	Pre-stim	Post-stim	Pre-stim	Post-stim
Wake - N1	$t = -17.84$ $p < .0001$	$t = -22.61$ $p < .0001$	$t = 24.53$ $p < .0001$	$t = 27.92$ $p < .0001$	$t = -13.68$ $p < .0001$	$t = -36.50$ $p < .0001$	$t = 21.11$ $p < .0001$	$t = 45.67$ $p < .0001$
Wake -N2	$t = -32.13$ $p < .0001$	$t = -34.71$ $p < .0001$	$t = 36.57$ $p < .0001$	$t = 39.84$ $p < .0001$	$t = -31.02$ $p < .0001$	$t = -76.63$ $p < .0001$	$t = -33.23$ $p < .0001$	$t = 76.13$ $p < .0001$
Wake - REM	$t = -23.29$ $p < .0001$	$t = -31.98$ $p < .0001$	$t = 30.05$ $p < .0001$	$t = 37.80$ $p < .0001$	-	-	-	-

Table S4.4. Statistical differences of the PSD values at alpha and delta frequencies between wake and different sleep stages during pre-stimulation (-1s to 0) and post-stimulation (0 to 8s) periods.

	K	PE θ	SE	wSMI θ	PSD $ \gamma $	PSD $ \beta $	PSD $ \alpha $	PSD $ \theta $	PSD $ \delta $
Wake - N1	$t = 9.88$ $p < .0001$	$t = 21.08$ $p < .0001$	$t = 12.37$ $p < .0001$	$t = 6.29$ $p < .0001$	$t = 9.54$ $p < .0001$	$t = 13.63$ $p < .0001$	$t = 25.91$ $p < .0001$	$t = -12.44$ $p < .0001$	$t = -17.95$ $p < .0001$
Wake - N2	$t = 27.01$ $p < .0001$	$t = 33.30$ $p < .0001$	$t = 28.90$ $p < .0001$	$t = 8.90$ $p < .0001$	$t = 17.76$ $p < .0001$	$t = 22.08$ $p < .0001$	$t = 38.66$ $p < .0001$	$t = -12.38$ $p < .0001$	$t = -32.48$ $p < .0001$
Wake - N3	$t = 44.86$ $p < .0001$	$t = 33.84$ $p < .0001$	$t = 39.14$ $p < .0001$	$t = 6.24$ $p < .0001$	$t = 19.70$ $p < .0001$	$t = 26.95$ $p < .0001$	$t = 31.16$ $p < .0001$	$t = -1.53$ $p = 0.14$	$t = -37.69$ $p < .0001$
Wake - REM	$t = 13.63$ $p < .0001$	$t = 24.95$ $p < .0001$	$t = 15.78$ $p < .0001$	$t = 8.08$ $p < .0001$	$t = 10.35$ $p < .0001$	$t = 14.35$ $p < .0001$	$t = 31.50$ $p < .0001$	$t = -10.51$ $p < .0001$	$t = -23.44$ $p < .0001$
N1 - N2	$t = 13.30$ $p < .0001$	$t = 6.62$ $p < .0001$	$t = 12.28$ $p < .0001$	$t = 1.06$ $p = 0.31$	$t = 5.41$ $p < .0001$	$t = 4.82$ $p < .0001$	$t = 6.18$ $p < .0001$	$t = 2.55$ $p = 0.13$	$t = -9.12$ $p < .0001$
N1 - N3	$t = 34.63$ $p < .0001$	$t = 14.63$ $p < .0001$	$t = 27.09$ $p < .0001$	$t = 0.68$ $p = 0.51$	$t = 10.83$ $p < .0001$	$t = 14.36$ $p < .0001$	$t = 8.07$ $p < .0001$	$t = 8.98$ $p < .0001$	$t = -20.72$ $p < .0001$
N1 - REM	$t = 3.55$ $p = .0005$	$t = 3.83$ $p = .0002$	$t = 3.29$ $p = 0.001$	$t = 1.71$ $p = 0.1$	$t = 0.90$ $p = 0.39$	$t = 0.88$ $p = 0.39$	$t = 5.48$ $p < .0001$	$t = -1.53$ $p = 0.14$	$t = -5.16$ $p < .0001$
N2 - N3	$t = 29.05$ $p < .0001$	$t = 11.36$ $p < .0001$	$t = 21.00$ $p < .0001$	$t = -0.15$ $p = 0.88$	$t = 7.93$ $p < .0001$	$t = 12.68$ $p < .0001$	$t = 3.95$ $p < .0001$	$t = 8.35$ $p < .0001$	$t = -16.32$ $p < .0001$
N2 - REM	$t = -8.91$ $p < .0001$	$t = -1.89$ $p = 0.06$	$t = -8.20$ $p < .0001$	$t = 1.06$ $p = 0.31$	$t = -4.31$ $p < .0001$	$t = -3.73$ $p = 0.0002$	$t = 0.59$ $p = 0.56$	$t = -0.66$ $p = 0.52$	$t = 2.79$ $p = 0.006$
N3 - REM	$t = -29.82$ $p < .0001$	$t = -10.51$ $p < .0001$	$t = -22.85$ $p < .0001$	$t = 0.90$ $p = 0.39$	$t = -9.53$ $p < .0001$	$t = -12.90$ $p < .0001$	$t = -2.73$ $p = 0.007$	$t = -7.18$ $p < .0001$	$t = 15.23$ $p < .0001$

Table S4.5. Details of the multiple comparisons of neurophysiological markers in different sleep stages in NP. K for Kolmogorov Complexity; PE θ for Permutation Entropy in the theta band; SE for Sample Entropy; and wSMI θ for weighted symbolic mutual information in the theta band. All p-values are FDR corrected for multiple comparisons. Statistically significant comparisons ($p < 0.05$) are highlighted.

	K	PE θ	SE	wSMI θ	PSD $ \gamma $	PSD $ \beta $	PSD $ \alpha $	PSD $ \theta $	PSD $ \delta $
Wake - N1	$t = 6.66$ $p < .0001$	$t = 17.12$ $p < .0001$	$t = 6.37$ $p < .0001$	$t = 6.59$ $p < .0001$	$t = 2.56$ $p = 0.013$	$t = 4.47$ $p < .0001$	$t = 22.52$ $p < .0001$	$t = -6.58$ $p < .0001$	$t = -13.93$ $p < .0001$
Wake -N2	$t = 33.86$ $p < .0001$	$t = 34.39$ $p < .0001$	$t = 34.53$ $p < .0001$	$t = 10.79$ $p < .0001$	$t = 22.36$ $p < .0001$	$t = 13.18$ $p < .0001$	$t = 25.37$ $p < .0001$	$t = -6.06$ $p < .0001$	$t = -31.23$ $p < .0001$
Wake - N3	$t = 38.01$ $p < .0001$	$t = 23.42$ $p < .0001$	$t = 29.93$ $p < .0001$	$t = 5.92$ $p < .0001$	$t = 13.96$ $p < .0001$	$t = 14.74$ $p < .0001$	$t = 20.26$ $p < .0001$	$t = 4.52$ $p < .0001$	$t = -26.74$ $p < .0001$
Wake - REM	$t = 24.34$ $p < .0001$	$t = 20.19$ $p < .0001$	$t = 26.56$ $p < .0001$	$t = 7.34$ $p < .0001$	$t = 18.79$ $p < .0001$	$t = 13.72$ $p < .0001$	$t = 21.37$ $p < .0001$	$t = -5.41$ $p < .0001$	$t = -21.65$ $p < .0001$
N1 - N2	$t = 18.67$ $p < .0001$	$t = 8.46$ $p < .0001$	$t = 19.50$ $p < .0001$	$t = 1.29$ $p = 0.22$	$t = 14.20$ $p < .0001$	$t = 5.36$ $p < .0001$	$t = 3.77$ $p = 0.0002$	$t = 2.13$ $p = 0.04$	$t = -9.28$ $p < .0001$
N1 - N3	$t = 30.44$ $p < .0001$	$t = 10.39$ $p < .0001$	$t = 23.25$ $p < .0001$	$t = 1.14$ $p = 0.28$	$t = 11.10$ $p < .0001$	$t = 10.59$ $p < .0001$	$t = 4.05$ $p < .0001$	$t = 8.35$ $p < .0001$	$t = -15.46$ $p < .0001$
N1 - REM	$t = 15.32$ $p = .0009$	$t = 3.08$ $p = 0.003$	$t = 17.48$ $p < .0001$	$t = 0.69$ $p = 0.53$	$t = 13.98$ $p < .0001$	$t = 8.03$ $p < .0001$	$t = -0.36$ $p = 0.73$	$t = 0.84$ $p = 0.43$	$t = -6.93$ $p < .0001$
N2 - N3	$t = 21.20$ $p < .0001$	$t = 5.72$ $p < .0001$	$t = 12.41$ $p < .0001$	$t = 0.37$ $p = 0.74$	$t = 2.39$ $p = 0.02$	$t = 8.20$ $p < .0001$	$t = 1.89$ $p = 0.07$	$t = 7.99$ $p < .0001$	$t = -10.91$ $p < .0001$
N2 - REM	$t = 0.03$ $p = 0.98$	$t = -5.00$ $p < .0001$	$t = 1.96$ $p = 0.06$	$t = -0.48$ $p = 0.66$	$t = 3.03$ $p = 0.003$	$t = 4.72$ $p < .0001$	$t = -4.46$ $p < .0001$	$t = -1.17$ $p = 0.27$	$t = 0.87$ $p = 0.42$
N3 - REM	$t = -19.41$ $p < .0001$	$t = -8.36$ $p < .0001$	$t = -10.15$ $p < .0001$	$t = -0.64$ $p = 0.55$	$t = -0.29$ $p = 0.78$	$t = -4.57$ $p < .0001$	$t = -4.51$ $p < .0001$	$t = -8.05$ $p < .0001$	$t = 10.54$ $p < .0001$

Table S4.6. Details of the multiple comparisons of neurophysiological markers in different sleep stages in HP. K for Kolmogorov Complexity; PE θ for Permutation Entropy in the theta band; SE for Sample Entropy; and wSMI θ for weighted symbolic mutual information in the theta band. All p-values are FDR corrected for multiple comparisons. Statistically significant comparisons ($p < 0.05$) are highlighted.

Participants with Narcolepsy (NP)									
	K	PE θ	SE	wSMI θ	PSD $ \gamma $	PSD $ \beta $	PSD $ \alpha $	PSD $ \theta $	PSD $ \delta $
Wake	$t = 2.63$ $p = 0.024$	$t = 0.14$ $p = 0.96$	$t = 3.15$ $p = 0.007$	$t = -0.22$ $p = 0.93$	$t = 2.55$ $p = 0.025$	$t = 0.84$ $p = 0.53$	$t = 0.65$ $p = 0.66$	$t = -0.07$ $p = 0.99$	$t = -1.18$ $p = 0.35$
N1	$t = 4.52$ $p < .0001$	$t = 1.48$ $p = 0.21$	$t = 3.87$ $p = 0.0006$	$t = -0.01$ $p = 0.99$	$t = 2.60$ $p = 0.025$	$t = 2.57$ $p = 0.025$	$t = 2.30$ $p = 0.043$	$t = -0.63$ $p = 0.66$	$t = -4$ $p = 0.0005$
N2	$t = 4.94$ $p < .0001$	$t = 1.85$ $p = 0.11$	$t = 5.03$ $p < .0001$	$t = -0.51$ $p = 0.71$	$t = 5.32$ $p < .0001$	$t = 2.28$ $p = 0.043$	$t = 0.56$ $p = 0.69$	$t = -0.86$ $p = 0.53$	$t = -1.47$ $p = 0.21$
REM	$t = 3.91$ $p = 0.0006$	$t = 2.63$ $p = 0.02$	$t = 3.5$ $p = 0.002$	$t = 1.62$ $p = 0.18$	$t = 2.34$ $p = 0.041$	$t = 2.94$ $p = 0.012$	$t = 1.87$ $p = 0.11$	$t = 0.05$ $p = 0.99$	$t = -2.93$ $p = 0.012$
Healthy Participants (HP)									
	K	PE θ	SE	wSMI θ	PSD $ \gamma $	PSD $ \beta $	PSD $ \alpha $	PSD $ \theta $	PSD $ \delta $
Wake	$t = 2.42$ $p = 0.048$	$t = 3.78$ $p = 0.005$	$t = 1.26$ $p = 0.40$	$t = -0.46$ $p = 0.76$	$t = 0.21$ $p = 0.87$	$t = 2.32$ $p = 0.056$	$t = 2.67$ $p = 0.035$	$t = -2.44$ $p = 0.048$	$t = -1.97$ $p = 0.12$
N1	$t = 3.29$ $p = 0.007$	$t = 0.90$ $p = 0.55$	$t = 2.70$ $p = 0.035$	$t = 0.99$ $p = 0.51$	$t = 1.71$ $p = 0.2$	$t = 1.36$ $p = 0.36$	$t = -0.36$ $p = 0.78$	$t = -0.08$ $p = 0.94$	$t = -0.71$ $p = 0.61$
N2	$t = 2.46$ $p = 0.048$	$t = 0.65$ $p = 0.63$	$t = 3.29$ $p = 0.007$	$t = -1.22$ $p = 0.40$	$t = 3.27$ $p = 0.007$	$t = 1.06$ $p = 0.49$	$t = -0.41$ $p = 0.77$	$t = 0.76$ $p = 0.60$	$t = -0.86$ $p = 0.55$

Table S4.7 Statistical differences of the neurophysiological markers between responsive and non-responsive trials in different sleep stages, in non-lucid naps, for HP and NP. K for Kolmogorov Complexity; PE θ for Permutation Entropy in the theta band; SE for Sample Entropy; and wSMI θ for weighted symbolic mutual information in the theta band. All p-values are FDR corrected for multiple comparisons. Statistically significant comparisons ($p < 0.05$) are highlighted.

Marker	Sleep Stage	Participants with narcolepsy (NP)		Healthy participants (HP)	
		Responsive trials	Unresponsive trials	Responsive trials	Unresponsive trials
K	Wake	0.6803754	0.6759375	0.6759382	0.6781734
	N1	0.6715431	0.6657330	0.6719169	0.6690935
	N2	0.6608676	0.6540851	0.6524095	0.6439975
	N3	0.6184315	0.6201406	-	-
	REM	0.6641869	0.6586848	0.6477605	0.6458158
PE θ	Wake	0.9438212	0.9607482	0.9553089	0.9487543
	N1	0.9089780	0.9061032	0.9178698	0.9242548
	N2	0.9068446	0.9024781	0.9057451	0.9034864
	N3	0.8785161	0.8788696	-	-
	REM	0.9110372	0.9046189	0.9275586	0.9045421
SE	Wake	0.7667154	0.7137313	0.7226942	0.7604313
	N1	0.6969705	0.6614606	0.6936492	0.7003899
	N2	0.6314248	0.5938238	0.5807554	0.5415817
	N3	0.4410244	0.4680347	-	-
	REM	0.6326181	0.6070131	0.5471580	0.5503706
wSMI θ	Wake	0.05851454	0.06273602	0.06149339	0.06386605
	N1	0.05114335	0.05127260	0.05559300	0.05590678
	N2	0.05047093	0.05062645	0.05073267	0.05295049
	N3	0.05035443	0.04943042	-	-
	REM	0.05267189	0.05029265	0.05458694	0.05269153
PSD $ \delta $	Wake	0.3194139	0.2605850	0.3072278	0.3533609
	N1	0.4503646	0.5030020	0.4671423	0.4538805
	N2	0.5119116	0.5370847	0.5442573	0.5576962
	N3	0.7045447	0.6870387	-	-
	REM	0.5025181	0.5284724	0.5086240	0.5643875
PSD $ \theta $	Wake	0.2068933	0.1418656	0.2007460	0.1939149
	N1	0.2656362	0.2414224	0.2475708	0.2244246
	N2	0.2575809	0.2429896	0.2323852	0.2305370
	N3	0.2000923	0.1947102	-	-
	REM	0.2399718	0.2332216	0.2438726	0.2417497
PSD $ \alpha $	Wake	0.25245023	0.39240107	0.31084653	0.2446519
	N1	0.11708552	0.10398341	0.12343722	0.1485939
	N2	0.10530406	0.09841525	0.09927345	0.1027312
	N3	0.05095843	0.06146279	-	-
	REM	0.11324187	0.10276048	0.15921852	0.1004059
PSD $ \beta $	Wake	0.1699562	0.17224221	0.14886467	0.16731716
	N1	0.1332042	0.12198210	0.13141251	0.13987564
	N2	0.1032444	0.10267684	0.11045073	0.09906883
	N3	0.0383426	0.04763254	-	-
	REM	0.1207973	0.11569344	0.07990251	0.08175934
PSD $ \gamma $	Wake	0.05128644	0.032906174	0.032315047	0.040755087
	N1	0.03370946	0.029610126	0.030437162	0.033225455
	N2	0.02195909	0.018833625	0.013633360	0.009966815
	N3	0.00606192	0.009155819	-	-
	REM	0.02347083	0.019852047	0.008382299	0.011697608

Table S4.8. Average values of neurophysiological markers in different sleep stages in NP and HP.

K for Kolmogorov Complexity; PE θ for Permutation Entropy in the theta band; SE for Sample Entropy; and wSMI θ for weighted symbolic mutual information in the theta band. Note that these are non z-scored trial averages. For the statistical comparisons (Figure 4.5A and Table S4.5), trial values were z-scored and estimated marginal means were computed. Figure 4.5A shows the differences between the estimated means of responsive and non-responsive trials.

Participants with Narcolepsy (NP)						
	True positives (TP)	False positives (FP)	True negatives (TN)	False negatives (FN)	Balanced accuracy	F1 score
Wake	671 (80.1%)	33 (25.2%)	98 (74.8%)	159 (19.2%)	0.78 (78%)	0.87
N1	181 (59%)	72 (36.4%)	126 (63.6%)	126 (41%)	0.61 (61%)	0.64
N2	187 (67%)	448 (35.6%)	810 (64.4%)	92 (33%)	0.66 (66%)	0.41
REM	151 (65.9%)	101 (28.2%)	257 (71.8%)	78 (34.1%)	0.67 (67%)	0.61
Healthy Participants (HP)						
	True positives (TP)	False positives (FP)	True negatives (TN)	False negatives (FN)	Balanced accuracy	F1 score
N2	29 (39.7%)	318 (25.1%)	948 (74.9%)	44 (60.3%)	0.58 (58%)	0.14

Table S4.9. Confusion matrix and performance scores of the random forest classifier (responsive vs non-responsive trials) in different sleep stages, for HP and NP.

Lucid REM Sleep	K	PE θ	SE	wSMI θ	PSD γ	PSD β	PSD α	PSD θ	PSD δ
Responsive vs. Non-responsive trials	$t = 1.26$ $p = 0.62$ BF = 0.17	$t = 0.05$ $p = 0.96$ BF = 0.08	$t = 1.18$ $p = 0.53$ BF = 0.18	$t = -0.58$ $p = 0.75$ BF = 0.10	$t = 0.55$ $p = 0.75$ BF = 0.10	$t = -1.31$ $p = 0.53$ BF = 0.21	$t = -0.70$ $p = 0.75$ BF = 0.11	$t = 1.20$ $p = 0.53$ BF = 0.17	$t = -0.06$ $p = 0.96$ BF = 0.08

Table S4.10. Statistical differences of the neurophysiological markers between responsive and non-responsive trials in lucid REM sleep (participants with narcolepsy). K for Kolmogorov Complexity; PE θ for Permutation Entropy in the theta band; SE for Sample Entropy; and wSMI θ for weighted symbolic mutual information in the theta band. All p-values are FDR corrected for multiple comparisons. BF: Bayes Factor of the comparison between the full model (response + subject identity) and a null model (subject identity only).

Lucid REM sleep vs. REM sleep	K	PE θ	SE	wSMI θ	PSD $ \gamma $	PSD $ \beta $	PSD $ \alpha $	PSD $ \theta $	PSD $ \delta $
All trials	$t = 2.08$ $p = 0.067$	$t = 2.33$ $p = 0.045$	$t = 2.99$ $p = 0.024$	$t = -1.13$ $p = 0.33$	$t = 2.73$ $p = 0.024$	$t = 1.90$ $p = 0.087$	$t = 0.96$ $p = 0.38$	$t = 0.72$ $p = 0.47$	$t = -2.66$ $p = 0.024$
Responsive trials	$t = 1.49$ $p = 0.31$ BF = 0.17	$t = -0.07$ $p = 0.94$ BF = 0.14	$t = 1.97$ $p = 0.31$ BF = 0.28	$t = -1.62$ $p = 0.31$ BF = 0.17	$t = 1.55$ $p = 0.31$ BF = 0.21	$t = -0.36$ $p = 0.81$ BF = 0.19	$t = -0.74$ $p = 0.69$ BF = 0.14	$t = 1.37$ $p = 0.31$ BF = 0.21	$t = -0.54$ $p = 0.76$ BF = 0.20

Table S4.11. Statistical differences of the neurophysiological markers between lucid and non-lucid trials (REM sleep), for all trials and for responsive trials only. K for Kolmogorov Complexity; PE θ for Permutation Entropy in the theta band; SE for Sample Entropy; and wSMI θ for weighted symbolic mutual information in the theta band. All p-values are FDR corrected for multiple comparisons. Statistically significant comparisons ($p < 0.05$) are highlighted. BF: Bayes Factor of the comparison between the full model (response + subject identity) and a null model (subject identity only).

Group	Nap	Wake		N1		N2		N3		REM		Sleep Latency		Micro-arousals		TST		Micro-arousal Index		WASO		Efficiency	
		%	std	%	std	%	std	%	std	%	std	min	std	number	std	min	std	number/H	std	min	std	%	std
Participants with Narcolepsy	Nap 1	10	21.21	16.33	17.85	24.55	23.7	2.63	9.44	46.5	31.57	2.86	4.65	11.85	8.37	15.7	5.51	52.05	50.56	1.43	3.32	90	21.21
	Nap 2	4.86	14.65	25.06	23.46	40.73	24.7	7.02	15.17	21.88	30.34	3.33	4.63	9.8	7.76	16.01	5.16	36.85	29.16	0.66	1.67	95.14	14.65
	Nap 3	5.05	7.06	24.74	23.3	41.03	24.03	13.33	22.48	15.85	28.61	3.48	4.01	9.19	7.08	15.77	4.23	39.73	35.44	0.75	0.99	94.95	7.06
	Nap 4	8.3	13.93	18.47	15.75	42.16	28.44	11.93	21.01	19.15	30.76	2.31	2.44	10.7	6.74	16.28	3.59	42.43	29.5	1.41	2.49	91.7	13.93
	Nap 5	7.58	13.31	19.49	15.85	26.04	22.41	7.91	21.7	38.97	34.12	4.22	4.19	9.79	7.09	14.73	4.77	38.67	32.56	1.05	1.87	92.42	13.31
	Total	7.158	14.032	20.818	19.242	34.902	24.656	8.564	17.96	28.47	31.08	3.24	3.984	10.266	7.408	15.698	4.652	41.946	35.444	1.06	2.068	92.842	14.032
Healthy Participants	Morning N = 14	18.82	18.08	20.69	7.39	36.63	14.04	10.07	13.7	13.79	12.13	16.52	13.02	35.36	15.23	69.5	21.98	33.65	16.3	13.98	10.89	81.18	18.08
	Afternoon N = 8	42.37	18.43	26.64	18.07	29.18	25.44	1.81	4.71	0	0	18.02	25.83	36.75	15.12	47.04	22.32	57.61	39.16	34.94	19.51	57.63	18.43
	Total	27.38	21.21	22.85	12.3	33.92	18.74	7.07	11.84	8.78	11.71	17.07	18.11	35.86	14.84	61.33	24.24	42.36	28.54	21.6	17.52	72.62	21.21

Table S4.12. Detailed information on the sleep characteristics of the participants with narcolepsy and healthy participants.

CHAPTER V

GENERAL DISCUSSION

GENERAL DISCUSSION

In this thesis, our main objective was to investigate the interplay between ongoing brain dynamics and conscious perception. We conducted three distinct experiments, testing several hypotheses:

- Study 1 - Chapter II: We examined the conscious processing of complex and ecologically valid stimuli during wakefulness.
- Study 2 - Chapter III: We focused on the conscious processing of threshold auditory stimuli during wakefulness.
- Study 3 - Chapter IV: We investigated both brain and behavioral responses to verbal stimuli across different stages of sleep.

In the subsequent sections, we will present our initial hypotheses and discuss the implications of the findings derived from the three studies. Then, we will address the limitations of our research and outline avenues for future explorations.

5.1. Going back to the initial hypotheses

Hypothesis (i): Conscious processing influences ongoing brain dynamics

In the first study (Chapter II), we adopted an ecologically valid and dynamic approach to investigate how conscious processing of supra-threshold naturalistic movies affects the ongoing brain dynamics resulting from brain networks' interactions. Instead of solely examining local activations in the visual and auditory cortices, we chose to analyze the dynamics of brain networks, reflecting the integration of diverse stimuli to create a coherent understanding of the narrative. Our findings revealed that the brain dynamics were synchronized among participants who watched the same intact movie. Importantly, this synchronization did not occur when participants viewed a scrambled version of the same movie, despite the scrambled scenes being presented in the same order. This result indicated that the synchronization of brain patterns was not solely influenced by the physical characteristics of the stimulus, but rather by the holistic understanding and subjective experience of the movie. Moreover, the level of synchronization varied based on the suspense level of the scenes, further supporting the notion that brain dynamics track high-level stimulus features.

The third study (Chapter IV) further confirmed the impact of conscious perception on subsequent brain network interactions. In this study, we employed a more traditional experimental paradigm involving the presentation of simple auditory stimuli at the detection threshold. We found that brain connectivity patterns favorable for conscious perception occurred more frequently following a detection. This suggests that once the brain detects and consciously processes a stimulus, it tends to remain or transition into complex states that are conducive to conscious perception. This stability in the brain's susceptibility to the external world over a certain period of time aligns with the concept of perceptual hysteresis, which refers to the influence of an immediately preceding perception on the current one (for an example in the auditory domain, see Chambers & Pressnitzer, 2014). In our perceptual detection experiment, participants likely transitioned into or remained in these favorable states after a detection, thereby increasing their chances of detecting subsequent stimuli. We observed that previous detections increased the likelihood of current detections, indicating a hysteresis effect. Although the interaction with the pattern type was only marginally significant, we believe that all these findings reflect a common hysteresis phenomenon facilitated by the transition to rich brain patterns. Further studies are required to explore and validate this interpretation thoroughly.

Hypothesis (ii): Conscious processing of information is a fluctuating phenomenon that can vary even within traditionally defined states of consciousness

The literature extensively demonstrated fluctuations in the conscious perception of stimuli presented at the detection threshold during wakefulness, even when the intensity of the stimulus remains fixed. Numerous studies have explored the brain responses associated with subjective experience by comparing conscious and unconscious perception of the same stimulus (Pins & Ffytche, 2003; Sergent et al., 2005; Del Cul et al., 2007), as well as by using bistable stimuli (Kornmeier & Bach, 2012; Frässle et al., 2014). In Study 2 (Chapter III) of our research, we replicate these findings by demonstrating that auditory stimuli presented at the detection threshold are perceived only in half of the trials. Importantly, we extend this observation beyond wakefulness to different sleep stages and supra-threshold stimuli. In Study 3 (Chapter IV), we illustrate that participants can process and respond to supra-threshold verbal stimuli during N1, N2, REM sleep, as well as in lucid REM sleep. However, this responsiveness is not constant over time, as a stimulus elicits a response only in certain trials. We attribute these fluctuations to variations in ongoing brain dynamics, which will be explored in detail in the

following sections. Collectively, these results indicate that cognitive abilities and the capacity for conscious processing of external information oscillate within traditionally defined states of consciousness and provide support for our initial hypothesis.

Hypothesis (iii): Ongoing brain dynamics also have an impact on the capacity for conscious perception, with some brain states facilitating such processing while others do not

The findings from Studies 2 and 3 (Chapters III and IV) demonstrated that the fate of a presented stimulus is influenced by the brain activity preceding the stimulation. Both studies, using different neuroimaging techniques and analytic approaches, consistently revealed that specific configurations of brain activity are favorable for conscious processing and significantly enhance the chances of detecting the presented stimulus in a given state of consciousness.

In Study 2, using fMRI, we demonstrate that brain coordination patterns, previously associated with conscious states and found to be less prevalent in patients with disorders of consciousness and under anesthesia (Demertzi et al., 2019), are also linked with the capacity to perceive external stimuli. Auditory stimuli at the individual detection threshold were more likely to be detected if they were delivered when the participants were exhibiting the consciousness-related patterns, indicating a functional role of these patterns in information processing. Similarly, Study 3 indicated that EEG spectral, connectivity, and complexity markers, previously associated with higher cognitive states and capable of distinguishing between MCS *vs.* VS (King et al., 2013; Sitt et al., 2014; Engemann et al., 2018) or wakefulness *vs.* REM sleep (Bourdillon et al., 2020), predicted responsiveness to verbal stimuli across different sleep stages. Once again, responsiveness was not constant within a sleep stage (e.g. always responding in N1 and never in N2) but rather fluctuated depending on the preceding EEG characteristics.

Hypothesis (iv): Traditional definitions of states of consciousness do not fully capture the richness and variability within each state.

Study 2 and 3 reveal that traditionally defined states of consciousness, such as wakefulness or specific sleep stages, exhibit variations in brain activity and behavior. Our findings indicate that the conventional definitions and boundaries of these macro states (e.g., wakefulness or N2 sleep) fail to capture the diversity within a state. Therefore, a more detailed description is

necessary, considering micro-level variations in brain activity and cognitive abilities. These temporary fluctuations in ongoing brain dynamics within a state can lead to different subjective experiences and behavioral outcomes. However, in the current framework, these diverse cognitive and behavioral profiles within a state are grouped under a single category.

Recent studies have also highlighted similar points concerning subjective experiences within traditionally defined states. It has been demonstrated that a more detailed description of neural activity, beyond standard polysomnographic evaluation, can explain why patients who are sleeping (at least according to the current classification) report not having slept (Andrillon et al., 2020). Similarly, localized sleep-like activity during wakefulness can result in subjective experiences of mind-wandering and mind-blanking, along with distinct corresponding behaviors (Andrillon et al., 2021). Despite these significant changes in behavior and subjective experience, these moments of local sleep-like activity are still classified as wakefulness within the current classification of consciousness states. Hence, a revision of the classification system is necessary to account for the richness and variability within each state.

We acknowledge the usefulness of discretizing consciousness states based on general features, especially in clinical settings where determining a patient's level of consciousness or sleep state is crucial. This discretization provides a simplified model of the actual phenomena and allows for easy categorization using accessible tools like clinical evaluation or global EEG traces. Incorporating transient variations to characterize transitions within a state would add more detail and sub-states to the model while still maintaining a discrete framework. On the other hand, real-life phenomena may represent a continuous spectrum of consciousness where the proportions of certain features vary. Considering our results and previous findings, we propose two potential perspectives:

1. States of consciousness are distinct continua: According to this view, the transitions between different states of consciousness are abrupt, resulting in discrete states (e.g., wakefulness, different sleep stages, anesthesia, MCS, VS, psychedelic states). However, each individual state exists on a continuum, allowing for variability in neural activity, subjective experience, and behavior.
2. States of consciousness are part of one comprehensive multidimensional consciousness space: In this perspective, states are not discrete from one another but rather exhibit continuity. The transitions between states are therefore gradual. This allows for

variability within states and the possibility of certain features of one state manifesting in another (e.g., wakefulness characteristic of responsiveness appearing during sleep).

At this moment, it is difficult to firmly affirm which view best reflects the structure of consciousness states. While our findings support the second perspective, we cannot completely dismiss the first view. However, based on previous findings, including our own, we can assert that each state of consciousness encompasses a spectrum of different behavioral, physiological, and subjective profiles. The current descriptions of states based on rigid categories are insufficient to fully explain empirical observations. We believe that this can stimulate an important discussion in the field regarding the frontiers of consciousness states and how to study them, as well as their interactions, within a multidimensional space.

5.2. Limitations

Limitations of specific studies have already been discussed in the corresponding chapters. In this section, we will focus on some general considerations regarding our research.

One technical challenge we encountered relates to the limited temporal resolution of fMRI for investigating ongoing brain dynamics. The BOLD response delay makes it difficult to accurately determine when the observed neural activity changes actually occurred. A commonly employed approach is convolving the BOLD signal with a gamma function when analyzing brain activations triggered by specific stimuli. However, in resting-state scans conducted prior to stimulation, where neural activity naturally fluctuates without external stimuli, accurately estimating the actual timing of neural events becomes challenging, especially when focusing on network connectivity rather than local activations. It is possible that the delay in the BOLD signal differs between resting-state and task conditions. Incorporating neuroimaging techniques with higher temporal resolution, such as combining fMRI with EEG, may offer additional insights into the timing of neural events. Nevertheless, accurately aligning the fMRI and EEG timeseries remains a current challenge, as estimating the time lag between these modalities proves difficult (slower reactivity of the BOLD signal compared to the EEG). Advancements in neuroimaging methods hold promise for addressing these timing issues in the future.

A crucial aspect of our research was establishing a link between pre-stimulus brain activity and subsequent behavior. To accomplish this, we focused on specific time windows preceding the stimulation. In Study 2, we targeted the fMRI volume coinciding with the stimulus

presentation. The rationale behind this choice was to be as close as possible in time to the stimulus presentation to capture the neural activity genuinely preceding the stimulation while avoiding stimulus-induced neural activity. Given the lag in the fMRI response, previous volumes would be too distant from the stimulation, while subsequent volumes would represent a mixture of ongoing brain dynamics and stimulus-induced responses. In Study 3, which employed EEG recordings, we focused on a 1-second time window preceding the stimulation. This duration allowed us to capture the baseline brain activity just before the stimulus presentation, while ensuring the epochs were long enough to compute our EEG markers. However, it is important to note that the selection of these time windows, although based on careful considerations, still involved some arbitrariness. It is possible that other time windows might be more suitable for examining the effect of pre-stimulus activity on behavior. For instance, a window as short as 100 milliseconds before the stimulus presentation could potentially better predict subsequent behavior. Due to current limitations in neuroimaging techniques, we were unable to explore the optimal timing to reveal such effects. Future research should focus on investigating how pre-stimulus brain activity at different distances from the stimulus onset influences information processing.

The extent to which stimulus-induced activity contributes to brain dynamics after stimulation remains an unresolved question, as the dynamics observed following a stimulus encompass a combination of stimulus-evoked responses and other ongoing processes (Fox et al., 2006). In Study 1, we demonstrate that brain patterns synchronize across participants during movie watching. The absence of synchronization in the scrambled movie condition indicates that this synchronization is not solely attributable to the sensory aspects of the stimuli but rather to the holistic experience. However, perfect synchronization was not achieved due to variations in participants' individual experiences of the movie. Furthermore, the observed brain dynamics may also reflect other internal processes that are not shared by all participants. Similarly, in Study 2, the detection of a stimulus was followed by a higher occurrence of consciousness-related patterns. Although we believe that this increase is indeed linked to participants detecting the stimulus, we cannot definitively rule out the possibility that this increase is the result of the summation with other processes. Thus, it is challenging to precisely determine the extent to which our measurements are exclusively associated with conscious processing.

5.3. Perspectives

This work raises several intriguing questions that remain unanswered, setting the stage for exciting future studies. In this section, we will briefly discuss potential follow-up investigations that would allow us to delve deeper into the complex interplay between ongoing brain dynamics and conscious perception.

We believe that it is crucial to provide a comprehensive description of the fMRI patterns discovered in Study 2 in order to gain insights into the underlying mechanisms of these brain patterns. For instance, thoroughly characterizing the network interactions within the brain patterns associated with conscious states (Demertzi et al., 2019) and the capacity for conscious perception (Study 2) could offer valuable information about the specific network interactions implicated in consciousness. This would contribute to the longstanding effort of identifying the true neural correlates of consciousness. Additionally, utilizing a more detailed atlas, beyond the 42 regions of interest employed in previous studies, could enable a more refined examination of these brain states.

The experimental designs employed in the Study 2 are highly adaptable and can be easily modified to investigate the interaction between ongoing brain dynamics and other cognitive processes. For example, by introducing an auditory tone that predicts a target at the detection threshold, we could explore how the ongoing brain dynamics prior to target presentation are influenced by anticipation. We expect that overall detection performance would be higher when the tone predicts the target compared to an unpredictable condition. Building upon our current findings, we hypothesize that participants would transition into consciousness-related patterns following a supra-threshold tone (as demonstrated in Study 2). Furthermore, we anticipate that participants would remain in these consciousness-related patterns for longer durations if the tone predicts the arrival of the target, facilitating enhanced processing of the target stimulus.

Investigating how consciousness-related patterns vary in ecological conditions, such as during movie watching, would also be intriguing. In Study 1, we identified brain patterns by applying k-means clustering to data obtained from movie watching, scrambled movie watching, and resting state conditions. This approach yielded patterns that were similar yet distinct from those found in Study 2. Instead of employing k-means clustering, we could label our data from Study 1 using the centroids derived from Study 2, thereby examining how consciousness-related

patterns are distributed across the three conditions and whether they play a specific role in synchronization during movie watching.

Through Studies 1 and 2, we explored the interplay between ongoing brain dynamics and conscious perception during wakefulness. Study 1 demonstrated that conscious processing of a naturalistic stimulus influenced ongoing brain dynamics (direction 1), while Study 2 provided compelling evidence for the reverse direction of the interaction, showing that pre-stimulus brain dynamics also affected stimulus processing (direction 2). However, we have only observed one side of this interaction during sleep. Study 3 focused on the effect of pre-stimulus brain activity on stimulus processing and responsiveness across sleep stages (direction 2) but lacked evidence on how conscious processing of stimuli in sleep influenced ongoing brain dynamics (direction 1). Future research should aim to shed light on the directionality of these interactions during sleep. For instance, it would be interesting to investigate whether processing a high-level stimulus in different sleep stages could induce synchronization across participants. Observing such synchronization during sleep would suggest that this interplay exists not only during wakefulness but also in other states of consciousness, hinting at the possibility that sleeping humans can share a common experience induced by the processing of external stimulation and opening up new and exciting research avenues for exploration.

The fact that sleeping humans can respond to external sensory stimuli indicates the possibility of two-way communication between sleepers and experimenters. Previous research has shown that lucid dreamers in REM sleep were able to perform complex tasks, such as solving simple mathematical problems instructed by the experimenter in real-time (Konkoly et al., 2021). Moreover, they were capable of responding behaviorally to auditory and tactile stimuli. Study 3 expands upon these findings by demonstrating that performing a lexical decision task and providing behavioral responses is also feasible during N1, N2, and REM sleep. These findings pave the way for studies that were previously considered far-fetched. For example, we could envision an experimental setup in which two sleeping individuals communicate with each other. By developing an algorithm that detects muscle contractions (similar to the one proposed in Study 3) and translates them into auditory signals, we could ask a sleeper in one room to contract their corrugator muscles a certain number of times (determined randomly by them). The contractions would be translated into vocalized auditory stimuli and delivered to the other sleeper in a separate room, who would be instructed to contract their muscles the same number of times as indicated by the auditory stimulus. By taking turns in this process, the two sleepers

could send and receive signals, proving the concept of inter-dream communication. While not directly linked to the current work, it would be incredibly exciting for any researcher in the field of sleep and dreams to explore this cutting-edge idea.

Finally, we could investigate the causal relationship between pre-stimulus brain dynamics and the capacity for conscious perception by tracking ongoing brain dynamics in real-time. We could target moments of consciousness-related patterns in wakefulness or periods of heightened EEG markers associated with responsiveness in sleep to trigger stimuli accordingly and examine their effect on perception. Establishing such a causal relationship would have significant implications for the scientific community. Tracking these moments of reactivity during sleep could facilitate real-time communication with the dreamer, enabling inquiries about dream content in the present moment rather than relying on post-awakening reports. This would represent an important paradigm shift in dream research. Furthermore, demonstrating the causal link between brain patterns and higher susceptibility to the external world would have important implications for medical practice. Quantifying the extent to which a patient exhibits consciousness-related patterns could serve as an effective diagnostic tool and predictor of prognosis. Additionally, targeting periods of heightened permeability to the external world in patients with DoC could allow for individually tailored patient care strategies. We hope that the modest contributions of this work will encourage scientists to pursue these exciting research avenues.

REFERENCES

- Abel, G. G., Murphy, W. D., Becker, J. V., & Bitar, A. (1979). Women's vaginal responses during REM Sleep. *Journal of Sex & Marital Therapy*, 5(1), 5–14. <https://doi.org/10.1080/00926237908403713>
- Allen, E. A., Damaraju, E., Plis, S. M., Erhardt, E. B., Eichele, T., & Calhoun, V. D. (2014). Tracking whole-brain connectivity dynamics in the resting state. *Cerebral Cortex (New York, N.Y.: 1991)*, 24(3), 663–676. <https://doi.org/10.1093/cercor/bhs352>
- Allen, P. J., Josephs, O., & Turner, R. (2000). A Method for Removing Imaging Artifact from Continuous EEG Recorded during Functional MRI. *NeuroImage*, 12(2), 230–239. <https://doi.org/10.1006/nimg.2000.0599>
- Andersson, J. L. R., Skare, S., & Ashburner, J. (2003). How to correct susceptibility distortions in spin-echo echo-planar images: Application to diffusion tensor imaging. *NeuroImage*, 20(2), 870–888. [https://doi.org/10.1016/S1053-8119\(03\)00336-7](https://doi.org/10.1016/S1053-8119(03)00336-7)
- Andrillon, T., Burns, A., Mackay, T., Windt, J., & Tsuchiya, N. (2021). Predicting lapses of attention with sleep-like slow waves. *Nature Communications*, 12(1), Article 1. <https://doi.org/10.1038/s41467-021-23890-7>
- Andrillon, T., & Kouider, S. (2020). The vigilant sleeper: Neural mechanisms of sensory (de)coupling during sleep. *Current Opinion in Physiology*, 15, 47–59. <https://doi.org/10.1016/j.cophys.2019.12.002>
- Andrillon, T., Kouider, S., Agus, T., & Pressnitzer, D. (2015). Perceptual Learning of Acoustic Noise Generates Memory-Evoked Potentials. *Current Biology*, 25(21), 2823–2829. <https://doi.org/10.1016/j.cub.2015.09.027>
- Andrillon, T., Poulsen, A. T., Hansen, L. K., Léger, D., & Kouider, S. (2016). Neural Markers of Responsiveness to the Environment in Human Sleep. *Journal of Neuroscience*, 36(24), 6583–6596. <https://doi.org/10.1523/JNEUROSCI.0902-16.2016>
- Andrillon, T., Solelhac, G., Bouchequet, P., Romano, F., Le Brun, M.-P., Brigham, M., Chennaoui, M., & Léger, D. (2020). Revisiting the value of polysomnographic data in insomnia: More than meets the eye. *Sleep Medicine*, 66, 184–200. <https://doi.org/10.1016/j.sleep.2019.12.002>
- Andrillon, T., Windt, J., Silk, T., Drummond, S. P. A., Bellgrove, M. A., & Tsuchiya, N. (2019). Does the Mind Wander When the Brain Takes a Break? Local Sleep in Wakefulness, Attentional Lapses and Mind-Wandering. *Frontiers in Neuroscience*, 13. <https://doi.org/10.3389/fnins.2019.00949>
- Arnulf, I. (2018). Sleepwalking. *Current Biology: CB*, 28(22), R1288–R1289. <https://doi.org/10.1016/j.cub.2018.09.062>
- Arzi, A., Holtzman, Y., Samnon, P., Eshel, N., Harel, E., & Sobel, N. (2014). Olfactory Aversive Conditioning during Sleep Reduces Cigarette-Smoking Behavior. *Journal of*

- Neuroscience*, 34(46), 15382–15393. <https://doi.org/10.1523/JNEUROSCI.2291-14.2014>
- Arzi, A., Shedlesky, L., Ben-Shaul, M., Nasser, K., Oksenberg, A., Hairston, I. S., & Sobel, N. (2012). Humans can learn new information during sleep. *Nature Neuroscience*, 15(10), Article 10. <https://doi.org/10.1038/nn.3193>
- Aserinsky, E., & Kleitman, N. (1953). Regularly Occurring Periods of Eye Motility, and Concomitant Phenomena, During Sleep. *Science*, 118(3062), 273–274. <https://doi.org/10.1126/science.118.3062.273>
- Atas, A., Faivre, N., Timmermans, B., Cleeremans, A., & Kouider, S. (2014). Nonconscious learning from crowded sequences. *Psychological Science*, 25(1), 113–119. <https://doi.org/10.1177/0956797613499591>
- Baars, B. J. (2005). Global workspace theory of consciousness: Toward a cognitive neuroscience of human experience. In S. Laureys (Ed.), *Progress in Brain Research* (Vol. 150, pp. 45–53). Elsevier. [https://doi.org/10.1016/S0079-6123\(05\)50004-9](https://doi.org/10.1016/S0079-6123(05)50004-9)
- Babiloni, C., Vecchio, F., Rossi, S., De Capua, A., Bartalini, S., Ulivelli, M., & Rossini, P. M. (2007). Human ventral parietal cortex plays a functional role on visuospatial attention and primary consciousness. A repetitive transcranial magnetic stimulation study. *Cerebral Cortex (New York, N.Y.: 1991)*, 17(6), 1486–1492. <https://doi.org/10.1093/cercor/bhl060>
- Bai, Y., Xia, X., & Li, X. (2017). A Review of Resting-State Electroencephalography Analysis in Disorders of Consciousness. *Frontiers in Neurology*, 8. <https://www.frontiersin.org/articles/10.3389/fneur.2017.00471>
- Baird, B., Mota-Rolim, S. A., & Dresler, M. (2019). The cognitive neuroscience of lucid dreaming. *Neuroscience and Biobehavioral Reviews*, 100, 305–323. <https://doi.org/10.1016/j.neubiorev.2019.03.008>
- Baird, B., Tononi, G., & LaBerge, S. (2022). Lucid dreaming occurs in activated rapid eye movement sleep, not a mixture of sleep and wakefulness. *Sleep*, zsab294. <https://doi.org/10.1093/sleep/zsab294>
- Balaban, C. D., & Weinstein, J. M. (1985). The human pre-saccadic spike potential: Influences of a visual target, saccade direction, electrode laterality and instructions to perform saccades. *Brain Research*, 347(1), 49–57. [https://doi.org/10.1016/0006-8993\(85\)90888-1](https://doi.org/10.1016/0006-8993(85)90888-1)
- Baria, A. T., Maniscalco, B., & He, B. J. (2017). Initial-state-dependent, robust, transient neural dynamics encode conscious visual perception. *PLOS Computational Biology*, 13(11), e1005806. <https://doi.org/10.1371/journal.pcbi.1005806>
- Barron, H. C., Garvert, M. M., & Behrens, T. E. J. (2016). Repetition suppression: A means to index neural representations using BOLD? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1705), 20150355. <https://doi.org/10.1098/rstb.2015.0355>

- Barttfeld, P., Uhrig, L., Sitt, J. D., Sigman, M., Jarraya, B., & Dehaene, S. (2015). Signature of consciousness in the dynamics of resting-state brain activity. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(3), 887–892. <https://doi.org/10.1073/pnas.1418031112>
- Bastuji, H., & García-Larrea, L. (1999). Evoked potentials as a tool for the investigation of human sleep. *Sleep Medicine Reviews*, *3*(1), 23–45. [https://doi.org/10.1016/s1087-0792\(99\)90012-6](https://doi.org/10.1016/s1087-0792(99)90012-6)
- Bastuji, H., García-Larrea, L., Franc, C., & Mauguière, F. (1995). Brain processing of stimulus deviance during slow-wave and paradoxical sleep: A study of human auditory evoked responses using the oddball paradigm. *Journal of Clinical Neurophysiology: Official Publication of the American Electroencephalographic Society*, *12*(2), 155–167. <https://doi.org/10.1097/00004691-199503000-00006>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beck, D. M., Muggleton, N., Walsh, V., & Lavie, N. (2006). Right parietal cortex plays a critical role in change blindness. *Cerebral Cortex (New York, N.Y.: 1991)*, *16*(5), 712–717. <https://doi.org/10.1093/cercor/bhj017>
- Bekinschtein, T. A., Dehaene, S., Rohaut, B., Tadel, F., Cohen, L., & Naccache, L. (2009). Neural signature of the conscious processing of auditory regularities. *Proceedings of the National Academy of Sciences*, *106*(5), 1672–1677. <https://doi.org/10.1073/pnas.0809667106>
- Bekinschtein, T. A., Manes, F. F., Villarreal, M., Owen, A. M., & Della-Maggiore, V. (2011). Functional imaging reveals movement preparatory activity in the vegetative state. *Frontiers in Human Neuroscience*, *5*, 5. <https://doi.org/10.3389/fnhum.2011.00005>
- Berry, R. B., Brooks, R., Gamaldo, C., Harding, S. M., Lloyd, R. M., Quan, S. F., Troester, M. T., & Vaughn, B. V. (2017). AASM Scoring Manual Updates for 2017 (Version 2.4). *Journal of Clinical Sleep Medicine: JCSM: Official Publication of the American Academy of Sleep Medicine*, *13*(5), 665–666. <https://doi.org/10.5664/jcsm.6576>
- Bezdek, M. A., Gerrig, R. J., Wenzel, W. G., Shin, J., Pirog Reville, K., & Schumacher, E. H. (2015). Neural evidence that suspense narrows attentional focus. *Neuroscience*, *303*, 338–345. <https://doi.org/10.1016/j.neuroscience.2015.06.055>
- Bezdek, M. A., Wenzel, W. G., & Schumacher, E. H. (2017). The effect of visual and musical suspense on brain activation and memory during naturalistic viewing. *Biological Psychology*, *129*, 73–81. <https://doi.org/10.1016/j.biopsycho.2017.07.020>
- Blanchette-Carrière, C., Julien, S.-H., Picard-Deland, C., Bouchard, M., Carrier, J., Paquette, T., & Nielsen, T. (2020). Attempted induction of signalled lucid dreaming by transcranial alternating current stimulation. *Consciousness and Cognition*, *83*, 102957. <https://doi.org/10.1016/j.concog.2020.102957>

- Boly, M., Baeteau, E., Schnakers, C., Degueldre, C., Moonen, G., Luxen, A., Phillips, C., Peigneux, P., Maquet, P., & Laureys, S. (2007). Baseline brain activity fluctuations predict somatosensory perception in humans. *Proceedings of the National Academy of Sciences*, *104*(29), 12187–12192. <https://doi.org/10.1073/pnas.0611404104>
- Bonneh, Y. S., Cooperman, A., & Sagi, D. (2001). Motion-induced blindness in normal observers. *Nature*, *411*(6839), 798–801. <https://doi.org/10.1038/35081073>
- Born, J., & Wilhelm, I. (2012). System consolidation of memory during sleep. *Psychological Research*, *76*(2), 192–203. <https://doi.org/10.1007/s00426-011-0335-6>
- Bourdillon, P., Hermann, B., Guénot, M., Bastuji, H., Isnard, J., King, J.-R., Sitt, J., & Naccache, L. (2020). Brain-scale cortico-cortical functional connectivity in the delta-theta band is a robust signature of conscious states: An intracranial and scalp EEG study. *Scientific Reports*, *10*(1), 14037. <https://doi.org/10.1038/s41598-020-70447-7>
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.
- Breitmeyer, B., & Ögmen, H. (2010). Visual Masking: Time Slices Through Conscious and Unconscious Vision. *Visual Masking: Time Slices Through Conscious and Unconscious Vision*, Vol. 41., 1–384. <https://doi.org/10.1093/acprof:oso/9780198530671.001.0001>
- Brown, R., Lau, H., & LeDoux, J. E. (2019). Understanding the Higher-Order Approach to Consciousness. *Trends in Cognitive Sciences*, *23*(9), 754–768. <https://doi.org/10.1016/j.tics.2019.06.009>
- Bruno, M.-A., Vanhaudenhuyse, A., Thibaut, A., Moonen, G., & Laureys, S. (2011). From unresponsive wakefulness to minimally conscious PLUS and functional locked-in syndromes: Recent advances in our understanding of disorders of consciousness. *Journal of Neurology*, *258*(7), 1373–1384. <https://doi.org/10.1007/s00415-011-6114-x>
- Busch, N. A., Dubois, J., & VanRullen, R. (2009). The Phase of Ongoing EEG Oscillations Predicts Visual Perception. *Journal of Neuroscience*, *29*(24), 7869–7876. <https://doi.org/10.1523/JNEUROSCI.0113-09.2009>
- Cabral, J., Kringelbach, M. L., & Deco, G. (2017). Functional connectivity dynamically evolves on multiple time-scales over a static structural connectome: Models and mechanisms. *NeuroImage*, *160*, 84–96. <https://doi.org/10.1016/j.neuroimage.2017.03.045>
- Canales-Johnson, A., Beerendonk, L., Blain, S., Kitaoka, S., Ezquerro-Nassar, A., Nuiten, S., Fahrenfort, J., Gaal, S. van, & Bekinschtein, T. A. (2020). Decreased Alertness Reconfigures Cognitive Control Networks. *Journal of Neuroscience*, *40*(37), 7142–7154. <https://doi.org/10.1523/JNEUROSCI.0343-20.2020>
- Carmel, D., Walsh, V., Lavie, N., & Rees, G. (2010). Right parietal TMS shortens dominance durations in binocular rivalry. *Current Biology*, *20*(18), R799–R800. <https://doi.org/10.1016/j.cub.2010.07.036>

- Casali, A. G., Gosseries, O., Rosanova, M., Boly, M., Sarasso, S., Casali, K. R., Casarotto, S., Bruno, M.-A., Laureys, S., Tononi, G., & Massimini, M. (2013). A theoretically based index of consciousness independent of sensory processing and behavior. *Science Translational Medicine*, 5(198), 198ra105. <https://doi.org/10.1126/scitranslmed.3006294>
- Casarotto, S., Comanducci, A., Rosanova, M., Sarasso, S., Fecchio, M., Napolitani, M., Pigorini, A., G Casali, A., Trimarchi, P. D., Boly, M., Gosseries, O., Bodart, O., Curto, F., Landi, C., Mariotti, M., Devalle, G., Laureys, S., Tononi, G., & Massimini, M. (2016). Stratification of unresponsive patients by an independently validated index of brain complexity. *Annals of Neurology*, 80(5), 718–729. <https://doi.org/10.1002/ana.24779>
- Chalmers, D. J. (1998). Facing Up to the Problem of Consciousness. In *Consciousness and Emotion in Cognitive Science*. Routledge.
- Chambers, C., & Pressnitzer, D. (2014). Perceptual hysteresis in the judgment of auditory pitch shift. *Attention, Perception, & Psychophysics*, 76(5), 1271–1279. <https://doi.org/10.3758/s13414-014-0676-5>
- Chanes, L., Chica, A. B., Quentin, R., & Valero-Cabré, A. (2012). Manipulation of Pre-Target Activity on the Right Frontal Eye Field Enhances Conscious Visual Perception in Humans. *PLOS ONE*, 7(5), e36232. <https://doi.org/10.1371/journal.pone.0036232>
- Chella, F., Pizzella, V., Zappasodi, F., & Marzetti, L. (2016). Impact of the reference choice on scalp EEG connectivity estimation. *Journal of Neural Engineering*, 13(3), 036016. <https://doi.org/10.1088/1741-2560/13/3/036016>
- Claassen, J., Doyle, K., Matory, A., Couch, C., Burger, K. M., Velazquez, A., Okonkwo, J. U., King, J.-R., Park, S., Agarwal, S., Roh, D., Megjhani, M., Eliseyev, A., Connolly, E. S., & Rohaut, B. (2019). Detection of Brain Activation in Unresponsive Patients with Acute Brain Injury. *New England Journal of Medicine*, 380(26), 2497–2505. <https://doi.org/10.1056/NEJMoA1812757>
- Cole, M. W., Bassett, D. S., Power, J. D., Braver, T. S., & Petersen, S. E. (2014). Intrinsic and Task-Evoked Network Architectures of the Human Brain. *Neuron*, 83(1), 238–251. <https://doi.org/10.1016/j.neuron.2014.05.014>
- Comsa, I. M., Bekinschtein, T. A., & Chennu, S. (2019). Transient Topographical Dynamics of the Electroencephalogram Predict Brain Connectivity and Behavioural Responsiveness During Drowsiness. *Brain Topography*, 32(2), 315–331. <https://doi.org/10.1007/s10548-018-0689-9>
- Cornsweet, T. N. (1962). The staircase-method in psychophysics. *The American Journal of Psychology*, 75, 485–491.
- Coste, C. P., Sadaghiani, S., Friston, K. J., & Kleinschmidt, A. (2011). Ongoing brain activity fluctuations directly account for intertrial and indirectly for intersubject variability in Stroop task performance. *Cerebral Cortex (New York, N.Y.: 1991)*, 21(11), 2612–2619. <https://doi.org/10.1093/cercor/bhr050>

- Cote, K. A., Lugt, D. R. D., & Campbell, K. B. (2002). Changes in the scalp topography of event-related potentials and behavioral responses during the sleep onset period. *Psychophysiology*, *39*(1), 29–37. <https://doi.org/10.1111/1469-8986.3910029>
- Cruse, D., Chennu, S., Chatelle, C., Bekinschtein, T. A., Fernández-Espejo, D., Pickard, J. D., Laureys, S., & Owen, A. M. (2011). Bedside detection of awareness in the vegetative state: A cohort study. *The Lancet*, *378*(9809), 2088–2094. [https://doi.org/10.1016/S0140-6736\(11\)61224-5](https://doi.org/10.1016/S0140-6736(11)61224-5)
- Cruse, D., Chennu, S., Chatelle, C., Fernández-Espejo, D., Bekinschtein, T. A., Pickard, J. D., Laureys, S., & Owen, A. M. (2012). Relationship between etiology and covert cognition in the minimally conscious state. *Neurology*, *78*(11), 816–822. <https://doi.org/10.1212/WNL.0b013e318249f764>
- Cruse, D., Chennu, S., Fernández-Espejo, D., Payne, W. L., Young, G. B., & Owen, A. M. (2012). Detecting Awareness in the Vegetative State: Electroencephalographic Evidence for Attempted Movements to Command. *PLOS ONE*, *7*(11), e49933. <https://doi.org/10.1371/journal.pone.0049933>
- Damoiseaux, J. S., Rombouts, S. A. R. B., Barkhof, F., Scheltens, P., Stam, C. J., Smith, S. M., & Beckmann, C. F. (2006). Consistent resting-state networks across healthy subjects. *Proceedings of the National Academy of Sciences*, *103*(37), 13848–13853. <https://doi.org/10.1073/pnas.0601417103>
- Dauvilliers, Y., Rompré, S., Gagnon, J.-F., Vendette, M., Petit, D., & Montplaisir, J. (2007). REM Sleep Characteristics in Narcolepsy and REM Sleep Behavior Disorder. *Sleep*, *30*(7), 844–849.
- de Gelder, B., Vroomen, J., Pourtois, G., & Weiskrantz, L. (1999). Non-conscious recognition of affect in the absence of striate cortex. *Neuroreport*, *10*(18), 3759–3763. <https://doi.org/10.1097/00001756-199912160-00007>
- Dehaene, S., & Changeux, J.-P. (2011a). Experimental and theoretical approaches to conscious processing. *Neuron*, *70*(2), 200–227. <https://doi.org/10.1016/j.neuron.2011.03.018>
- Dehaene, S., & Changeux, J.-P. (2011b). Experimental and Theoretical Approaches to Conscious Processing. *Neuron*, *70*(2), 200–227. <https://doi.org/10.1016/j.neuron.2011.03.018>
- Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends in Cognitive Sciences*, *10*(5), 204–211. <https://doi.org/10.1016/j.tics.2006.03.007>
- Dehaene, S., Lau, H., & Kouider, S. (2017). What is consciousness, and could machines have it? *Science*, *358*(6362), 486–492. <https://doi.org/10.1126/science.aan8871>
- Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition*, *79*(1–2), 1–37.

- Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J. F., Poline, J. B., & Rivière, D. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience*, *4*(7), 752–758. <https://doi.org/10.1038/89551>
- Dehaene, S., Naccache, L., Le Clec'H, G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., van de Moortele, P. F., & Le Bihan, D. (1998). Imaging unconscious semantic priming. *Nature*, *395*(6702), 597–600. <https://doi.org/10.1038/26967>
- Del Cul, A., Baillet, S., & Dehaene, S. (2007). Brain dynamics underlying the nonlinear threshold for access to consciousness. *PLoS Biology*, *5*(10), e260. <https://doi.org/10.1371/journal.pbio.0050260>
- Demertzi, A., Tagliazucchi, E., Dehaene, S., Deco, G., Barttfeld, P., Raimondo, F., Martial, C., Fernández-Espejo, D., Rohaut, B., Voss, H. U., Schiff, N. D., Owen, A. M., Laureys, S., Naccache, L., & Sitt, J. D. (2019). Human consciousness is supported by dynamic complex patterns of brain signal coordination. *Science Advances*, *5*(2), eaat7603. <https://doi.org/10.1126/sciadv.aat7603>
- Di, X., Zhang, Z., Xu, T., & Biswal, B. B. (2022). Dynamic and stationary brain connectivity during movie watching as revealed by functional MRI. *Brain Structure and Function*, *227*(7), 2299–2312. <https://doi.org/10.1007/s00429-022-02522-w>
- Dodet, P., Chavez, M., Leu-Semenescu, S., Golmard, J.-L., & Arnulf, I. (2015). Lucid Dreaming in Narcolepsy. *Sleep*, *38*(3), 487–497. <https://doi.org/10.5665/sleep.4516>
- Dresler, M., Eibl, L., Fischer, C., Wehrle, R., Spoormaker, V., Steiger, A., Czisch, M., & Pawlowski, M. (2014). Volitional components of consciousness vary across wakefulness, dreaming and lucid dreaming. *Frontiers in Psychology*, *4*. <https://www.frontiersin.org/article/10.3389/fpsyg.2013.00987>
- Dresler, M., Wehrle, R., Spoormaker, V. I., Koch, S. P., Holsboer, F., Steiger, A., Obrig, H., Sämann, P. G., & Czisch, M. (2012). Neural correlates of dream lucidity obtained from contrasting lucid versus non-lucid REM sleep: A combined EEG/fMRI case study. *Sleep*, *35*(7), 1017–1020. <https://doi.org/10.5665/sleep.1974>
- Duszyk-Bogorodzka, A., Zieleniewska, M., & Jankowiak-Siuda, K. (2022). Brain Activity Characteristics of Patients With Disorders of Consciousness in the EEG Resting State Paradigm: A Review. *Frontiers in Systems Neuroscience*, *16*, 654541. <https://doi.org/10.3389/fnsys.2022.654541>
- Ekman, M., Derrfuss, J., Tittgemeyer, M., & Fiebach, C. J. (2012). Predicting errors from reconfiguration patterns in human brain networks. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(41), 16714–16719. <https://doi.org/10.1073/pnas.1207523109>
- Engemann, D. A., Raimondo, F., King, J.-R., Rohaut, B., Louppe, G., Faugeras, F., Annen, J., Cassol, H., Gosseries, O., Fernandez-Slezak, D., Laureys, S., Naccache, L., Dehaene, S., & Sitt, J. D. (2018). Robust EEG-based cross-site and cross-protocol classification of states of consciousness. *Brain*, *141*(11), 3179–3192. <https://doi.org/10.1093/brain/awy251>

- Ergenoglu, T., Demiralp, T., Bayraktaroglu, Z., Ergen, M., Beydagi, H., & Uresin, Y. (2004). Alpha rhythm of the EEG modulates visual detection performance in humans. *Brain Research. Cognitive Brain Research*, *20*(3), 376–383. <https://doi.org/10.1016/j.cogbrainres.2004.03.009>
- Erlacher, D., & Schredl, M. (2004). Time required for motor activity in lucid dreams. *Perceptual and Motor Skills*, *99*(3 Pt 2), 1239–1242. <https://doi.org/10.2466/pms.99.3f.1239-1242>
- Erlacher, D., & Schredl, M. (2008). Do REM (lucid) dreamed and executed actions share the same neural substrate? *International Journal of Dream Research*, 7–14. <https://doi.org/10.11588/ijodr.2008.1.20>
- Everson, C. A., Bergmann, B. M., & Rechtschaffen, A. (1989). Sleep deprivation in the rat: III. Total sleep deprivation. *Sleep*, *12*(1), 13–21. <https://doi.org/10.1093/sleep/12.1.13>
- Faugeras, F., Rohaut, B., Weiss, N., Bekinschtein, T. A., Galanaud, D., Puybasset, L., Bolgert, F., Sergent, C., Cohen, L., Dehaene, S., & Naccache, L. (2011). Probing consciousness with event-related potentials in the vegetative state. *Neurology*, *77*(3), 264–268. <https://doi.org/10.1212/WNL.0b013e3182217ee8>
- Fernandez-Delgado, M., Cernadas, E., Barro, S., & Amorim, D. (2014). Do we Need Hundreds of Classifiers to Solve Real World Classification Problems? *Journal of Machine Learning Research*, *15*, 3133–3181.
- Fernández-Espejo, D., Bekinschtein, T., Monti, M. M., Pickard, J. D., Junque, C., Coleman, M. R., & Owen, A. M. (2011). Diffusion weighted imaging distinguishes the vegetative state from the minimally conscious state. *NeuroImage*, *54*(1), 103–112. <https://doi.org/10.1016/j.neuroimage.2010.08.035>
- Fernández-Espejo, D., & Owen, A. M. (2013). Detecting awareness after severe brain injury. *Nature Reviews Neuroscience*, *14*(11), Article 11. <https://doi.org/10.1038/nrn3608>
- Fernández-Espejo, D., Soddu, A., Cruse, D., Palacios, E. M., Junque, C., Vanhaudenhuyse, A., Rivas, E., Newcombe, V., Menon, D. K., Pickard, J. D., Laureys, S., & Owen, A. M. (2012). A role for the default mode network in the bases of disorders of consciousness. *Annals of Neurology*, *72*(3), 335–343. <https://doi.org/10.1002/ana.23635>
- Ferrand, L., Méot, A., Spinelli, E., New, B., Pallier, C., Bonin, P., Dufau, S., Mathôt, S., & Grainger, J. (2018). MEGALEX: A megastudy of visual and auditory word recognition. *Behavior Research Methods*, *50*(3), 1285–1307. <https://doi.org/10.3758/s13428-017-0943-1>
- Ferrarelli, F., Massimini, M., Sarasso, S., Casali, A., Riedner, B. A., Angelini, G., Tononi, G., & Pearce, R. A. (2010). Breakdown in cortical effective connectivity during midazolam-induced loss of consciousness. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(6), 2681–2686. <https://doi.org/10.1073/pnas.0913008107>

- Filevich, E., Dresler, M., Brick, T. R., & Kühn, S. (2015). Metacognitive Mechanisms Underlying Lucid Dreaming. *Journal of Neuroscience*, *35*(3), 1082–1088. <https://doi.org/10.1523/JNEUROSCI.3342-14.2015>
- Fischer, C., Morlet, D., Bouchet, P., Luaute, J., Jourdan, C., & Salord, F. (1999). Mismatch negativity and late auditory evoked potentials in comatose patients. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, *110*(9), 1601–1610. [https://doi.org/10.1016/s1388-2457\(99\)00131-5](https://doi.org/10.1016/s1388-2457(99)00131-5)
- Fisher, C., Gross, J., & Zuch, J. (1965). Cycle of Penile Erection Synchronous With Dreaming (REM) Sleep: Preliminary Report. *Archives of General Psychiatry*, *12*(1), 29–45. <https://doi.org/10.1001/archpsyc.1965.01720310031005>
- Formby, D. (1967). Maternal Recognition of Infant's Cry. *Developmental Medicine & Child Neurology*, *9*(3), 293–298. <https://doi.org/10.1111/j.1469-8749.1967.tb02271.x>
- Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (Third). Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Fox, K. C. R., Spreng, R. N., Ellamil, M., Andrews-Hanna, J. R., & Christoff, K. (2015). The wandering brain: Meta-analysis of functional neuroimaging studies of mind-wandering and related spontaneous thought processes. *NeuroImage*, *111*, 611–621. <https://doi.org/10.1016/j.neuroimage.2015.02.039>
- Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences*, *102*(27), 9673–9678. <https://doi.org/10.1073/pnas.0504136102>
- Fox, M. D., Snyder, A. Z., Zacks, J. M., & Raichle, M. E. (2006). Coherent spontaneous activity accounts for trial-to-trial variability in human evoked brain responses. *Nature Neuroscience*, *9*(1), Article 1. <https://doi.org/10.1038/nn1616>
- Frässle, S., Sommer, J., Jansen, A., Naber, M., & Einhäuser, W. (2014). Binocular rivalry: Frontal activity relates to introspection and action but not to perception. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *34*(5), 1738–1747. <https://doi.org/10.1523/JNEUROSCI.4403-13.2014>
- Gaser, C., Dahnke, R., Thompson, P. M., Kurth, F., Luders, E., & Initiative, A. D. N. (2022). *CAT – A Computational Anatomy Toolbox for the Analysis of Structural MRI Data* (p. 2022.06.11.495736). bioRxiv. <https://doi.org/10.1101/2022.06.11.495736>
- Gevers, W., Deliens, G., Hoffmann, S., Notebaert, W., & Peigneux, P. (2015). Sleep deprivation selectively disrupts top-down adaptation to cognitive conflict in the Stroop test. *Journal of Sleep Research*, *24*(6), 666–672. <https://doi.org/10.1111/jsr.12320>
- Giacino, J. T., Ashwal, S., Childs, N., Cranford, R., Jennett, B., Katz, D. I., Kelly, J. P., Rosenberg, J. H., Whyte, J., Zafonte, R. D., & Zasler, N. D. (2002). The minimally conscious state: Definition and diagnostic criteria. *Neurology*, *58*(3), 349–353.

- Giacino, J. T., Kalmar, K., & Whyte, J. (2004). The JFK Coma Recovery Scale-Revised: Measurement characteristics and diagnostic utility. *Archives of Physical Medicine and Rehabilitation*, 85(12), 2020–2029. <https://doi.org/10.1016/j.apmr.2004.02.033>
- Goldfine, A. M., Bardin, J. C., Noirhomme, Q., Fins, J. J., Schiff, N. D., & Victor, J. D. (2013). Reanalysis of “Bedside detection of awareness in the vegetative state: A cohort study”. *The Lancet*, 381(9863), 289–291. [https://doi.org/10.1016/S0140-6736\(13\)60125-7](https://doi.org/10.1016/S0140-6736(13)60125-7)
- Gonzalez-Castillo, J., & Bandettini, P. A. (2018). Task-based dynamic functional connectivity: Recent findings and open questions. *NeuroImage*, 180, 526–533. <https://doi.org/10.1016/j.neuroimage.2017.08.006>
- Gonzalez-Castillo, J., Hoy, C. W., Handwerker, D. A., Robinson, M. E., Buchanan, L. C., Saad, Z. S., & Bandettini, P. A. (2015). Tracking ongoing cognition in individuals using brief, whole-brain functional connectivity patterns. *Proceedings of the National Academy of Sciences*, 112(28), 8762–8767. <https://doi.org/10.1073/pnas.1501242112>
- Gramfort, A., Luessi, M., Larson, E., Engemann, D., Strohmeier, D., Brodbeck, C., Goj, R., Jas, M., Brooks, T., Parkkonen, L., & Hämäläinen, M. (2013). MEG and EEG data analysis with MNE-Python. *Frontiers in Neuroscience*, 7. <https://www.frontiersin.org/articles/10.3389/fnins.2013.00267>
- Grill-Spector, K., Kushnir, T., Hendler, T., & Malach, R. (2000). The dynamics of object-selective activation correlate with recognition performance in humans. *Nature Neuroscience*, 3(8), 837–843. <https://doi.org/10.1038/77754>
- Gujar, N., McDonald, S. A., Nishida, M., & Walker, M. P. (2011). A role for REM sleep in recalibrating the sensitivity of the human brain to specific emotions. *Cerebral Cortex (New York, N.Y.: 1991)*, 21(1), 115–123. <https://doi.org/10.1093/cercor/bhq064>
- Harris, C. R., Millman, K. J., van der Walt, S. J., Gommers, R., Virtanen, P., Cournapeau, D., Wieser, E., Taylor, J., Berg, S., Smith, N. J., Kern, R., Picus, M., Hoyer, S., van Kerkwijk, M. H., Brett, M., Haldane, A., del Río, J. F., Wiebe, M., Peterson, P., ... Oliphant, T. E. (2020). Array programming with NumPy. *Nature*, 585(7825), 357–362. <https://doi.org/10.1038/s41586-020-2649-2>
- Hartig, F. (2022). *DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. <http://florianhartig.github.io/DHARMA/>
- Hasson, U., Furman, O., Clark, D., Dudai, Y., & Davachi, L. (2008). Enhanced Intersubject Correlations during Movie Viewing Correlate with Successful Episodic Encoding. *Neuron*, 57(3), 452–462. <https://doi.org/10.1016/j.neuron.2007.12.009>
- Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., & Malach, R. (2004). Intersubject Synchronization of Cortical Activity During Natural Vision. *Science*, 303(5664), 1634–1640. <https://doi.org/10.1126/science.1089506>
- Haugg, A., Cusack, R., Gonzalez-Lara, L. E., Sorger, B., Owen, A. M., & Naci, L. (2018). Do Patients Thought to Lack Consciousness Retain the Capacity for Internal as Well as

- Haynes, J.-D., Driver, J., & Rees, G. (2005). Visibility Reflects Dynamic Changes of Effective Connectivity between V1 and Fusiform Cortex. *Neuron*, 46(5), 811–821. <https://doi.org/10.1016/j.neuron.2005.05.012>
- Hearne, K. (1978). *Lucid dreams: An electro-physiological and psychological study* [Ph.D., Liverpool University]. <https://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.458729>
- Heinke, W., Kenntner, R., Gunter, T. C., Sammler, D., Olthoff, D., & Koelsch, S. (2004). Sequential effects of increasing propofol sedation on frontal and temporal cortices as indexed by auditory event-related potentials. *Anesthesiology*, 100(3), 617–625. <https://doi.org/10.1097/00000542-200403000-00023>
- Helfrich, R. F., Knepper, H., Nolte, G., Strüber, D., Rach, S., Herrmann, C. S., Schneider, T. R., & Engel, A. K. (2014). Selective Modulation of Interhemispheric Functional Connectivity by HD-tACS Shapes Perception. *PLOS Biology*, 12(12), e1002031. <https://doi.org/10.1371/journal.pbio.1002031>
- Helfrich, R. F., Lendner, J. D., & Knight, R. T. (2021). Aperiodic sleep networks promote memory consolidation. *Trends in Cognitive Sciences*, 25(8), 648–659. <https://doi.org/10.1016/j.tics.2021.04.009>
- Hermann, B., Goudard, G., Courcoux, K., Valente, M., Labat, S., Despois, L., Bourmaleau, J., Richard-Gillis, L., Faugeras, F., Demeret, S., Sitt, J. D., Naccache, L., & Rohaut, B. (2019). Wisdom of the caregivers: Pooling individual subjective reports to diagnose states of consciousness in brain-injured patients, a monocentric prospective study. *BMJ Open*, 9(2), e026211. <https://doi.org/10.1136/bmjopen-2018-026211>
- Hermann, B., Salah, A. B., Perlberg, V., Valente, M., Pyatigorskaya, N., Habert, M.-O., Raimondo, F., Stender, J., Galanaud, D., Kas, A., Puybasset, L., Perez, P., Sitt, J. D., Rohaut, B., & Naccache, L. (2020). Habituation of auditory startle reflex is a new sign of minimally conscious state. *Brain*, 143(7), 2154–2172. <https://doi.org/10.1093/brain/awaa159>
- Hesselmann, G., Kell, C. A., Eger, E., & Kleinschmidt, A. (2008). Spontaneous local variations in ongoing neural activity bias perceptual decisions. *Proceedings of the National Academy of Sciences*, 105(31), 10984–10989.
- Hesselmann, G., Kell, C. A., & Kleinschmidt, A. (2008). Ongoing Activity Fluctuations in hMT+ Bias the Perception of Coherent Visual Motion. *The Journal of Neuroscience*, 28(53), 14481–14485. <https://doi.org/10.1523/JNEUROSCI.4398-08.2008>
- Hirshkowitz, M. (2004). Normal human sleep: An overview. *The Medical Clinics of North America*, 88(3), 551–565, vii. <https://doi.org/10.1016/j.mcna.2004.01.001>
- Honey, C. J., Kötter, R., Breakspear, M., & Sporns, O. (2007). Network structure of cerebral cortex shapes functional connectivity on multiple time scales. *Proceedings of the*

- National Academy of Sciences*, 104(24), 10240–10245.
<https://doi.org/10.1073/pnas.0701519104>
- Hutchison, R. M., Womelsdorf, T., Gati, J. S., Everling, S., & Menon, R. S. (2013). Resting-state networks show dynamic functional connectivity in awake humans and anesthetized macaques. *Human Brain Mapping*, 34(9), 2154–2177.
<https://doi.org/10.1002/hbm.22058>
- Ibáñez, A., López, V., & Cornejo, C. (2006). ERPs and contextual semantic discrimination: Degrees of congruence in wakefulness and sleep. *Brain and Language*, 98(3), 264–275.
<https://doi.org/10.1016/j.bandl.2006.05.005>
- Idir, Y., Oudiette, D., & Arnulf, I. (2022). Sleepwalking, sleep terrors, sexsomnia and other disorders of arousal: The old and the new. *Journal of Sleep Research*, 31(4), e13596.
<https://doi.org/10.1111/jsr.13596>
- Issa, E. B., & Wang, X. (2011). Altered Neural Responses to Sounds in Primate Primary Auditory Cortex during Slow-Wave Sleep. *The Journal of Neuroscience*, 31(8), 2965–2973. <https://doi.org/10.1523/JNEUROSCI.4920-10.2011>
- Jääskeläinen, I. P., Koskentalo, K., Balk, M. H., Autti, T., Kauramäki, J., Pomren, C., & Sams, M. (2008). Inter-Subject Synchronization of Prefrontal Cortex Hemodynamic Activity During Natural Viewing. *The Open Neuroimaging Journal*, 2, 14–19.
<https://doi.org/10.2174/18744440000802010014>
- Jagannathan, S. R., Bareham, C. A., & Bekinschtein, T. A. (2022). Decreasing Alertness Modulates Perceptual Decision-Making. *Journal of Neuroscience*, 42(3), 454–473.
<https://doi.org/10.1523/JNEUROSCI.0182-21.2021>
- Jagannathan, S. R., Ezquerro-Nassar, A., Jachs, B., Pustovaya, O. V., Bareham, C. A., & Bekinschtein, T. A. (2018). Tracking wakefulness as it fades: Micro-measures of alertness. *NeuroImage*, 176, 138–151.
<https://doi.org/10.1016/j.neuroimage.2018.04.046>
- James, W. (1890). *The principles of psychology, Vol I*. Henry Holt and Co.
<https://doi.org/10.1037/10538-000>
- Jas, M., Engemann, D. A., Bekhti, Y., Raimondo, F., & Gramfort, A. (2017). Autoreject: Automated artifact rejection for MEG and EEG data. *NeuroImage*, 159, 417–429.
<https://doi.org/10.1016/j.neuroimage.2017.06.030>
- Jennett, B., & Plum, F. (1972). Persistent vegetative state after brain damage. A syndrome in search of a name. *Lancet (London, England)*, 1(7753), 734–737.
[https://doi.org/10.1016/s0140-6736\(72\)90242-5](https://doi.org/10.1016/s0140-6736(72)90242-5)
- Kasper, L., Bollmann, S., Diaconescu, A. O., Hutton, C., Heinzle, J., Iglesias, S., Hauser, T. U., Sebold, M., Manjaly, Z.-M., Pruessmann, K. P., & Stephan, K. E. (2017). The PhysIO Toolbox for Modeling Physiological Noise in fMRI Data. *Journal of Neuroscience Methods*, 276, 56–72. <https://doi.org/10.1016/j.jneumeth.2016.10.019>

- Kauppi, J.-P., Jääskeläinen, I., Sams, M., & Tohka, J. (2010). Inter-subject correlation of brain hemodynamic responses during watching a movie: Localization in space and frequency. *Frontiers in Neuroinformatics*, 4. <https://www.frontiersin.org/article/10.3389/fninf.2010.00005>
- Kelleher, J. D., Namee, B. M., & D'Arcy, A. (2015). *Fundamentals of Machine Learning for Predictive Data Analytics: Algorithms, Worked Examples, and Case Studies*. MIT Press.
- Kentridge, R. W., Heywood, C. A., & Weiskrantz, L. (1999). Attention without awareness in blindsight. *Proceedings of the Royal Society B: Biological Sciences*, 266(1430), 1805–1811.
- Kentridge, R. W., Heywood, C. A., & Weiskrantz, L. (2004). Spatial attention speeds discrimination without awareness in blindsight. *Neuropsychologia*, 42(6), 831–835. <https://doi.org/10.1016/j.neuropsychologia.2003.11.001>
- Kessler, K., Schmitz, F., Gross, J., Hommel, B., Shapiro, K., & Schnitzler, A. (2005). Target consolidation under high temporal processing demands as revealed by MEG. *NeuroImage*, 26(4), 1030–1041. <https://doi.org/10.1016/j.neuroimage.2005.02.020>
- King, J.-R., & Dehaene, S. (2014). Characterizing the dynamics of mental representations: The temporal generalization method. *Trends in Cognitive Sciences*, 18(4), 203–210. <https://doi.org/10.1016/j.tics.2014.01.002>
- King, J.-R., Sitt, J. D., Faugeras, F., Rohaut, B., El Karoui, I., Cohen, L., Naccache, L., & Dehaene, S. (2013). Information sharing in the brain indexes consciousness in noncommunicative patients. *Current Biology: CB*, 23(19), 1914–1919. <https://doi.org/10.1016/j.cub.2013.07.075>
- Koch, C., Massimini, M., Boly, M., & Tononi, G. (2016). Neural correlates of consciousness: Progress and problems. *Nature Reviews. Neuroscience*, 17(5), 307–321. <https://doi.org/10.1038/nrn.2016.22>
- Konkoly, K. R., Appel, K., Chabani, E., Mangiaruga, A., Gott, J., Mallett, R., Caughran, B., Witkowski, S., Whitmore, N. W., Mazurek, C. Y., Berent, J. B., Weber, F. D., Türker, B., Leu-Semenescu, S., Maranci, J.-B., Pipa, G., Arnulf, I., Oudiette, D., Dresler, M., & Paller, K. A. (2021). Real-time dialogue between experimenters and dreamers during REM sleep. *Current Biology*, 31(7), 1417–1427.e6. <https://doi.org/10.1016/j.cub.2021.01.026>
- Kornmeier, J., & Bach, M. (2012). Ambiguous Figures – What Happens in the Brain When Perception Changes But Not the Stimulus. *Frontiers in Human Neuroscience*, 6. <https://www.frontiersin.org/articles/10.3389/fnhum.2012.00051>
- Koroma, M., Elbaz, M., Léger, D., & Kouider, S. (2022). Learning New Vocabulary Implicitly During Sleep Transfers With Cross-Modal Generalization Into Wakefulness. *Frontiers in Neuroscience*, 16. <https://www.frontiersin.org/articles/10.3389/fnins.2022.801666>

- Koroma, M., Lacaux, C., Andrillon, T., Legendre, G., Léger, D., & Kouider, S. (2020). Sleepers Selectively Suppress Informative Inputs during Rapid Eye Movements. *Current Biology*, *30*(12), 2411–2417.e3. <https://doi.org/10.1016/j.cub.2020.04.047>
- Kouider, S., Andrillon, T., Barbosa, L. S., Goupil, L., & Bekinschtein, T. A. (2014). Inducing Task-Relevant Responses to Speech in the Sleeping Brain. *Current Biology*, *24*(18), 2208–2214. <https://doi.org/10.1016/j.cub.2014.08.016>
- Kouider, S., Eger, E., Dolan, R., & Henson, R. N. (2009). Activity in face-responsive brain regions is modulated by invisible, attended faces: Evidence from masked priming. *Cerebral Cortex*, *19*(1), 13–23. <https://doi.org/10.1093/cercor/bhn048>
- Kranczioch, C., Debener, S., Schwarzbach, J., Goebel, R., & Engel, A. K. (2005). Neural correlates of conscious perception in the attentional blink. *NeuroImage*, *24*(3), 704–714. <https://doi.org/10.1016/j.neuroimage.2004.09.024>
- Kurtzberg, D., & Vaughan, H. G. (1982). Topographic analysis of human cortical potentials preceding self-initiated and visually triggered saccades. *Brain Research*, *243*(1), 1–9. [https://doi.org/10.1016/0006-8993\(82\)91115-5](https://doi.org/10.1016/0006-8993(82)91115-5)
- Kusnir, F., Chica, A. B., Mitsumasu, M. A., & Bartolomeo, P. (2011). Phasic auditory alerting improves visual conscious perception. *Consciousness and Cognition*, *20*(4), 1201–1210. <https://doi.org/10.1016/j.concog.2011.01.012>
- LaBerge, S., Baird, B., & Zimbardo, P. G. (2018). Smooth tracking of visual targets distinguishes lucid REM sleep dreaming and waking perception from imagination. *Nature Communications*, *9*(1), Article 1. <https://doi.org/10.1038/s41467-018-05547-0>
- LaBerge, S., Levitan, L., & Dement, W. C. (1986). Lucid dreaming: Physiological correlates of consciousness during REM sleep. *Journal of Mind and Behavior*, *7*, 251–258.
- LaBerge, S. P., Nagel, L. E., Dement, W. C., & Zarcone, V. P. (1981). Lucid dreaming verified by volitional communication during REM sleep. *Perceptual and Motor Skills*, *52*(3), 727–732. <https://doi.org/10.2466/pms.1981.52.3.727>
- Lacaux, C., Andrillon, T., Bastoul, C., Idir, Y., Fonteix-Galet, A., Arnulf, I., & Oudiette, D. (2021). Sleep onset is a creative sweet spot. *Science Advances*, *7*(50), eabj5866. <https://doi.org/10.1126/sciadv.abj5866>
- Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*(11), 494–501. <https://doi.org/10.1016/j.tics.2006.09.001>
- Lamme, V. A. F. (2010). How neuroscience will change our view on consciousness. *Cognitive Neuroscience*, *1*(3), 204–220. <https://doi.org/10.1080/17588921003731586>
- Lankinen, K., Saari, J., Hlushchuk, Y., Tikka, P., Parkkonen, L., Hari, R., & Koskinen, M. (2018). Consistency and similarity of MEG- and fMRI-signal time courses during movie viewing. *NeuroImage*, *173*, 361–369. <https://doi.org/10.1016/j.neuroimage.2018.02.045>
- Laumann, T. O., Gordon, E. M., Adeyemo, B., Snyder, A. Z., Joo, S. J., Chen, M.-Y., Gilmore, A. W., McDermott, K. B., Nelson, S. M., Dosenbach, N. U. F., Schlaggar, B. L.,

- Mumford, J. A., Poldrack, R. A., & Petersen, S. E. (2015). Functional System and Areal Organization of a Highly Sampled Individual Human Brain. *Neuron*, *87*(3), 657–670. <https://doi.org/10.1016/j.neuron.2015.06.037>
- Lechinger, J., Bothe, K., Pichler, G., Michitsch, G., Donis, J., Klimesch, W., & Schabus, M. (2013). CRS-R score in disorders of consciousness is strongly related to spectral EEG at rest. *Journal of Neurology*, *260*(9), 2348–2356. <https://doi.org/10.1007/s00415-013-6982-3>
- Lee, M. D., & Wagenmakers, E.-J. (2014). *Bayesian Cognitive Modeling: A Practical Course*. Cambridge University Press.
- Legendre, G., Andrillon, T., Koroma, M., & Kouider, S. (2019). Sleepers track informative speech in a multitalker environment. *Nature Human Behaviour*, *3*(3), Article 3. <https://doi.org/10.1038/s41562-018-0502-5>
- Lenth, R. V. (2021). *Emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.6.2-1*. <https://CRAN.R-project.org/package=emmeans>
- Leske, S., Ruhnau, P., Frey, J., Lithari, C., Müller, N., Hartmann, T., & Weisz, N. (2015). Prestimulus Network Integration of Auditory Cortex Predisposes Near-Threshold Perception Independently of Local Excitability. *Cerebral Cortex*, *25*(12), 4898–4907. <https://doi.org/10.1093/cercor/bhv212>
- Leslie, K., & Ogilvie, R. (1996). Vestibular dreams: The effect of rocking on dream mentation. *Dreaming*, *6*, 1–16. <https://doi.org/10.1037/h0094442>
- Lim, J., & Dinges, D. F. (2008). Sleep Deprivation and Vigilant Attention. *Annals of the New York Academy of Sciences*, *1129*(1), 305–322. <https://doi.org/10.1196/annals.1417.002>
- Mack, A. (2003). Inattentional Blindness: Looking Without Seeing. *Current Directions in Psychological Science*, *12*(5), 180–184. <https://doi.org/10.1111/1467-8721.01256>
- Marois, R., Yi, D.-J., & Chun, M. M. (2004). The neural fate of consciously perceived and missed events in the attentional blink. *Neuron*, *41*(3), 465–472. [https://doi.org/10.1016/s0896-6273\(04\)00012-1](https://doi.org/10.1016/s0896-6273(04)00012-1)
- Martínez Vivot, R., Pallavicini, C., Zamberlan, F., Vigo, D., & Tagliazucchi, E. (2020). Meditation Increases the Entropy of Brain Oscillatory Activity. *Neuroscience*, *431*, 40–51. <https://doi.org/10.1016/j.neuroscience.2020.01.033>
- Mashour, G. A., Roelfsema, P., Changeux, J.-P., & Dehaene, S. (2020). Conscious Processing and the Global Neuronal Workspace Hypothesis. *Neuron*, *105*(5), 776–798. <https://doi.org/10.1016/j.neuron.2020.01.026>
- Mason, M. F., Norton, M. I., Van Horn, J. D., Wegner, D. M., Grafton, S. T., & Macrae, C. N. (2007). Wandering Minds: The Default Network and Stimulus-Independent Thought. *Science*, *315*(5810), 393–395. <https://doi.org/10.1126/science.1131295>
- Massimini, M., Ferrarelli, F., Huber, R., Esser, S. K., Singh, H., & Tononi, G. (2005). Breakdown of cortical effective connectivity during sleep. *Science (New York, N.Y.)*, *309*(5744), 2228–2232. <https://doi.org/10.1126/science.1117256>

- Meer, J. N. van der, Breakspear, M., Chang, L. J., Sonkusare, S., & Cocchi, L. (2020). Movie viewing elicits rich and reliable brain state dynamics. *Nature Communications*, *11*(1), 5004. <https://doi.org/10.1038/s41467-020-18717-w>
- Monti, M. M., Coleman, M. R., & Owen, A. M. (2009). Executive functions in the absence of behavior: Functional imaging of the minimally conscious state. *Progress in Brain Research*, *177*, 249–260. [https://doi.org/10.1016/S0079-6123\(09\)17717-8](https://doi.org/10.1016/S0079-6123(09)17717-8)
- Monti, M. M., Pickard, J. D., & Owen, A. M. (2013). Visual cognition in disorders of consciousness: From V1 to top-down attention. *Human Brain Mapping*, *34*(6), 1245–1253. <https://doi.org/10.1002/hbm.21507>
- Monti, M. M., Vanhaudenhuyse, A., Coleman, M. R., Boly, M., Pickard, J. D., Tshibanda, L., Owen, A. M., & Laureys, S. (2010). Willful modulation of brain activity in disorders of consciousness. *The New England Journal of Medicine*, *362*(7), 579–589. <https://doi.org/10.1056/NEJMoa0905370>
- Monto, S., Palva, S., Voipio, J., & Palva, J. M. (2008). Very Slow EEG Fluctuations Predict the Dynamics of Stimulus Detection and Oscillation Amplitudes in Humans. *Journal of Neuroscience*, *28*(33), 8268–8272. <https://doi.org/10.1523/JNEUROSCI.1910-08.2008>
- Morey, R. D., & Rouder, J. N. (2013). *BayesFactor*.
- Mortaheb, S., Van Calster, L., Raimondo, F., Klados, M. A., Boulakis, P. A., Georgoula, K., Majerus, S., Van De Ville, D., & Demertzi, A. (2022). Mind blanking is a distinct mental state linked to a recurrent brain profile of globally positive connectivity during ongoing mentation. *Proceedings of the National Academy of Sciences*, *119*(41), e2200511119. <https://doi.org/10.1073/pnas.2200511119>
- Mudrik, L., Breska, A., Lamy, D., & Deouell, L. Y. (2011). Integration Without Awareness: Expanding the Limits of Unconscious Processing. *Psychological Science*, *22*(6), 764–770. <https://doi.org/10.1177/0956797611408736>
- Mudrik, L., Faivre, N., & Koch, C. (2014). Information integration without awareness. *Trends in Cognitive Sciences*, *18*(9), 488–496. <https://doi.org/10.1016/j.tics.2014.04.009>
- Naccache, L. (2018). Why and how access consciousness can account for phenomenal consciousness. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *373*(1755), 20170357. <https://doi.org/10.1098/rstb.2017.0357>
- Naci, L., Cusack, R., Anello, M., & Owen, A. M. (2014). A common neural code for similar conscious experiences in different individuals. *Proceedings of the National Academy of Sciences*, *111*(39), 14277–14282. <https://doi.org/10.1073/pnas.1407007111>
- Nir, Y., Vyazovskiy, V. V., Cirelli, C., Banks, M. I., & Tononi, G. (2015). Auditory Responses and Stimulus-Specific Adaptation in Rat Auditory Cortex are Preserved Across NREM and REM Sleep. *Cerebral Cortex*, *25*(5), 1362–1378. <https://doi.org/10.1093/cercor/bht328>

- Nummenmaa, L., Glerean, E., Viinikainen, M., Jääskeläinen, I. P., Hari, R., & Sams, M. (2012). Emotions promote social interaction by synchronizing brain activity across individuals. *Proceedings of the National Academy of Sciences*, *109*(24), 9599–9604. <https://doi.org/10.1073/pnas.1206095109>
- Ogilvie, R. D. (2001). The process of falling asleep. *Sleep Medicine Reviews*, *5*(3), 247–270. <https://doi.org/10.1053/smr.v.2001.0145>
- Oizumi, M., Albantakis, L., & Tononi, G. (2014). From the Phenomenology to the Mechanisms of Consciousness: Integrated Information Theory 3.0. *PLOS Computational Biology*, *10*(5), e1003588. <https://doi.org/10.1371/journal.pcbi.1003588>
- Oudiette, D., Dodet, P., Ledard, N., Artru, E., Rachidi, I., Similowski, T., & Arnulf, I. (2018). REM sleep respiratory behaviours match mental content in narcoleptic lucid dreamers. *Scientific Reports*, *8*(1), Article 1. <https://doi.org/10.1038/s41598-018-21067-9>
- Oudiette, D., & Paller, K. A. (2013). Upgrading the sleeping brain with targeted memory reactivation. *Trends in Cognitive Sciences*, *17*(3), 142–149. <https://doi.org/10.1016/j.tics.2013.01.006>
- Owen, A. M., Coleman, M. R., Boly, M., Davis, M. H., Laureys, S., & Pickard, J. D. (2006). Detecting Awareness in the Vegetative State. *Science*, *313*(5792), 1402–1402. <https://doi.org/10.1126/science.1130197>
- Palva, S., Linkenkaer-Hansen, K., Näätänen, R., & Palva, J. M. (2005). Early Neural Correlates of Conscious Somatosensory Perception. *Journal of Neuroscience*, *25*(21), 5248–5258. <https://doi.org/10.1523/JNEUROSCI.0141-05.2005>
- Paul, F., Schädlich, M., & Erlacher, D. (2014). Lucid dream induction by visual and tactile stimulation. *International Journal of Dream Research*, *7*, 61–66. <https://doi.org/10.11588/ijodr.2014.1.13044>
- Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., Blondel, M., Prettenhofer, P., Weiss, R., Dubourg, V., Vanderplas, J., Passos, A., Cournapeau, D., Brucher, M., Perrot, M., & Duchesnay, É. (2011). Scikit-learn: Machine Learning in Python. *Journal of Machine Learning Research*, *12*(85), 2825–2830.
- Pennartz, C. M. A. (2022). What is neurorepresentationalism? From neural activity and predictive processing to multi-level representations and consciousness. *Behavioural Brain Research*, *432*, 113969. <https://doi.org/10.1016/j.bbr.2022.113969>
- Penny, W. D., Friston, K. J., Ashburner, J. T., Kiebel, S. J., & Nichols, T. E. (2011). *Statistical Parametric Mapping: The Analysis of Functional Brain Images*. Elsevier.
- Perea, M., Marcet, A., Vergara-Martínez, M., & Gomez, P. (2016). On the Dissociation of Word/Nonword Repetition Effects in Lexical Decision: An Evidence Accumulation Account. *Frontiers in Psychology*, *7*. <https://www.frontiersin.org/article/10.3389/fpsyg.2016.00215>
- Perrin, F., Bastuji, H., & Garcia-Larrea, L. (2002). Detection of verbal discordances during sleep. *Neuroreport*, *13*(10), 1345–1349.

- Perrin, F., García-Larrea, L., Mauguière, F., & Bastuji, H. (1999). A differential brain response to the subject's own name persists during sleep. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, *110*(12), 2153–2164.
- Pessiglione, M., Schmidt, L., Draganski, B., Kalisch, R., Lau, H., Dolan, R. J., & Frith, C. D. (2007). How the brain translates money into force: A neuroimaging study of subliminal motivation. *Science (New York, N.Y.)*, *316*(5826), 904–906. <https://doi.org/10.1126/science.1140459>
- Pincham, H. L., & Szűcs, D. (2012). Conscious Access Is Linked to Ongoing Brain State: Electrophysiological Evidence from the Attentional Blink. *Cerebral Cortex*, *22*(10), 2346–2353. <https://doi.org/10.1093/cercor/bhr314>
- Pins, D., & Ffytche, D. (2003). The Neural Correlates of Conscious Vision. *Cerebral Cortex*, *13*(5), 461–474. <https://doi.org/10.1093/cercor/13.5.461>
- Pitts, M. A., Metzler, S., & Hillyard, S. A. (2014). Isolating neural correlates of conscious perception from neural correlates of reporting one's perception. *Frontiers in Psychology*, *5*. <https://www.frontiersin.org/articles/10.3389/fpsyg.2014.01078>
- Ploner, M., Lee, M. C., Wiech, K., Bingel, U., & Tracey, I. (2010). Prestimulus functional connectivity determines pain perception in humans. *Proceedings of the National Academy of Sciences*, *107*(1), 355–360. <https://doi.org/10.1073/pnas.0906186106>
- R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ragazzoni, A., Pirulli, C., Veniero, D., Feurra, M., Cincotta, M., Giovannelli, F., Chiaramonti, R., Lino, M., Rossi, S., & Miniussi, C. (2013). Vegetative versus minimally conscious states: A study using TMS-EEG, sensory and event-related potentials. *PloS One*, *8*(2), e57069. <https://doi.org/10.1371/journal.pone.0057069>
- Rahimi, S., Naghibi, S. M., Mokhber, N., Schredl, M., Assadpour, H., Ramezani Farkhani, A., Nemati Karimoui, H. A., Mohajeri, S. M. R., Darvish, A., Naghibi, S. S., & Sadjadi, S. A. (2015). *Sophisticated evaluation of possible effect of distinct auditory stimulation during REM sleep on dream content*. <https://doi.org/10.11588/IJODR.2015.2.24881>
- Railo, H., Salminen-Vaparanta, N., Henriksson, L., Revonsuo, A., & Koivisto, M. (2012). Unconscious and Conscious Processing of Color Rely on Activity in Early Visual Cortex: A TMS Study. *Journal of Cognitive Neuroscience*, *24*(4), 819–829. https://doi.org/10.1162/jocn_a_00172
- Rasch, B., & Born, J. (2013). About sleep's role in memory. *Physiological Reviews*, *93*(2), 681–766. <https://doi.org/10.1152/physrev.00032.2012>
- Rasch, B., Büchel, C., Gais, S., & Born, J. (2007). Odor Cues During Slow-Wave Sleep Prompt Declarative Memory Consolidation. *Science*, *315*(5817), 1426–1429. <https://doi.org/10.1126/science.1138581>

- Reber, T. P., & Henke, K. (2012). Integrating unseen events over time. *Consciousness and Cognition*, *21*(2), 953–960. <https://doi.org/10.1016/j.concog.2012.02.013>
- Recio, G., Shmuilovich, O., & Sommer, W. (2014). Should I smile or should I frown? An ERP study on the voluntary control of emotion-related facial expressions. *Psychophysiology*, *51*(8), 789–799. <https://doi.org/10.1111/psyp.12220>
- Ric, F., & Muller, D. (2012). Unconscious addition: When we unconsciously initiate and follow arithmetic rules. *Journal of Experimental Psychology. General*, *141*(2), 222–226. <https://doi.org/10.1037/a0024608>
- Richman, J. S., & Moorman, J. R. (2000). Physiological time-series analysis using approximate entropy and sample entropy. *American Journal of Physiology. Heart and Circulatory Physiology*, *278*(6), H2039-2049. <https://doi.org/10.1152/ajpheart.2000.278.6.H2039>
- Rivera-García, A. P., Ramírez-Salado, I., Corsi-Cabrera, M., & Calvo, J. M. (2011). Facial muscle activation during sleep and its relation to the rapid eye movements of REM sleep. *Journal of Sleep Research*, *20*(1pt1), 82–91. <https://doi.org/10.1111/j.1365-2869.2010.00853.x>
- Rohaut, B., & Naccache, L. (2017). Disentangling conscious from unconscious cognitive processing with event-related EEG potentials. *Revue Neurologique*, *173*(7–8), 521–528. <https://doi.org/10.1016/j.neurol.2017.08.001>
- Rosanova, M., Gosseries, O., Casarotto, S., Boly, M., Casali, A. G., Bruno, M.-A., Mariotti, M., Boveroux, P., Tononi, G., Laureys, S., & Massimini, M. (2012). Recovery of cortical effective connectivity and recovery of consciousness in vegetative patients. *Brain: A Journal of Neurology*, *135*(Pt 4), 1308–1320. <https://doi.org/10.1093/brain/awr340>
- Rossetti, Y. (1998). Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Consciousness and Cognition*, *7*(3), 520–558. <https://doi.org/10.1006/ccog.1998.0370>
- Rowley, J. T., Stickgold, R., & Hobson, J. A. (1998). Eyelid movements and mental activity at sleep onset. *Consciousness and Cognition*, *7*(1), 67–84. <https://doi.org/10.1006/ccog.1998.0333>
- Ruby, P., Caclin, A., Boulet, S., Delpuech, C., & Morlet, D. (2008). Odd sound processing in the sleeping brain. *Journal of Cognitive Neuroscience*, *20*(2), 296–311. <https://doi.org/10.1162/jocn.2008.20023>
- Ruby, P. M. (2020). The Neural Correlates of Dreaming Have Not Been Identified Yet. Commentary on “The Neural Correlates of Dreaming. Nat Neurosci. 2017”. *Frontiers in Neuroscience*, *14*. <https://www.frontiersin.org/articles/10.3389/fnins.2020.585470>
- Ruch, S., Alain Züst, M., & Henke, K. (2022). Sleep-learning impairs subsequent awake-learning. *Neurobiology of Learning and Memory*, *187*, 107569. <https://doi.org/10.1016/j.nlm.2021.107569>

- Rudoy, J. D., Voss, J. L., Westerberg, C. E., & Paller, K. A. (2009). Strengthening individual memories by reactivating them during sleep. *Science (New York, N.Y.)*, *326*(5956), 1079. <https://doi.org/10.1126/science.1179013>
- Sadaghiani, S., Hesselmann, G., & Kleinschmidt, A. (2009). Distributed and Antagonistic Contributions of Ongoing Activity Fluctuations to Auditory Stimulus Detection. *Journal of Neuroscience*, *29*(42), 13410–13417.
- Sadaghiani, S., Poline, J.-B., Kleinschmidt, A., & D'Esposito, M. (2015). Ongoing dynamics in large-scale functional connectivity predict perception. *Proceedings of the National Academy of Sciences*, *112*(27), 8463–8468. <https://doi.org/10.1073/pnas.1420687112>
- Sanchez, G., Hartmann, T., Fuscà, M., Demarchi, G., & Weisz, N. (2020). Decoding across sensory modalities reveals common supramodal signatures of conscious perception. *Proceedings of the National Academy of Sciences*, *117*(13), 7437–7446. <https://doi.org/10.1073/pnas.1912584117>
- Sapir, A., d'Avossa, G., McAvoy, M., Shulman, G. L., & Corbetta, M. (2005). Brain signals for spatial attention predict performance in a motion discrimination task. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(49), 17810–17815. <https://doi.org/10.1073/pnas.0504678102>
- Sateia, M. J. (2014). International classification of sleep disorders-third edition: Highlights and modifications. *Chest*, *146*(5), 1387–1394. <https://doi.org/10.1378/chest.14-0970>
- Saunders, D. T., Roe, C. A., Smith, G., & Clegg, H. (2016). Lucid dreaming incidence: A quality effects meta-analysis of 50years of research. *Consciousness and Cognition*, *43*, 197–215. <https://doi.org/10.1016/j.concog.2016.06.002>
- Schnakers, C., Majerus, S., Goldman, S., Boly, M., Van Eeckhout, P., Gay, S., Pellas, F., Bartsch, V., Peigneux, P., Moonen, G., & Laureys, S. (2008). Cognitive function in the locked-in syndrome. *Journal of Neurology*, *255*(3), 323–330. <https://doi.org/10.1007/s00415-008-0544-0>
- Schnakers, C., Perrin, F., Schabus, M., Majerus, S., Ledoux, D., Damas, P., Boly, M., Vanhauzenhuysse, A., Bruno, M.-A., Moonen, G., & Laureys, S. (2008). Voluntary brain processing in disorders of consciousness. *Neurology*, *71*(20), 1614–1620. <https://doi.org/10.1212/01.wnl.0000334754.15330.69>
- Schnakers, C., Vanhauzenhuysse, A., Giacino, J., Ventura, M., Boly, M., Majerus, S., Moonen, G., & Laureys, S. (2009). Diagnostic accuracy of the vegetative and minimally conscious state: Clinical consensus versus standardized neurobehavioral assessment. *BMC Neurology*, *9*, 35. <https://doi.org/10.1186/1471-2377-9-35>
- Schooler, J. (2015). Bridging the Objective/Subjective Divide Towards a Meta-Perspective of Science and Experience. In T. Metzinger & J. M. Windt (Eds). *Open MIND: 34(T)*. Frankfurt Am Main: MIND Group. <https://doi.org/10.15502/9783958570405>
- Schurger, A., Cowey, A., Cohen, J. D., Treisman, A., & Tallon-Baudry, C. (2008). Distinct and independent correlates of attention and awareness in a hemianopic patient.

- Schwartz, S., Dang-Vu, T. T., Ponz, A., Duhoux, S., & Maquet, P. (2005). Dreaming: A neuropsychological view. *Schweizer Archiv Für Neurologie Und Psychiatrie*, 156, 426–439. <https://doi.org/10.4414/sanp.2005.01657>
- Sergent, C., Baillet, S., & Dehaene, S. (2005). Timing of the brain events underlying access to consciousness during the attentional blink. *Nature Neuroscience*, 8(10), 1391–1400. <https://doi.org/10.1038/nn1549>
- Sergent, C., Corazzol, M., Labouret, G., Stockart, F., Wexler, M., King, J.-R., Meyniel, F., & Pressnitzer, D. (2021). Bifurcation in brain dynamics reveals a signature of conscious processing independent of report. *Nature Communications*, 12(1), Article 1. <https://doi.org/10.1038/s41467-021-21393-z>
- Siclari, F., Baird, B., Perogamvros, L., Bernardi, G., LaRocque, J. J., Riedner, B., Boly, M., Postle, B. R., & Tononi, G. (2017). The neural correlates of dreaming. *Nature Neuroscience*, 20(6), Article 6. <https://doi.org/10.1038/nn.4545>
- Siclari, F., LaRocque, J., Postle, B., & Tononi, G. (2013). Assessing sleep consciousness within subjects using a serial awakening paradigm. *Frontiers in Psychology*, 4. <https://www.frontiersin.org/articles/10.3389/fpsyg.2013.00542>
- Simons, D. J., & Chabris, C. F. (1999). Gorillas in our midst: Sustained inattention blindness for dynamic events. *Perception*, 28(9), 1059–1074. <https://doi.org/10.1068/p281059>
- Simons, D. J., & Levin, D. T. (1997). Change blindness. *Trends in Cognitive Sciences*, 1(7), 261–267. [https://doi.org/10.1016/S1364-6613\(97\)01080-2](https://doi.org/10.1016/S1364-6613(97)01080-2)
- Simons, D. J., & Rensink, R. A. (2005). Change blindness: Past, present, and future. *Trends in Cognitive Sciences*, 9(1), 16–20. <https://doi.org/10.1016/j.tics.2004.11.006>
- Simony, E., Honey, C. J., Chen, J., Lositsky, O., Yeshurun, Y., Wiesel, A., & Hasson, U. (2016). Dynamic reconfiguration of the default mode network during narrative comprehension. *Nature Communications*, 7(1), 12141. <https://doi.org/10.1038/ncomms12141>
- Sitt, J. D., King, J.-R., El Karoui, I., Rohaut, B., Faugeras, F., Gramfort, A., Cohen, L., Sigman, M., Dehaene, S., & Naccache, L. (2014). Large scale screening of neural signatures of consciousness in patients in a vegetative or minimally conscious state. *Brain*, 137(8), 2258–2270. <https://doi.org/10.1093/brain/awu141>
- Smith, S. M., Jenkinson, M., Woolrich, M. W., Beckmann, C. F., Behrens, T. E. J., Johansen-Berg, H., Bannister, P. R., De Luca, M., Drobnjak, I., Flitney, D. E., Niazy, R. K., Saunders, J., Vickers, J., Zhang, Y., De Stefano, N., Brady, J. M., & Matthews, P. M. (2004). Advances in functional and structural MR image analysis and implementation as FSL. *NeuroImage*, 23 Suppl 1, S208-219. <https://doi.org/10.1016/j.neuroimage.2004.07.051>

- Solomonova, E., & Carr, M. (2019). *Incorporation of External Stimuli into Dream Content* (pp. 213–218).
- Song, H., Park, B., Park, H., & Shim, W. M. (2021). Cognitive and Neural State Dynamics of Narrative Comprehension. *Journal of Neuroscience*, *41*(43), 8972–8990. <https://doi.org/10.1523/JNEUROSCI.0037-21.2021>
- Strauss, M., Sitt, J. D., King, J.-R., Elbaz, M., Azizi, L., Buiatti, M., Naccache, L., Wassenhove, V. van, & Dehaene, S. (2015). Disruption of hierarchical predictive coding during sleep. *Proceedings of the National Academy of Sciences*, *112*(11), E1353–E1362. <https://doi.org/10.1073/pnas.1501026112>
- Strauss, M., Sitt, J. D., Naccache, L., & Raimondo, F. (2022). Predicting the loss of responsiveness when falling asleep in humans. *NeuroImage*, *251*, 119003. <https://doi.org/10.1016/j.neuroimage.2022.119003>
- Strüber, D., Rach, S., Trautmann-Lengsfeld, S. A., Engel, A. K., & Herrmann, C. S. (2014). Antiphase 40 Hz Oscillatory Current Stimulation Affects Bistable Motion Perception. *Brain Topography*, *27*(1), 158–171. <https://doi.org/10.1007/s10548-013-0294-x>
- Stumbrys, T., Erlacher, D., & Schredl, M. (2013). Testing the involvement of the prefrontal cortex in lucid dreaming: A tDCS study. *Consciousness and Cognition*, *22*(4), 1214–1222. <https://doi.org/10.1016/j.concog.2013.08.005>
- Supèr, H., Spekreijse, H., & Lamme, V. A. (2001). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience*, *4*(3), 304–310. <https://doi.org/10.1038/85170>
- Tagliazucchi, E., von Wegner, F., Morzelewski, A., Brodbeck, V., & Laufs, H. (2012). Dynamic BOLD functional connectivity in humans and its electrophysiological correlates. *Frontiers in Human Neuroscience*, *6*, 339. <https://doi.org/10.3389/fnhum.2012.00339>
- Tasserie, J., Uhrig, L., Sitt, J. D., Manasova, D., Dupont, M., Dehaene, S., & Jarraya, B. (2022). Deep brain stimulation of the thalamus restores signatures of consciousness in a nonhuman primate model. *Science Advances*, *8*(11), eab15547. <https://doi.org/10.1126/sciadv.ab15547>
- Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. *Trends in Cognitive Sciences*, *10*(11), 502–511. <https://doi.org/10.1016/j.tics.2006.09.003>
- Tononi, G., Boly, M., Massimini, M., & Koch, C. (2016). Integrated information theory: From consciousness to its physical substrate. *Nature Reviews Neuroscience*, *17*(7), Article 7. <https://doi.org/10.1038/nrn.2016.44>
- Trotter, K., Dallas, K., & Verdone, P. (1988). Olfactory stimuli and their effects on REM dreams. *Psychiatric Journal of the University of Ottawa: Revue De Psychiatrie De l'Universite d'Ottawa*, *13*(2), 94–96.
- Tse, P. U., Martinez-Conde, S., Schlegel, A. A., & Macknik, S. L. (2005). Visibility, visual awareness, and visual masking of simple unattended targets are confined to areas in the

- occipital cortex beyond human V1/V2. *Proceedings of the National Academy of Sciences*, 102(47), 17178–17183. <https://doi.org/10.1073/pnas.0508010102>
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, 8(8), Article 8. <https://doi.org/10.1038/nn1500>
- Tsuchiya, N., Wilke, M., Frässle, S., & Lamme, V. A. F. (2015). No-Report Paradigms: Extracting the True Neural Correlates of Consciousness. *Trends in Cognitive Sciences*, 19(12), 757–770. <https://doi.org/10.1016/j.tics.2015.10.002>
- Türker, B., Belloli, L., Owen, A. M., Naci, L., & Sitt, J. D. (2023). *Processing of the Same Narrative Stimuli Elicits Common Functional Connectivity Dynamics Between Individuals* (p. 2022.11.25.517964). bioRxiv. <https://doi.org/10.1101/2022.11.25.517964>
- Uhrig, L., Sitt, J. D., Jacob, A., Tasserie, J., Barttfeld, P., Dupont, M., Dehaene, S., & Jarraya, B. (2018). Resting-state Dynamics as a Cortical Signature of Anesthesia in Monkeys. *Anesthesiology*, 129(5), 942–958. <https://doi.org/10.1097/ALN.0000000000002336>
- Unsworth, N., & Robison, M. K. (2016). Pupillary correlates of lapses of sustained attention. *Cognitive, Affective, & Behavioral Neuroscience*, 16(4), 601–615. <https://doi.org/10.3758/s13415-016-0417-4>
- Vallat, R. (2018). Pingouin: Statistics in Python. *Journal of Open Source Software*, 3(31), 1026. <https://doi.org/10.21105/joss.01026>
- Vallat, R., & Walker, M. (2021). An open-source, high-performance tool for automated sleep staging. *ELife*, 10. <https://doi.org/10.7554/eLife.70092>
- van den Heuvel, M. P., & Hulshoff Pol, H. E. (2010). Exploring the brain network: A review on resting-state fMRI functional connectivity. *European Neuropsychopharmacology*, 20(8), 519–534. <https://doi.org/10.1016/j.euroneuro.2010.03.008>
- van Gaal, S., Lamme, V. A. F., Fahrenfort, J. J., & Ridderinkhof, K. R. (2011). Dissociable brain mechanisms underlying the conscious and unconscious control of behavior. *Journal of Cognitive Neuroscience*, 23(1), 91–105. <https://doi.org/10.1162/jocn.2010.21431>
- Van Rossum, G., & Drake, F. L. (2009). *Python 3 Reference Manual*. CreateSpace.
- van Vugt, B., Dagnino, B., Vartak, D., Safaai, H., Panzeri, S., Dehaene, S., & Roelfsema, P. R. (2018). The threshold for conscious report: Signal loss and response bias in visual and frontal cortex. *Science*, 360(6388), 537–542. <https://doi.org/10.1126/science.aar7186>
- Vanhaudenhuyse, A., Demertzi, A., Schabus, M., Noirhomme, Q., Bredart, S., Boly, M., Phillips, C., Soddu, A., Luxen, A., Moonen, G., & Laureys, S. (2011). Two distinct neuronal networks mediate the awareness of environment and of self. *Journal of Cognitive Neuroscience*, 23(3), 570–578. <https://doi.org/10.1162/jocn.2010.21488>
- Virtanen, P., Gommers, R., Oliphant, T. E., Haberland, M., Reddy, T., Cournapeau, D., Burovski, E., Peterson, P., Weckesser, W., Bright, J., van der Walt, S. J., Brett, M.,

- Wilson, J., Millman, K. J., Mayorov, N., Nelson, A. R. J., Jones, E., Kern, R., Larson, E., ... van Mulbregt, P. (2020). SciPy 1.0: Fundamental algorithms for scientific computing in Python. *Nature Methods*, *17*(3), 261–272. <https://doi.org/10.1038/s41592-019-0686-2>
- Voss, U., Holzmann, R., Hobson, A., Paulus, W., Koppehele-Gossel, J., Klimke, A., & Nitsche, M. A. (2014). Induction of self awareness in dreams through frontal low current stimulation of gamma activity. *Nature Neuroscience*, *17*(6), Article 6. <https://doi.org/10.1038/nn.3719>
- Voss, U., Holzmann, R., Tuin, I., & Hobson, J. A. (2009). Lucid dreaming: A state of consciousness with features of both waking and non-lucid dreaming. *Sleep*, *32*(9), 1191–1200.
- Vuilleumier, P., Sagiv, N., Hazeltine, E., Poldrack, R. A., Swick, D., Rafal, R. D., & Gabrieli, J. D. E. (2001). Neural fate of seen and unseen faces in visuospatial neglect: A combined event-related functional MRI and event-related potential study. *Proceedings of the National Academy of Sciences*, *98*(6), 3495–3500. <https://doi.org/10.1073/pnas.051436898>
- Weiskrantz, L., Warrington, E. K., Sanders, M. D., & Marshall, J. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain: A Journal of Neurology*, *97*(4), 709–728. <https://doi.org/10.1093/brain/97.1.709>
- Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., McLaren, D. G., Somerville, L. H., McLean, A. A., Maxwell, J. S., & Johnstone, T. (2004). Human Amygdala Responsivity to Masked Fearful Eye Whites. *Science*, *306*(5704), 2061–2061. <https://doi.org/10.1126/science.1103617>
- Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *The Journal of Neuroscience*, *18*(1), 411–418. <https://doi.org/10.1523/JNEUROSCI.18-01-00411.1998>
- Whitfield-Gabrieli, S., & Nieto-Castanon, A. (2012). Conn: A functional connectivity toolbox for correlated and anticorrelated brain networks. *Brain Connectivity*, *2*(3), 125–141.
- Wong, W., Noreika, V., Móró, L., Revonsuo, A., Windt, J., Valli, K., & Tsuchiya, N. (2020). The Dream Catcher experiment: Blinded analyses failed to detect markers of dreaming consciousness in EEG spectral power. *Neuroscience of Consciousness*, *2020*(1), niaa006. <https://doi.org/10.1093/nc/niaa006>
- Wühle, A., Mertiens, L., Rüter, J., Ostwald, D., & Braun, C. (2010). Cortical processing of near-threshold tactile stimuli: An MEG study. *Psychophysiology*, *47*(3), 523–534. <https://doi.org/10.1111/j.1469-8986.2010.00964.x>
- Wühle, A., Preissl, H., & Braun, C. (2011). Cortical processing of near-threshold tactile stimuli in a paired-stimulus paradigm – an MEG study. *European Journal of Neuroscience*, *34*(4), 641–651. <https://doi.org/10.1111/j.1460-9568.2011.07770.x>

- Wyart, V., & Tallon-Baudry, C. (2009). How Ongoing Fluctuations in Human Visual Cortex Predict Perceptual Awareness: Baseline Shift versus Decision Bias. *Journal of Neuroscience*, 29(27), 8715–8725. <https://doi.org/10.1523/JNEUROSCI.0962-09.2009>
- Xia, T., Yao, Z., Guo, X., Liu, J., Chen, D., Liu, Q., Paller, K. A., & Hu, X. (2023). Updating memories of unwanted emotions during human sleep. *Current Biology*, 33(2), 309-320.e5. <https://doi.org/10.1016/j.cub.2022.12.004>
- Züst, M. A., Ruch, S., Wiest, R., & Henke, K. (2019). Implicit Vocabulary Learning during Sleep Is Bound to Slow-Wave Peaks. *Current Biology*, 29(4), 541-553.e7. <https://doi.org/10.1016/j.cub.2018.12.038>

