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# Toward a better understanding of dreaming: electrophysiological and behavioral investigations

Aurelien de la Chapelle

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**Toward a better understanding of dreaming**  
—  
**Electrophysiological and behavioural  
investigations**

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# Abstract

People from every era have found dreams to be a source of fascination, leading to many hypotheses about their meaning and interpretation. And while curiosity generally leads to answers, much remains to be understood about dreaming, notably because of its subjective and fleeting nature. Throughout this thesis, we confronted these challenges by using varied methodologies, allowing us to investigate several unanswered questions about dreaming. We first tested the contribution of cognitive abilities to dream recall frequency (DRF) in a thorough investigation of memory and attention (using the MEMAT paradigm) in low- and high-frequency dream recallers (respectively LR and HR), both at the behavioural scale (Study 1a) and with MEG recordings (Studies 1b, 1c). Then, we capitalised on the study of epilepsy, a condition associated with abnormal brain activity generally activated by sleep, to investigate the neural bases of dream content and dream recall thanks to intracranial recordings (Study 2a, 2b). Finally, we investigated the content and frequency of grief-related dreams during the first year of mourning after the death of a relative to test the emotion regulation hypothesis of dreaming (Study 3).

Memory performance and its cerebral correlates did not differ between LR and HR in the MEMAT task, supporting the hypothesis that short-term memory abilities during wakefulness are not a determinant factor of DRF. In addition, the MEMAT paradigm enabled us to confirm attention-related cerebral differences between LR and HR and to show for the first time attentional performance differences between LR and HR. Attentional processes may modulate DRF via the promotion of intra-sleep wakefulness (bottom-up attention) and/or by orienting the focus of attention toward the dream content (top-down attention). According to the preliminary results of the Studies 2a and 2b, intrasleep wakefulness is associated with DRF in epileptic patients as is the case in healthy subjects. Notably, the increased rate of nocturnal awakenings due to epilepsy seems to increase DRF in this population. Finally, the results of the Study 3 suggest that dreaming is strongly influenced by emotion regulation processes. We indeed observed a correlation at the within-subject level between grief intensity (as assessed by the Inventory of Complicated Grief scale) and the frequency of grief-related dreams. The mourning process evolves all the more favourably that grief-related dreams are recalled often and integrate positive emotions. As such, the brain activity underlying emotion regulation during sleep seems to influence the dream experience. As a conclusion, the broad investigations we conducted using rare methodologies offer a new perspective on the landscape of dream research, which we hope will one day contribute to a comprehensive understanding of dreaming.

**Keywords:** Dream, sleep, emotion regulation, memory, attention, epilepsy, behaviour, MEG, SEEG

# Résumé

À toutes les époques, les humains ont trouvé les rêves fascinants, ce qui a entraîné de nombreuses interprétations quant à leur sens et à leur interprétation. Et si la curiosité mène généralement à des réponses, il reste encore beaucoup à comprendre sur le rêve, en particulier à cause de sa nature subjective et fugace. Au cours de cette thèse, nous avons relevé ces défis en utilisant des méthodologies variées, ce qui nous a permis d'étudier plusieurs questions restées sans réponse sur les rêves. Nous avons d'abord testé la contribution des capacités cognitives à la fréquence de rappel des rêves (DRF) à travers une étude approfondie de la mémoire et de l'attention (grâce au paradigme MEMAT) chez des personnes se rappelant rarement ou souvent de leurs rêves (respectivement LR et HR), à la fois à l'échelle comportementale (Étude 1a) et à l'aide d'enregistrements MEG (Études 1b, 1c). Nous avons également tiré partie de l'étude de l'épilepsie, une maladie neurologique associée à une activité cérébrale pathologique généralement activée par le sommeil, afin d'investiguer les bases cérébrales du contenu et du rappel des rêves à l'aide d'enregistrements intracrâniens (Études 2a, 2b). Enfin, nous nous sommes intéressés au contenu et à la fréquence des rêves en lien avec le deuil pendant la première année suivant le décès d'un proche pour tester l'hypothèse de régulation émotionnelle du rêve (Étude 3).

Les performances mnésiques et leurs corrélats cérébraux étaient similaires entre LR et HR dans le paradigme MEMAT (Études 1a, 1b et 1c), soutenant l'hypothèse selon laquelle les capacités de mémoire à court-terme pendant la veille ne sont pas un facteur déterminant de la fréquence de rappel des rêves. Par ailleurs, ce paradigme nous a permis de confirmer des différences cérébrales liées à l'attention entre LR et HR, et de montrer pour la première fois des différences comportementales de capacités attentionnelles entre LR et HR. De tels processus attentionnels pourraient moduler la fréquence de rappel des rêves en favorisant l'éveil intra-sommeil (attention exogène) et/ou en orientant notre attention vers le contenu des rêves (attention endogène). D'après les résultats préliminaires des Études 2a et 2b, l'éveil intrasommeil est associé à la fréquence de rappel des rêves chez les patients épileptiques, tout comme c'est le cas chez les personnes en bonne santé. Un taux accru d'éveils nocturnes dû à l'épilepsie semble notamment augmenter la fréquence de rappel des rêves dans cette population. Enfin, les résultats de l'Étude 3 suggèrent que les rêves sont fortement influencés par les processus de régulation émotionnelle. Nous avons en effet observé une corrélation intra-sujet entre intensité du deuil (évaluée avec l'échelle de l'Inventaire du Deuil Complicqué) et la fréquence des rêves liés au défunt. Le processus de deuil évolue d'autant plus favorablement que l'on se souvient fréquemment de ces rêves et qu'ils intègrent des émotions positives. Ainsi, l'activité cérébrale qui sous-tend la régulation des émotions pendant le sommeil semble influencer l'expérience onirique. En conclusion, les diverses investigations que nous avons menées à l'aide de méthodologies originales et complémentaires offrent une nouvelle perspective

sur le paysage de la recherche sur les rêves, perspective qui, nous l'espérons, contribuera un jour à une compréhension approfondie des rêves.

**Mots-cléf:** Rêve, sommeil, régulation émotionnelle, mémoire, attention, épilepsie, comportement, MEG, SEEG

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# Abbreviations

BFI – Big five inventory  
DD – Dream of the deceased  
DLPFC – Dorsolateral prefrontal cortex  
DMN – Default mode network  
DRF – Dream recall frequency  
DSM-5 – Diagnostic and statistical manual of mental disorders, fifth edition  
EEG – Electroencephalography  
ECG – Electrocardiography  
ECoG – Electrocorticography  
EMG – Electromyography  
EOG – Electrooculography  
ERF – Event-related field  
ERP – Event-related potential  
FD – Flying dream  
fMRI – Functional magnetic resonance imaging  
HR – High-frequency dream recaller  
iEEG – Intracerebral EEG  
IRT – Imagery rehearsal therapy  
LR – Low-frequency dream recaller  
LTM – Long-term memory  
MEG – Magnetoencephalography  
MEMAT – Memory and attention paradigm  
MPFC – Medial prefrontal cortex  
NREM – Non-rapid eye movement (sleep)  
OD – Other dream  
PET – Positron emission tomography  
PSG – Polysomnography  
REM – Rapid eye movement (sleep)  
SEEG – Stereoencephalography  
STM – Short-term memory  
TPJ – Temporo-parietal junction



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# I. Introduction

## Dreaming: definitions

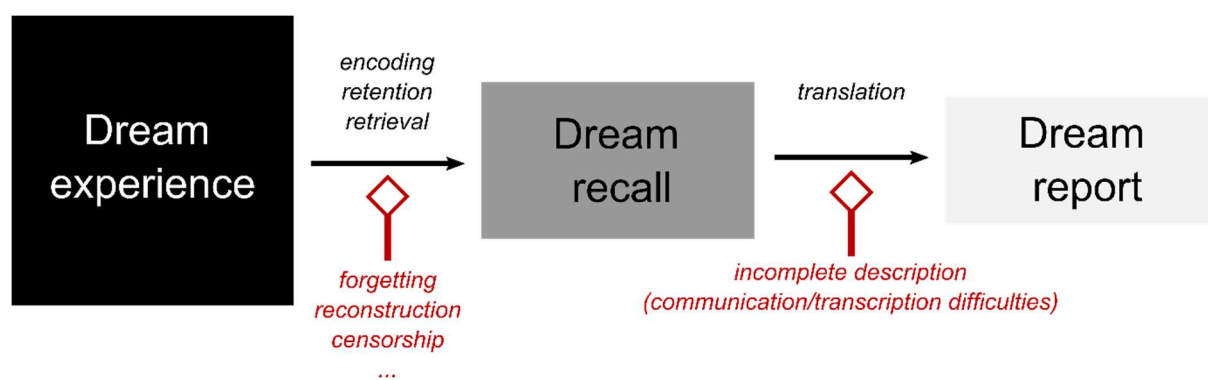
As a part of our sleep, dreaming has always taken a place in our minds. During Antiquity, Greeks, Romans and Egyptians considered for instance dreams as prophecies or messages from the gods (De Koninck, 2012). Cambodians believe that their soul is roaming around during dreaming, potentially meeting other souls like those of the deceased who can't cross over to the afterlife (Hinton et al., 2013). Likewise, many are also fascinated by the interpretation of dreams.

Except to the rare people who report never dreaming, dreaming is an obvious phenomenon. People can report that they dreamt, even what they dreamt about, and it seems at first glance obvious what a dream is. Paradoxically, a single definition of dreaming has not yet been established as the concept is still being debated (Pagel et al., 2001). It is generally admitted that dreaming is a subjective mental immersive experience characterised by sensory hallucinations, emotions, narrative elements, and vivid experiences that occur during sleep and can be recalled and recounted upon awakening (Nielsen, 2000; Guérolé & Nicolas, 2010; Windt et al., 2016; Montangero, 2018). This definition encompasses the impossibility to have an objective evaluation of dreams, the complexity of their content and their realism, as well as the opposition between their production during sleep and their recall during wake. These aspects make the study of dreaming all the more difficult to conduct.

To reflect this complexity, Guérolé (2009) distinguished three successive phases of dreaming (see Figure 1): the dream experience, the dream memory and the dream report. The dream experience consists in the mental processes happening during sleep that lead to a dream. After awakening, the subjective remaining trace of the dream experience that persists in memory is called the dream memory. This implies that not all dream experiences are remembered, and some parts may be temporarily forgotten until later that day, when they may resurface for instance because of a cue (Botman & Crovitz, 1989). The transcription of the dream memory on an external support (by being written, said, drawn...) results in a dream report. Each of these steps is accompanied by a loss of information. We don't know when dream experiences take place during sleep (Ruby, 2020), making them unavailable to an external observer, and even the dreamer cannot remember every single detail of the whole dream experience after awakening. The resulting dream memory can suffer from distortion, forgetting and reconstruction. The report may subsequently be biased by rationality, culture and/or censorship, especially as time since awakening increases (Schwartz & Maquet, 2002; Schwartz et al., 2005). Because of this, most dream studies investigate dream reports as they are the only objective and methodologically usable information about dreaming. Despite being an incomplete and potentially biased transcript of the dream experience, the dream report is an interesting object of study in at least two aspects: dream recall (which dreams are

remembered more and why) and dream content (what is represented in recalled dream memories), which will be detailed in the next sections.

The presented-above limitations of the study of dreaming have long limited (and still do limit) our understanding of dreaming. The temporality of dreaming, the mechanisms behind dream content generation, the differences in dream recall between different people and different nights, the functions of dreaming, and many others, are still open questions that have been progressively addressed for decades by the scientific community. The goal of this thesis is to contribute to this existing knowledge by providing additional arguments for existing theories of dreaming and by bringing fresh insights in this growing literature.



*Figure 1 - The successive steps of dream recall, adapted from Guénolé (2009). Each step is associated with possible loss or transformations of information, illustrated by the changing size and color of the rectangles.*



# Dream recall

## Measures of dream recall frequency

### Methods

As dreams are usually rapidly forgotten after awakening, dream recall can be difficult to assess and can vary both at the inter- and intra-individual scales (see next sections), but also depending on the method used to measure it. However, an efficient and scientific study of dream recall necessitates a standardised way to measure and report dreams. Three methods have been tested, developed, and used over the course of dream research: retrospective dream recall assessments, dream diaries, and laboratory awakenings (Schredl, 1999).

In the first case, participants are generally asked how often they remember dreams in the last week or month. This method provides quick answers (a single question) and allows testing in a large population as it is inexpensive, but it depends on the dreams memory, which quickly fades over time. Because of this, retrospective assessments are sensitive to retrospective memory biases, contrary to dream diaries and laboratory awakenings.

Dream diaries consist in reporting whether a dream was recalled every morning for a set period of time (2 weeks according to Schredl & Fulda, 2005). This method is more accurate than retrospective assessments regarding potential forgetting of the dreams, but the induced elevated and unusual focus on dreams may increase dream recall for people who usually don't remember their dreams (Schredl, 2002; Mediano et al., 2022; Aspy, 2016). On the contrary, dream diaries generally don't influence or even decrease the dream recall frequency (DRF) DRF of High-frequency dream recaller (HR) (Bernstein & Belicki, 1996; Schredl, 2002).

Awakenings in a laboratory setting allow for a more controlled and generally shorter version of the dream diary previously presented. It can consist in one or several awakenings in a nap, a single night or several nights, followed by the question whether the participant remembered a dream or thoughts they had when awoken. The instructions used can modify the answer, as participants are less likely to report recalling a dream after the question "were you dreaming?" than "was anything going through your mind?", because of the subjective labeling by the participants of what is or is not a dream (Foulkes, 1962). Importantly, this method can be combined with concurrent sleep polysomnography recordings (EEG, EOG, EMG, ECG), allowing to categorise a dream report according to the sleep stage that preceded it. It is however an expensive, resource-intensive and time-consuming method, and similarly to dream diaries, the focus on dreaming may increase DRF. Likewise, repeated awakenings increase DRF in this situation.

## Average dream recall frequency

As mentioned earlier, the DRF depends on the used measuring method. A retrospective assessment of the DRF in a representative German sample (N=931) identified  $0.8 \pm 1.6$  recalls per week (Schredl, 2008). On the other hand, dream diaries tend to increase DRF overall: for instance, Schredl & Fulda (2005) observed in 196 German students an average DRF of  $3.9 \pm 1.82$  recalls per week. This increase can also be explained by the higher involvement of the participant required in a dream diary study compared to a simple retrospective assessment, which necessarily leads to a more likely recruitment of people interested in their dreams, who are known to have a higher DRF (Schredl et al., 2003). For instance, Beaulieu-Prévost & Zadra (2005) evaluated the retrospective DRF and the diary DRF in 82 students who were informed of the objectives of the study. The estimated DRF was 4.3 dreams/week, the diary DRF was 4.9 dreams/week (both above average), and in both cases the participant with the lowest DRF remembered 0.8-1 dreams/week, which should already be average (Schredl, 2008).

In other words, the average DRF is around 1 dream per week but is generally higher in most dream studies because of selection biases, as a large array of factors (section *Factors of variability in dream recall frequency*) contribute to inter- and intra-individual variability of the DRF

## Inter-individual variability

The means presented above do not reflect every aspect of dream recall in the general population: some people rarely recall dreams while others can report dreams every morning. For instance, Schredl & Göritz (2017) showed a skewed distribution of the dream recall frequency in the representative samples of Schredl (2008) and Schredl (2013), with 54.59% of the sample (N=1841) remembering a dream at most once per month and only 13.2% having more than one dream per week. These two extremes are often considered when studying dream recall, with comparisons between High-frequency (HR, report a dream several mornings per week) and Low-frequency (LR, report at most 2 dreams per month) dream recallers (e.g., Goodenough et al., 1959; Eichenlaub, Bertrand, et al., 2014; van Wyk et al., 2019). Factors contributing to these inter-individual differences are detailed in the section *Factors of variability in dream recall frequency*.

### Intra-individual variability

Even among LR and among HR, day-to-day fluctuations of dream recall happen. Nevertheless, over longer periods of time, it was shown that DRF was rather stable. Schredl & Fulda (2005) measured DRF with dream diaries in 196 participants during one month and it stayed stable over this period. Using the same scale, Schredl & Göritz (2015) confirmed in 1340 individuals that DRF was stable over a period of three years, despite a very small but significant decrease (from  $3.54 \pm 1.80$  to  $3.42 \pm 1.83$  dreams per week, effect size  $d=0.161$ ). They replicated this result in 279 women over the course of their pregnancy and first years of maternity, during 4 years, by showing no difference in retrospective DRF between all tested time points (Schredl et al., 2020).

These large inter- and intra-individual differences can be explained by several factors that will be presented in the next section.

## Factors of variability in dream recall frequency

A lot of factors were identified to play a role on DRF, both at the inter-individual (i.e. trait factors) and intra-individual scale (i.e. state factors). More specifically, trait factors refer to personality and any other variable that is stable over time within an individual, while state factors refer to time- and situation-dependent factors. It should however be noted that the large majority of the factors involved in DRF explain only a small part of the variance in DRF (Schredl et al., 2003), which reminds us that our understanding of dream recall is still incomplete.

### Trait factors

#### Cognitive abilities

Inter-individual differences in DRF could be explained by cognitive abilities, and notably memory. For instance, an efficient short-term memory (STM) could contribute to a better recall of a dream preceding an awakening, while long-term memory (LTM) could logically be useful for remembering dreams on a long period of time. The role of memory in dream recall has been further discussed in the arousal-retrieval model proposed by Koulack & Goodenough (1976) (presented in the section *Models of dream recall*). Consequently, both STM and LTM have been thoroughly investigated by dream researchers (Belicki et al., 1978; Blagrove & Akehurst, 2000; Bloxham, 2018; Butler & Watson, 1985; D. B. Cohen, 1971; Cory et al., 1975; Eichenlaub, Nicolas, et al., 2014; Martinetti, 1983, 1985; Nakagawa et al., 2016; Schredl et al., 1995; Schredl, Hebel, et al., 2009; Schredl et al., 1997; Solms, 1997; Waterman, 1991). A relation between LTM and dream recall has received little support despite its expected effect. The literature regarding STM and dreaming shows mixed and inconclusive results, as detailed in the introduction of the Study 1a (the summary table of Study 1a is also reported below in Table 1). Interestingly, contrary to the hypothesis that visual short-term memory would have a greater impact on dream recall compared to other sensory modalities (because of the very frequent and intense contribution of the visual dimension of dream reports, see section *General dream characteristics*), the existing studies yielded inconsistent results across all sensory modalities. Note that all studies with significant results find an effect in the same direction, i.e. HR having higher STM abilities during wakefulness than LR. However, as the effect of STM on DRF appears to be actually unclear, this common finding may have resulted from experimenter/publishing biases towards the expected finding of increased STM abilities in HR, and should therefore be considered with caution. The high amount of inconclusive studies suggests that if an effect exists (which is unclear), it is most probably a

small one. It should also be noted that it is unclear whether STM characteristics at wake are the same as (or at least proportional to) STM characteristics during sleep. The interaction between STM abilities during wakefulness and dream recall will be further addressed in the studies 1a, 1b, and 1c of the current thesis.

Reference	N	Type of short-term memory	Type of test	Results
Butler & Watson, 1985	12	Auditory verbal	Digit span	HR > LR (corr. DS & DRF, $r = 0.69$ )
Martinetti, 1983	30	Auditory verbal	Digit span	(13 ± 3) HR > LR (9 ± 2)
Martinetti, 1985	70	Auditory verbal	Digit span	(14 ± 2) HR > LR (11 ± 2)
Nakagawa et al., 2016	779	Visual verbal	Digit span	=
		Visuo-spatial	Visuo-spatial span	HR > LR (corr. DS & DRF, $r = 0.07$ )
Solms, 1997 <sup>a</sup>	361	Auditory verbal	Digit span	=
		Visuo-spatial	Pictures recall	(14/36) HR > LR (11/36)
Cohen, 1971	?	Auditory verbal	Story recall	=
	20	Visual	Pictures recall	=
Belicki et al., 1978	44	Visual	Pictures recall	=
		? verbal	Words recall	=
Cory et al., 1975	100	Visual implicit	Pictures recall	(12/50) HR > LR (10/50)
		Visual explicit	Pictures recall	(24/40) HR > LR (21/40)
Schredl et al., 1995	50	Visual	Pictures recall	=
		Visuo-spatial	Route recall	HR > LR (corr. test & DRF, $r = 0.36$ )
		Visual	Movie recall	=
Schredl et al., 1997	51	Visual	Pictures recall	=
		Visuo-spatial	Route recall	=
Schredl et al., 2009	444	Visual	Pictures recall	=
		Visuo-spatial	Route recall	=
		Visual	Movie recall	=
Waterman, 1991	93 + 80	Visual	Movie recall	=
Bloxham, 2018	57	Visual verbal	Story recall	=
Blagrove & Akehurst, 2000	93	Auditory verbal	Story recall	=

corr., correlation between; DRF, dream recall frequency; DS, digit span; HR, high dream recallers; LR, low dream recallers

=, no significant link between DRF and memory performance was observed.

HR > LR, HR showed significantly better performance than LR (each group scores are between brackets), or a significant correlation between DRF and memory score was observed.

<sup>a</sup>In this study the population tested was mainly patients with cerebral lesions.

Table 1 – Review of studies investigating the role of short-term memory in HR and in LR (from Blain, de la Chapelle et al. 2022).

Attention is another cognitive ability which could influence dream recall but has received little attention (Ruby et al., 2022). By orienting attention towards the content of the mind, top-down attention may contribute to gaining consciousness of dream content during the transition between sleep and wakefulness. Bottom-up attention may also contribute to DRF by facilitating arousals or awakenings during sleep caused by surrounding stimulations, therefore promoting dream recall (Koulack & Goodenough, 1976; Vallat, Lajnef, et al., 2017; see sections Models of dream recall and Sleep architecture: a state and trait factor). The only study so far which tested for bottom-up and top-down differences between LR and HR did not

manage to identify any behavioural difference between the two groups, while evidencing differences in the electrophysiological signature of bottom-up and top-down processes. Compared to LR, HR showed increased amplitude of the components associated with both bottom-up and top-down attention (Ruby et al., 2022). Several other works identified cerebral differences between HR and LR, and notably higher brain reactivity to external stimuli in HR (Ruby et al., 2013; Eichenlaub, Bertrand, et al., 2014; Moyne et al., 2022). Previous results thus suggest that LR and HR likely have different attentional abilities, orchestrated by different cerebral organisations. Ruby et al. (2022) proposed that HR have a higher distractibility because of their higher bottom-up attention, but that they also recruit more top-down resources to compensate for these task-irrelevant processes: overall, an attentional balance would be reached in HR with the increase of both bottom-up and top-down processes compared to LR. This aspect will be further investigated in the studies 1a, 1b, and 1c of the current thesis.

In addition to memory and attention, cognitive skills such as problem-solving and pattern recognition can aid in interpreting and making sense of dream narratives, further enhancing recall. While these specific abilities were not investigated, several studies reported associations between increased DRF and high scores of creativity (Fitch & Armitage, 1989; Schredl, 1995; Schredl et al., 2003; Vallat et al., 2022) and intelligence (Schonbar, 1959; Connor & Boblitt, 1970). Visual imagination and the related concepts of daydreaming and fantasy proneness have also been associated with a high DRF (e.g., Hiscock & Cohen, 1973; Martinetti, 1989; Tonay, 1993).

#### Interest in dreams

DRF has been repeatedly shown to be influenced by interest in dreams, also referred to as “positive attitude toward dreaming” in some studies (Schredl et al., 2003; Beaulieu-Prévost & Zadra, 2007). The exact mechanism underlying this effect still remains to be understood, but one explication could come from the effect of attention mentioned above, as proposed by Ruby et coll. (2022). Motivation to recall a dream may for instance increase top-down attention on the content of the mind (Bourgeois et al., 2016) and the subsequent ability to recall it (Xiao & Nie, 2023).

#### Other personality traits

Several other aspects of personality have been associated with DRF. Following the repression hypothesis of Freud (which is detailed in the next section), several studies between 1950 and 1980 investigated the effect of this personality trait, which refers to a defence mechanism that the mind employs to avoid experiencing distressing or traumatic thoughts,

feelings, memories, or impulses. Their results were however limited and do not allow to conclude on an effect of repression on DRF (Schredl & Montasser, 1996).

Hartmann (1989) identified a correlation between DRF and psychological boundaries, which refer to the psychological or emotional limits and distinctions that individuals establish to protect their sense of self, personal space, and well-being. More specifically, people with thin boundaries, who he defines as “being sensitive, easily hurt, creative, non-conventional, having unusual sensual experiences as well as intense, conflict-laden interpersonal relationships”, report more dreams. Likewise, the concept of absorption, which refers to an individual's capacity to become deeply immersed or absorbed in their sensory experiences, thoughts, or activities, has also received some interest, as absorption is what happens in a dream. Individuals with a high absorption were indeed found to have a higher DRF (Spanos et al., 1980). It should however be noted that thin-thinck boundaries and absorption are strongly correlated (Zamore & Barrett, 1989). Moreover, in a meta-analysis, Beaulieu-Prévost & Zadra (2007) proposed that both boundaries and absorption scores explained retrospective evaluation biases better than DRF: a high score on these scales indeed led to a systematically increased DRF compared to dream diary studies.

These two personality traits also relate to openness to experience, one of the traits measured by the Big Five Inventory (BFI). Openness to experience has reliably been associated with an increased DRF in several studies (Schredl & Göritz, 2017; Schredl & Montasser, 1996). Among the other “Big Five” of the BFI, neuroticism has also been found to be associated with an increased DRF, or more precisely to an increase in nightmare frequency (Schredl & Göritz, 2017, 2021).

#### Age and gender

An effect of age and gender has also been identified in several studies, although the effect size is small, and especially for gender. Women generally report more dreams than men, and DRF tends to decrease with age (Schredl & Reinhard, 2008; Nielsen, 2012; Schredl et al., 2014; Settineri et al., 2019). Interestingly, Schredl & Reinhard (2008) identified in their meta-analysis an interaction between age and gender as the effect size was smaller in young children (< 10 years old) and larger in adolescents. The authors interpreted this effect as a gender difference in dream socialisation, i.e. any interaction leading to an increased interest in dreaming (Schredl et al., 2015).

## State factors

Unlike trait factors, state factors have a transient influence on dream recall. For instance, stress and negative pre-sleep mood tend to increase DRF (D. B. Cohen, 1974; Schredl & Reinhard, 2010). This increased recall may be caused by the incorporation of the waking life emotion in the dreams, which may increase their salience and thus dream recall (detailed further in the sections *Models of dream recall* and *Dream content formation*), or by the increased intra-sleep awakenings possibly induced by stress, as will be presented in the next section.

Brain lesions in the medial prefrontal cortex and in the TPJ can also induce a loss of dream recall, as will be detailed in the section *Brain lesions and dream recall alterations*. While brain lesions can never fully recover, the formidable plasticity of the brain generally leads to a recovery of the ability to recall dreams in these patients (Solms, 2000), supporting the temporary effect of brain lesions on dream recall.

Interference with the dream memory/consciousness processes during the sleep-wake transition can also hamper dream recall, as was shown by Cohen & Wolfe (1973). This effect, which is at the core of their Interference hypothesis of dreaming, will be further detailed in the section *Models of dream recall*.

## Sleep architecture: a state and trait factor

Dreams were previously defined as an experience happening during sleep. Some sleep and circadian characteristics have coherently been identified to have an influence on dream recall. As some sleep characteristics exhibit both inter- (e.g. usual sleep duration, chronotype, Fabbian et al., 2016) and intra-individual variability (e.g. sleep duration, awakening time, social jetlag, Slavish et al., 2019), sleep is considered here as both a state and a trait factor in DRF variability.

Sleep architecture is generally recorded with at least electroencephalography (EEG) to measure brain activity, electrooculography (EOG) to monitor eye movements, and electromyography (EMG) to detect muscular activity. Based on these recordings, sleep has been divided in several stages with specific electrophysiological properties. Originally, Rechtschaffen and Kales (1968) distinguished 5 vigilance states (REM sleep, and non-REM sleep I, II, III, IV). Because of the similar properties of the stages III and IV (slow oscillations) and the evolution of our understanding of sleep, the American Academy of Sleep Medicine (Iber et al., 2007) later proposed updated nomenclature for the sleep stages (REM, N1, N2, N3), with N3 being the fusion of stages III and IV. An overview of their electrophysiological properties is reported in Figure 2. In regards to dreams, extensive literature identified a smaller percentage of dream reports after awakenings from non-REM sleep compared to REM sleep.



However this stage effect has been overestimated in early investigations and updated to: 84% of awakenings with a dream recall in REM sleep vs 51% in NREM sleep (Nielsen, 2000). Dream reports obtained after REM sleep awakenings are also generally longer, more intense, vivid, emotional, bizarre, complex and story-like than dreams obtained after non-REM awakenings (Martin et al., 2020; Monroe et al., 1965). The circadian effect is probably stronger than the stage effect and explains that more dreams are reported at awakenings in the morning than at the beginning of sleep (Chellappa & Cajochen, 2013).

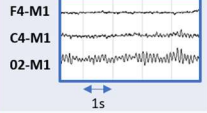
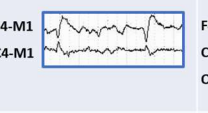
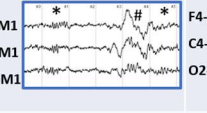
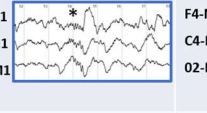
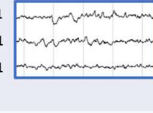
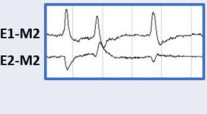
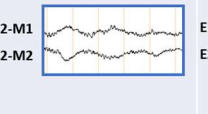
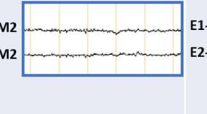
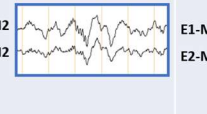
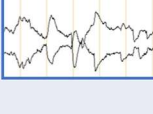

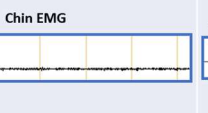
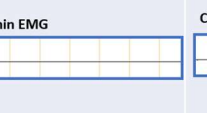

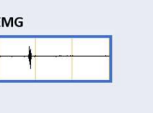
	Wake	N1	N2	N3	REM
EEG	>50% alpha/beta 	<50% alpha; mixed frequencies (4-7Hz); vertex sharp waves 	Sigma (sleep spindles*), K-complex (#) 	delta (slow waves), spindles, K-complex 	mixed frequencies (theta, alpha...); sawtooth waves 
EOG	eyeblinks, reading eye movements 	slow, rolling eye movements 	none 	none (but slow waves can be seen in EOG) 	rapid eye movements 
EMG	high tension 	low 	lower 	lower 	Lowest + phasic bursts 

Figure 2 - Electrophysiological properties of the AASM-defined sleep stages. Polysomnography traces from [polysomnograph-e.fr](http://polysomnograph-e.fr).

The scoring guidelines established by the AASM (2007) partition sleep into 30-second epochs, with each epoch being linked to a specific sleep stage. This results in graphical descriptions of the sleep course called hypnogram (see Figure 3), with which several observations can be made about normal (Hirshkowitz, 2004) and pathological sleep (e.g., Lehner et al., 2022). Sleep stages generally alternate in stereotyped cycles (N1->N2->N3->REM) of 90-120 minutes, that are repeated 3 to 5 times and whose content evolves across the night. In each successive cycle, as time asleep increases, REM sleep duration increases while NREM sleep duration decreases.

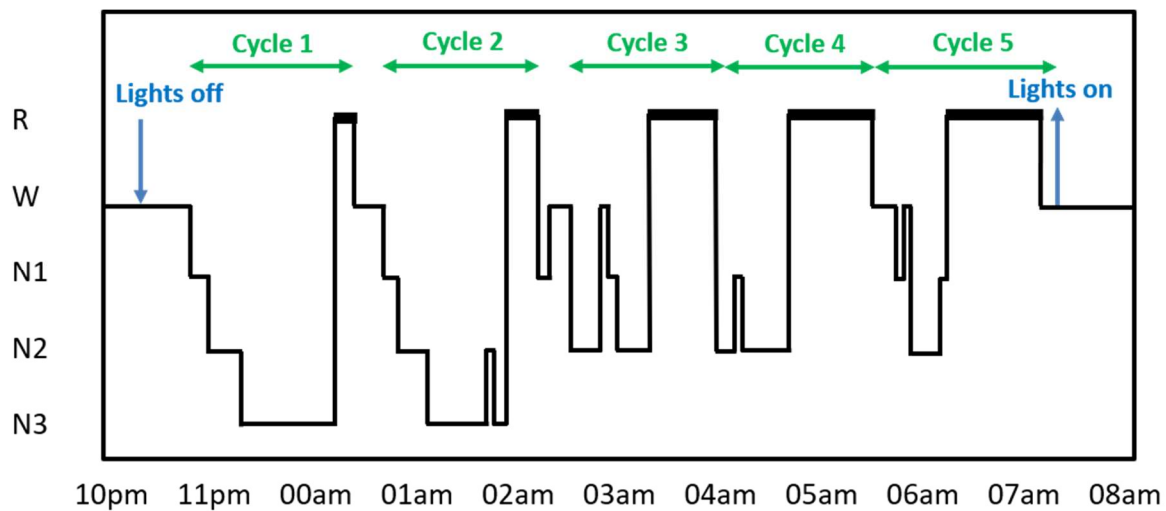


Figure 3 - Example of an hypnogram (adapted from [polysomnograph-e.fr](http://polysomnograph-e.fr)). Note the varying composition of the sleep cycles across the night.

This typical sleep architecture is also characterised by regular and short periods of intra-sleep wakefulness, i.e. 30-second epochs of wake in between epochs of sleep. While hypnograms are a useful tool in clinical practice and provide a general overview of the sleep course, the 30-second timescale hides microstructural components of sleep such as arousals. Contrary to intra-sleep wakefulness, an arousal lasts between 3 and 15 seconds only and consists in an “abrupt shift in EEG frequency, which may include theta, alpha and/or frequencies greater than 16Hz but not spindles” (Bonnet et al., 2007). They become more and more frequent as we age, from 10 per hour in 18-34 years old to 20 in 65-79 years old (Boulos et al., 2019). HR show more intra-sleep wakefulness than LR (about 30 vs 15 min in average; Eichenlaub, Bertrand, et al., 2014; Vallat, Lajnef, et al., 2017), and longer awakenings (2 vs 1 min in average; Eichenlaub, Bertrand, et al., 2014; Vallat, Lajnef, et al., 2017), but they don’t show any difference in their arousal frequency nor in other parameters of the sleep microstructure (Vallat, Lajnef, et al., 2017; van Wyk et al., 2019).

Finally, dream recall may be affected by the sleep-wake transition, and more specifically by sleep inertia, which is usually defined as a transitional state characterised by impaired vigilance, cognition, and a desire to return to sleep, typically subsiding within the initial 30 minutes after waking (Trotti, 2017; Ruby et al., in press). In support of this hypothesis, Vallat et al. (2020) identified increased connectivity in HR compared to LR within the Default Mode Network (DMN) and between the DMN and regions involved in memory right after awakening, suggesting that the brain state of HR at awakening is more favourable to dream recall than the one of LR.

## Models of dream recall

Several models were proposed along the history of dream research to explain how dreams are memorised or forgotten and present the main modulating parameters of these processes. It should be noted that most of these theories are compatible. In his PhD thesis, Raphael Vallat proposed in 2017 a comprehensive model of dream recall integrating the main modulating parameters of dream recall evidenced so far, which will be presented in the last paragraph of this section.

### Repression Hypothesis

Freud (1900) proposed in the early 20<sup>th</sup> century that dreams were a manifestation of unconscious desires, and in order to not disturb sleep, only abstract dreams or showing acceptable desires could be remembered. All other dreams would be repressed and forgotten. This theory is methodologically difficult to test as it supposes that the repressed dreams are not remembered, and thus cannot be investigated. Nevertheless, some studies investigated the relation between the repression personality trait and DRF. Authors hypothesised that a more repressive personality would censor more dreams, and therefore would result in a decreased DRF. Their results turned out to be mostly inconclusive (as discussed in the section *Factors of variability in dream recall frequency*).

### Life-Style Hypothesis

The Life-Style Hypothesis (Schonbar, 1965) opposed two life-styles: “inner-acceptant” people with a high DRF, and “inner-rejectant” people with a low DRF. Inner-acceptant people would have an increased focus on their inner consciousness, more creativity, they would be more introverted, more prone to fantasies, and more open to experience. The characteristics of this life style would lead to an increased awareness of dreams, and therefore an increased DRF. Several of these characteristics were confirmed to actually be related to increased DRF, as presented in the section *Factors of variability in dream recall frequency*.

## Interference Hypothesis

The interference hypothesis was developed by Cohen & Wolfe (1973) who questioned the life-style hypothesis of dream recall, as it cannot explain intra-individual variability in DRF. They focused on interference at the moment of the dream memorisation process, and showed that people who were focused on a task when awakening were less likely to report a dream than when they were not focused on a task. Also, abrupt rather than gradual awakenings had been associated with more dream-like than thought-like memories: the interference hypothesis explains this effect by proposing that abrupt awakenings prevent random thoughts to interfere with the dream memory (Shapiro et al., 1965; Goodenough et al., 1965; Parke & Horton, 2009). In other words, according to the interference hypothesis, the memory trace of the dream is maintained as long as no other thought or stimulus interferes with it. Any goal-directed behaviour at wake (e.g. getting out of bed, getting dressed-up, eating) or distracting stimuli or thoughts would substitute the dream memory from short-term memory stores.

## Salience Hypothesis

Cohen also proposed that the salience of a dream (i.e. more vivid, more emotional, more bizarre...) would increase its recallability (D. B. Cohen & MacNeilage, 1974). This hypothesis is however difficult to investigate, as to test it we would need to access the unrecalled dreams. And as both salient and non-salient dreams are reported, we have to at least hypothesize that salience is only one of the parameters influencing dream recall. Some studies using indirect strategies showed supporting results (e.g., Parke & Horton, 2009) and others did not, notably regarding the effect of dream bizarreness (supported by Cipolli et al., 1993; not supported by Schredl, 2000b; D. B. Cohen & MacNeilage, 1974) and dream emotionality (supported by Schredl & Doll, 1998; not supported by Schredl, 2000b) on dream recall.

## Arousal-Retrieval Model

Koulack & Goodenough (1976) proposed the arousal-retrieval model to account for reported dream recall and dream forgetting observations in both at-home and experimental conditions. They proposed that dream recall could only occur under two conditions. First, during sleep, it is assumed that the dream memory is short-lived and cannot transfer from working memory to long-term memory stores unless an arousal/awakening occurs. Second, during this arousal, the dream memory can only be transferred if the dream content is salient

enough and not interfered with by repression or internal or external interference, as proposed in the models of dream recall presented above. The arousal-retrieval model has been supported by several studies on the relation between sleep and dream recall showing more dream recall when intra-sleep wakefulness increased (Eichenlaub, Bertrand, et al., 2014; Vallat, Lajnef, et al., 2017; Nicolas & Ruby, 2020; van Wyk et al., 2019; Schredl et al., 2003; De Gennaro et al., 2010). Among the sleep parameters contributing to this difference in intra-sleep wakefulness, the number of awakenings or of arousals did not differ between LR and HR in these studies, contrary to the mean duration of their awakenings (2 min in average for HR vs 1 min in LR). This suggests that encoding the dream in memory would need enough time after an awakening to take place more than short opportunities.

### State-Shift Model

The functional state-shift hypothesis of Koukkou & Lehmann (1983) is based on sleep electrophysiological recordings, which show very different functional brain activity (i.e. functional state) in wake and in the different sleep stages. Each state would be associated with different properties and cognitive abilities, and the more two states differ, the more compromised would be the survival of the short-term memory content in the transition from one state to the other. For instance, the frequency content of the EEG in wakefulness (alpha, beta) is more similar to the frequency content of REM sleep (alpha, theta) than to the frequency content of N3 (slow oscillations). According to the state-shift model, this would explain a better dream recall rate at awakening from REM sleep than from N3. These states would also have a hierarchy, so that information stored in a higher functional state (such as wakefulness) would be easier to access in lower functional states (sleep states), which would explain why nocturnal mental activity (i.e. dreams) can incorporate information from the awake life but also why dreams are so difficult to recall when awake.

### An integrative model of dream recall

In order to account for the various factors modulating DRF at the inter- and intra-individual level, Vallat (2017) proposed an integrative model of dream recall presented in Figure 4. Neurophysiology and personality (which are most likely related), are at the core of this model, in line with the repression hypothesis (Freud, 1900) and the life-style hypothesis (Schonbar, 1965). This comprehensive model also integrates all the other models presented above.

Similarly to the arousal-retrieval model (Koulack & Goodenough, 1976), this model assumes that the short-term memory of dreams has to survive the sleep-wake transition and then be transferred from short-term to long-term memory (as defended in the section *Arousal-Retrieval Model*). To survive in short-term memory during the sleep-wake transition, the dream experience would need to be salient enough, as defended by Cohen & MacNeilage (1974), and the brain would need to be in the appropriate state (Vallat et al., 2020) as defended in the state-shift model (Koukkou & Lehmann 1983). These two aspects would depend on personality parameters such as interest in dreams, creativity, and openness to experience (e.g., Vallat et al., 2022). During the sleep-wake transition, interferences (thoughts, stimulations, actions...) would induce a vanishing of the short-term memory content and thus prevent the dream memory transfer from short-term to long-term memory, as suggested by Cohen & Wolfe (1973). Finally, specific cognitive abilities would increase (increased bottom-up attention) or decrease (increased top-down attention) sensibility to interferences.

This model elegantly shows how the existing models of dream recall can coexist and offers the satisfaction of taking into account all the main parameters known to influence DRF. The detail of how cognitive abilities influence dream recall remains unclear, especially the role of memory abilities and attention (see section section *Factors of variability in dream recall frequency*). This question will be addressed in the Studies 1a, 1b, and 1c of the present thesis.

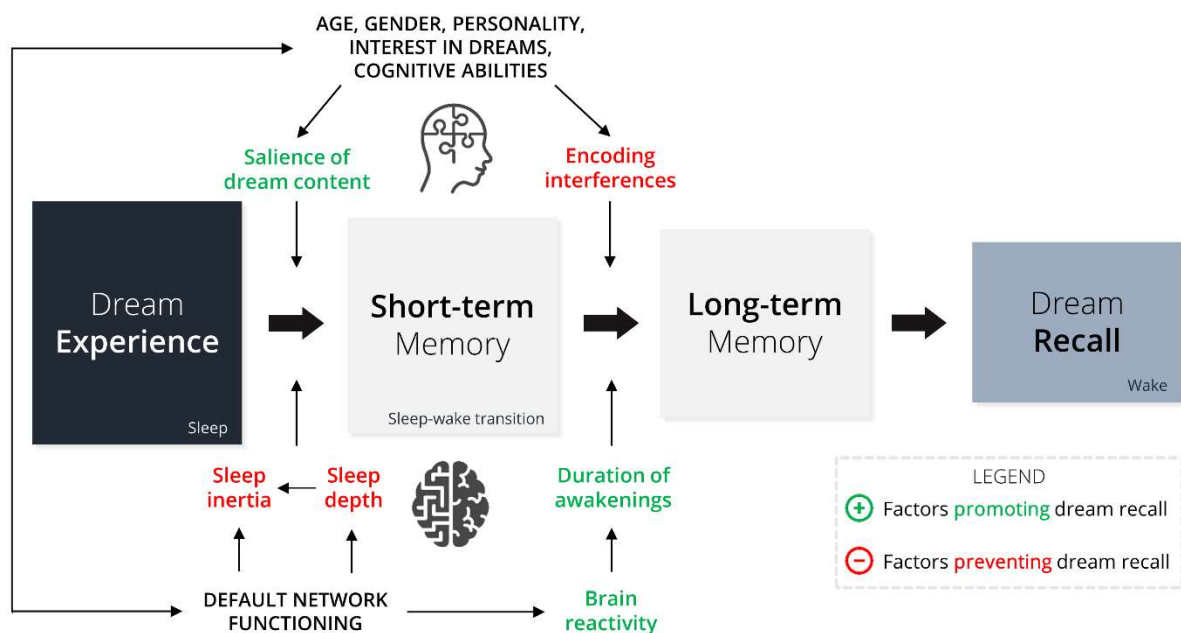


Figure 4 - Integrative model of Dream Recall (from Vallat 2017).

## Functional role of dream memories

Unless repeated or immediately written after waking up, dreams are often quickly forgotten. As dream science mainly relies on dream reports, the forgetting of dream memories induces a major methodological issue, and gives importance to the understanding the mechanisms involved in dream memorisation.

As we don't have any reliable means to observe the experience of a dream, and as we only have access to the dreamer subjective report after awakening, it is impossible to know whether a dream was experienced or not if no memory can be recalled after waking up (Ruby, 2020) (Ruby 2020). In some cases, the memory of having dreamt can remain without remembering the details of the dream content, a phenomenon dubbed "contentless" or "white" dreaming (D. B. Cohen, 1972). An awakening leads to white dreams in 20 to 40% of the cases, depending on the sleep stage and the study, with either a laboratory serial awakening paradigm (Noreika et al., 2009; Siclari et al., 2013) or diary reports (D. B. Cohen, 1972; D. B. Cohen & Wolfe, 1973). It is however unclear whether white dreams reflect the inability to retrieve the dream memory, as suggested by interference studies (D. B. Cohen & Wolfe, 1973), or only lower quality dream experiences, with fewer sensations and details, as proposed by Windt and coll. (2016) and Fazekas and coll. (2019), or even the false impression of having dreamt.

The study of dreaming has mostly focused on dream reports so far as they are the only observable trace of dreaming (Figure 1). Nevertheless, the fast forgetting of dream memories and the general tendency to not recall one's dreams (Schredl & Göritz, 2017: 54% of the population with at most one dream per month) suggest that dream recall is not useful or at least not necessary for human survival. It suggests a dissociation between the function of dreaming (i.e. emotional regulation, creativity...) and the function of dream recall (introspection, culture...) and also points towards the fact that the function of dreaming is most probably independent of dream recall, i.e. applies whether or not a dream is recalled or not. Several observations and theoretical points support this hypothesis. First, if dreams were remembered as well as waking memories, it would lead to a non-adaptive confusion between some dream memories and actual awake memories. This phenomenon is very rarely reported in healthy subjects, has been observed only in traumatic or pathological cases, and can be accompanied by intense emotions or violent behaviours (Nielsen, 2011). Second, while dreams incorporate parts of waking memories, the dream experience is generally not realistic, logic or applicable during waking life, and therefore does not have a clear adaptive value for the awake self. Processes underlying the formation of dreams (functions of dreaming) may be the most important for the awake self, and dream memories would only be a witness that the function happened. Finally, the large inter-individual variability in dream recall is associated with small inter-individual cognitives differences as described in the section

*Factors of variability in dream recall* frequency, which underlines that remembering one's dreams or not does not have a critical impact on everyday life.

In short, the roles of the dream and of the dream memory are most likely dissociated. Understanding dream recall is an important step toward understanding dreaming itself, but dream content may be more likely to address the functions of dreaming. We will review in the next section our current knowledge about dream content.



# Dream content

## Methods to assess dream content

### External scoring

As dreams are subjective perceptions that are incompletely described in a dream report, scientific analyses of dream content must rely on reproducible data that represents the dream as accurately as possible.

To address this issue, dream researchers have looked into asking external judges to rate and score dream reports as objectively as possible. This technique has been proposed as early as in 1893 by Mary Calkins (Calkins, 1893) who was the first to propose statistics about dreams content. Since then, the system proposed by Hall & Van de Castle (1966) has become the most widely used for dream scoring. Its fundamental concept involves the segmentation of dream content into distinct empirical categories, such as settings, objects, characters, interactions, emotions, and misfortunes. Subsequently, these categories can be employed to discern recurring patterns, providing norms for various contents, allowing for comparisons with specific populations. It is important to acknowledge that the norms developed by Hall & Van de Castle (1966) are tailored to the cultural context of their time, which is more than 60 years ago. Even though close scores were found in similar populations from 30 years later (Hall et al., 1982), comparisons with the 1966 norms should be done with consideration of the changing social context.

Dream scoring using the Hall & Van de Castle method has been widely used but is time-consuming, as the several scorers required will need to score each dream as many times as there are scales (Schredl, 2010a). Similarly, investigating a new scale implies confirming its validity (i.e., is it measuring the expected parameter) and its reliability (i.e., do different scorers attribute similar scores to the same dream), which is all the more time-consuming. Scorer biases are limited by reliability tests but remain present, as two people may have a different understanding of the dreams (especially the shortest ones). Alternative methods using an objective analysis of the words of the dream report have been proposed to bypass these issues. These methods generally employ keyword searches (Bulkeley, 2014) or natural language processing (NLP) tools, for instance for categorisation of word psychological attributes (Nadeau et al., 2006) or for semantic similarity analyses (e.g., Mota et al., 2020). Despite showing results similar to manual scorings, these methods are challenged by spelling mistakes, negation, irony detection, domain-specific lexicon, language-specific models (which are mostly created for English texts) and, in some cases, the time-consuming labeling of data similar to the target text (Nandwani & Verma, 2021). However, both manual and automated external scorings imply transforming the dream report in subscales, which induces a loss of dimensionality of the data and therefore a loss of information (Schredl, 2010a).

## Self-scoring

The accuracy of external ratings has been questioned over the course of dream research. How accurately can someone describe the subjective perception of someone else? In this sense, another way to get measurements of dream content is to ask the dreamers themselves to rate their dreams on one or several scales after awakening. As the dreamer is the only person who truly experienced the dream, they should be able to more accurately describe the dream memory with specific scales than what can be extracted from a potentially incomplete dream report by an external scorer. This method is less flexible than external ratings as self-ratings must be made as soon as possible after waking up and only the dreamer may rate the dream (by definition). This technique is therefore limited to prospective studies as dream memories are quickly forgotten. Moreover, all participants may have a different understanding of a same scale, censor themselves, or be otherwise biased.

Self-ratings and external ratings are generally correlated, although studies comparing these methods suggest that self-ratings are more reliable than external ratings (Schredl & Doll, 1998; Röver & Schredl, 2017; Sikka et al., 2014). Indeed, external ratings tend to underestimate some aspects of dream content compared to self-ratings, like emotions in dreams (Sikka et al., 2014; Röver & Schredl, 2017). The results of Röver & Schredl (2017) also show that, at least for negative emotions, shorter dreams are associated with a lower correspondence between self-ratings and external ratings, suggesting an incomplete description of the negative emotions in the dream report; positive emotions may be not affected as they are less striking and therefore may be less described, whatever the dream length. As the dreamer is the only one who lived through the dream experience, and based on the evidence above, self-ratings appear to describe better the dream than an external rating would.

## General dream characteristics

The use of dream content analysis methods led to the identification of several typical characteristics of dream content between subjects (Ruby, 2011).

In dreams all the senses can be experienced with a similar hierarchy of predominance between senses as in wake : vision > audition > touch > olfaction > taste (Zadra et al., 1998; Schwartz & Maquet, 2002; Lovati et al., 2014; Plailly et al., 2019). Of interest, olfaction and gustation seem particularly rare in dreams (Zadra et al., 1998; Schredl, Atanasova, et al., 2009; Weitz et al., 2010) even though only few studies addressed the comparison of senses representation in wake vs dreaming so far (Lovati et al., 2014). A survey addressing this issue

has been launched as part of my PhD project (data is still being acquired) to test whether all the senses were experienced with different intensities in wake and dreams.

Dreams generally contain elements from the waking life, though not exactly identical. Fosse et al. (2003) showed that exact replays of episodic memories were present in barely 2% of the 299 dreams they investigated, while fragments of these memories were identified 65% of them. The dream characters in the dreams collected by Vallat et al. (2017) were mostly people existing in waking life (54% of the dream characters) or presenting some traits from existing people (11%). These dream characters, which are frequent (4.7 characters in average in Vallat, Chatard, et al., 2017, with 96% dreams presenting at least 1 character), show some autonomy, thoughts and feelings (Kahn & Hobson, 2005), although they seem highly dependent on the dreamer's ego (Schmidt et al., 2014; Windt et al., 2014). Likewise, places in dreams share similar properties with existing places (Vallat, Chatard, et al., 2017).

One of the most reported is the emotional nature of dreams, especially after an awakening from REM sleep (Foulkes, 1962). In Vallat et al. (2017), 86% of dreams were emotional and about 56% were of high emotional intensity. Similar results were obtained (78% of emotional dreams) with a similar methodology (home dreams self-scored on 2 separate scales for positive and negative emotions) and numerous subject (N=413) (Röver & Schredl, 2017). Furthermore, it has been widely reported that dreams were often more negative than positive (e.g., Hall & Van de Castle, 1966; Kramer et al., 1971). This generally accepted observation should however be considered carefully, as results are not as clear when comparing self-ratings vs external ratings (Sikka et al., 2014, 2018; Schredl & Doll, 1998; Röver & Schredl, 2017) or home dreams vs lab dreams (B. Domhoff & Kamiya, 1964; e.g. Röver & Schredl, 2017 for home dreams; e.g. Schredl et al., 2012 for lab dreams). As described in the previous section, self-ratings appear more reliable than external ratings, and lab dreams do not exactly reflect an ordinary situation. Such studies generally found as much positive as negative emotion intensity, or a slightly more negative content in some cases. For instance, Röver and Schredl (2017), who used a large sample (N=425 participants and 1207 dreams), found that positive emotions ( $1.3 \pm 0.8 / 5$ ) and negative emotions ( $1.5 \pm 0.8 / 5$ ) did not differ (personnel communication with the author). This effect may also depend on the considered population, as Schredl et al. (2012) reported more positive dreams in healthy people than in people with sleep disorders, and more negative dreams are reported in depressed as non-depressed persons (Tribl et al., 2013).

Finally, dreams can be bizarre (Hobson et al., 1987; Nemeth & Bányai, 2022), without alerting or bothering the dreamer's consciousness (Dresler et al., 2015). Realistic situations do happen, but the unique characteristic of dreams is that the dreamer is not aware of any temporal, spatial, logical... incoherence. The only exception is the rare case of lucid dreaming, which is defined by an awareness that one is dreaming (LaBerge, 1980).

## Dream content formation

Dreams stage very various and sometimes seemingly unrelated elements, without necessarily following the real world rules and constraints, which leads to frequent feelings of bizarreness after waking up (e.g., Hobson et al., 1987). To account for this specific phenomenology, several authors have proposed that dreams are metaphorical representations of memories or emotions, and that these metaphors may reflect underlying dream functions (Hartmann, 1996; Malinowski & Horton, 2015; Ruby, 2021). These metaphors would correspond to mapping between common features of different memories, allowing for indirect incorporation in dreams and for the emergence of original experiences able to integrate in an existing network (Malinowski & Horton, 2015).

However, it is not clear which features of our memories drive the formation of a dream. Emotional memories seem to be preferably incorporated in dream content (Schredl, 2006; Malinowski & Horton, 2014; Eichenlaub et al., 2018; Vallat, Chatard, et al., 2017), but they are not the only ones. For instance, Vallat et al. (2017) reported that 73% of the waking life elements identified as incorporated in dreams were only feebly or moderately emotional. Interestingly, there is no preferred incorporation of positive vs negative (Schredl, 2006; Eichenlaub et al., 2018) or stressful (Malinowski & Horton, 2015) waking-life events in dreams: emotional intensity was the determinant parameter in all cases. Hartmann (2008) further proposed that emotional memory are not only incorporated, but also drive the construction of dreams, to allow for the formation of new connections with an adaptive value between memories. This hypothesis remains however to be confirmed.

Incorporation of external and internal stimuli may also affect the course of the dream (Solomonova & Carr, 2019). Direct and indirect incorporations of somatosensory (electric, Koulack, 1969; water, Dement & Wolpert, 1958; Koulack, 1969; pressure, Nielsen, 1993), auditory (Berger, 1963; Hoelscher et al., 1981), and olfactory (Schredl, Atanasova, et al., 2009) stimuli have been reported with varying success rates (9 to 87% depending on the study, the stimulus modality, and the methodology), while visual stimuli, like objects presented in front of the sleeper open eyes (Rechtschaffen & Foulkes, 1965), are less successfully incorporated (see also Conduit et al., 1997). Incorporation of visual cues has however seen some success as a lucid dreaming induction method (LaBerge & Levitan, 1995; Carr et al., 2020). It is not clear why incorporation of visual stimuli has been less successful than other stimulations or what controls their incorporation. On a similar note, the incorporation of auditory stimuli in dream content has also been tested using Targeted-Memory Reactivation (TMR); this technique consists in presenting during sleep a specific cue or stimulus that was previously paired with the encoding of a specific information during wake, leading to improved memory consolidation. Existing studies suggest an indirect and/or delayed incorporation of TMR-related memories

in dream content (Schwartz et al., 2022; Picard-Deland et al., 2021, 2021). It was suggested that the processing of external stimuli disrupts the ongoing sleep-related brain processes, potentially leading to an arousal or an awakening. To prevent such interference and maintain uninterrupted sleep, incoming stimuli are then adjusted to align with ongoing dreams and thoughts as well as possible, resulting in their direct or indirect incorporation into the dream content, in line with the sleep protection theory of dreaming initially formulated by Freud (Guénolé et al., 2013).

In comparison, less research was conducted regarding the incorporation of internal stimuli in dreams. Dement & Wolpert (1958) and Bokert (1967) had contradictory findings regarding the influence of thirst on dream content. In the pathological case of sleep apnea, where respiratory events could lead to breathing-related dream content, no direct incorporation of sleep apnea symptoms could be made (Schredl et al., 1999; Carrasco et al., 2006; Gross & Lavie, 1994). While not internally generated but still internally perceived, transcranial brain stimulations have been shown to influence dream content; for instance, Speth & Speth (2016) used tDCS to stimulate the motor cortex during sleep, which led to increased rates of motor imagery. It is overall less clear whether internal stimuli are incorporated in dreams, and we will address this question further in the framework of this thesis with the study of a pathological situation, i.e. epilepsy-generated internal stimuli (Studies 2a and 2b).

Building on the existing literature, De Koninck (2012) proposed a mechanism of REM sleep-related dream content formation (Figure 5). His model is one of the rare showing a respective contribution of distinct and hierarchically organised factors on dream content formation. As such, it is a precious tool for dream research, although some limits should be considered.

First, the respective contribution of each factor has never clearly been addressed by the author nor has it been experimentally tested. Importantly, the author did not describe how these factors interacted to create a dream scene, and how each of them specifically contributed. While internal and external stimuli seem to adapt to the existing dream, supporting their position as a low-importance factor in dream formation, it is less clear how culture and past experiences interact, as both reflect waking-life events which may be incorporated into dreams. This uncertainty is also visible by the changes in the hierarchy between the factors of the author's model across his own publications (e.g., De Koninck, 2012; Lortie-Lussier et al., 2019), seemingly reflecting the evolution of the corresponding scientific literature. Second, and on a similar note, the influence of presleep experiences, mood, concerns, their emotional components, and even culture or gender all at least partly reflect the same waking-life and therefore severely overlap, blurring their distinction in this model. Finally, there is limited or contradictory evidence for some blocks of this model. The effect of brain organisation for instance intertwines so much with dreaming and dream report abilities that their effect on dream content is unclear and has received too little attention (Kramer et al.,

1975; Sándor et al., 2014). On the contrary, the effect of internal stimuli on dream content has received limited support so far, despite its logical involvement on dreaming. This last aspect will be further studied through the studies 2a and 2b of this thesis.

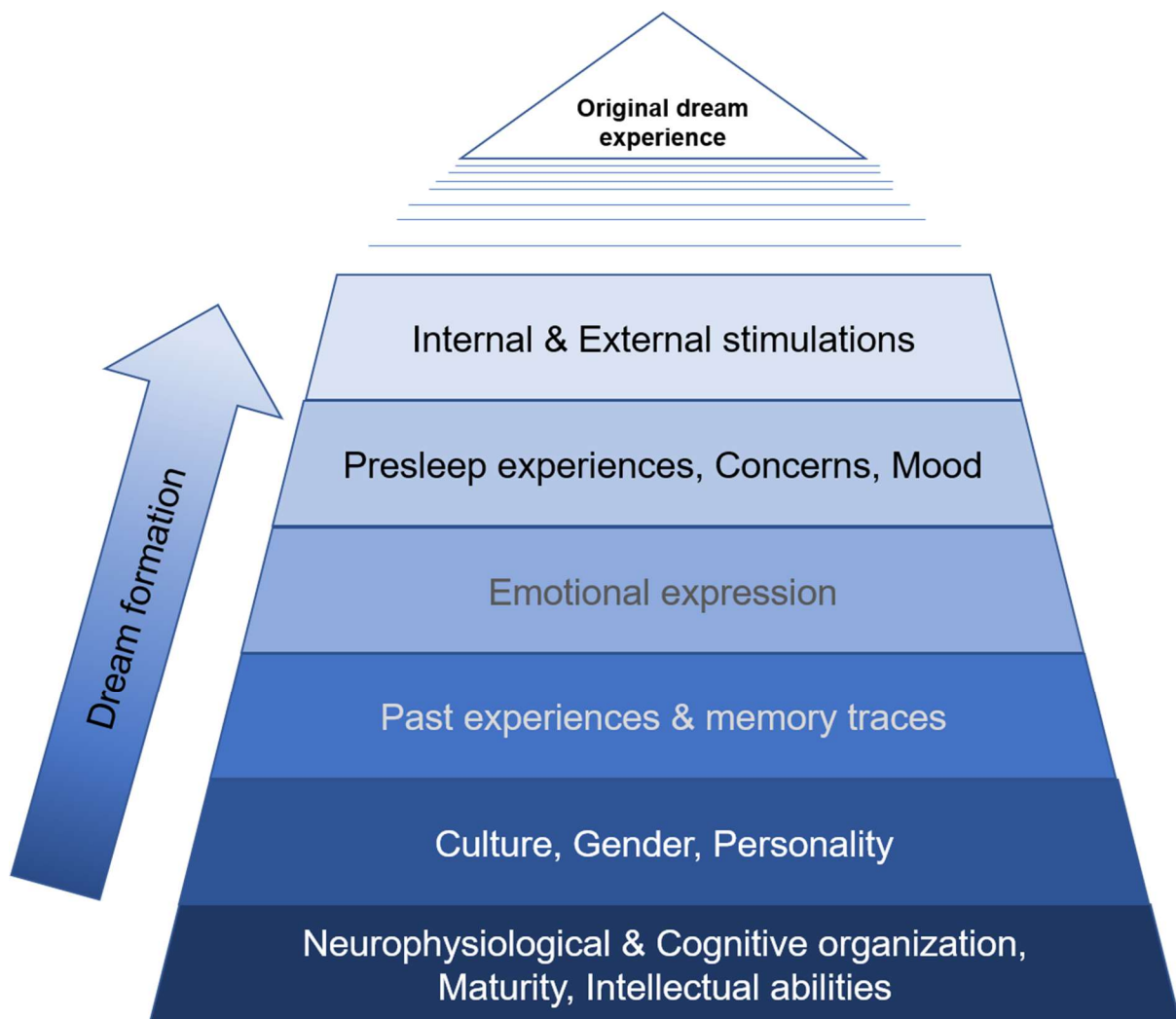


Figure 5 – The various factors involved in the formation of dream content according to De Koninck, represented as a pyramid to illustrate the relative influence of each parameter (adapted from De Koninck, 2012, and Lortie-Luissier et al., 2019). It should be noted that the model does not explicit how these factors are used to generate the dream and how each category contributes to the dream experience.

## Nightmares and bad dreams

According to the DSM-5 (American Psychiatric Association, 2013), nightmares are “extended, extremely dysphoric, and well-remembered dreams that usually involve threats to survival, security, or physical integrity” (Schredl & Göritz, 2018), like falling, being chased, being paralysed, being late, seeing a close person disappear or die (Schredl, 2010b). The fear component of nightmares is usually strong and usually induces an awakening, contrary to bad dreams, which are just negative dreams; because of this distinction, some researchers have proposed an alternate definition of nightmares as intense negative dreams leading to an awakening (Fireman et al., 2014; Levin & Nielsen, 2007).

While anyone can have nightmares, they are generally rare: in a representative German sample of 2019 people, only 9.0% had a nightmare once per month or more often (Schredl, 2010b). Several studies report frequent ( $\geq 1$ /week) nightmares in 2 to 5% of adults, with an effect of age, gender, and personality (Li et al., 2010; Schredl, 2010b; Carr et al., 2022; Gessert & Schredl, 2023). Frequent nightmares, when associated with clinically significant impairments like a fear to sleep or day-time mood disturbances, are considered pathological (“nightmare disorder”). They can also co-occur with PTSD (van Liempt et al., 2013), insomnia (Nakajima et al., 2014; Li et al., 2010; Sandman et al., 2013) and depression (Nakajima et al., 2014; Ohayon et al., 1997; Sandman et al., 2013). As nightmares are often associated with sleep and/or emotion-related pathologies, it has been proposed that they reflected a failure of emotion regulation processes occurring during sleep (Levin & Nielsen, 2007; Nielsen & Levin, 2007), as will be described in the section *Emotion regulation*.

Drug treatments for nightmares are mostly ineffective, except maybe prazosin for PTSD nightmares (Augedal et al., 2013), but imagery rehearsal therapy (IRT) has been found to have moderate to high efficiency in reducing nightmare frequency. The principle is to change the nightmare story to a positive one and to rehearse this new imagery several times a day (Krakow et al., 1995; Krakow & Zadra, 2010; Putois et al., 2019; Lüth et al., 2021).

## The functions of dreaming

The variability of dream recall questions all the more the function of dreaming. This question is even more difficult to answer that dreams cannot be directly manipulated (they can, at most, be influenced with external stimuli; see section *Dream content formation*) and that they are subjective and complex phenomenon that don't even have a clear and unique definition. Similarly, as dreams are deeply intertwined with sleep, the current hypotheses for a role of dreaming are based on functional hypotheses of sleep. Despite these constraints, knowledge about dream content, dream recall, sleep neurophysiology and DRF cerebral correlates allowed several authors to formulate functional hypotheses about the function(s) of dreaming (Ruby, 2011), among which the most influential will be detailed in this section. It should be noted that these theories are not incompatible between each other, and some of them even integrate other theories in their framework.

### Dreaming as an epiphenomenon of sleep brain activity

A first hypothesis came from neurophysiological studies of REM sleep, which was supposedly associated with dreaming for a long time (further detailed in the section *Neural correlates of REM sleep*). In this sense, Hobson proposed that dreaming is nothing more than an epiphenomenon of REM sleep (Hobson et al., 1998). According to Hobson's activation-synthesis model (Hobson & McCarley, 1977), dream imagery arises as cortical centers attempt to derive meaning from brainstem-driven signals occurring during REM sleep. Although dreaming would therefore have no adaptive value, he still agreed that it is possible to extract meaning from dreaming, which may show wake concerns, reflect unconscious processes... but only a posteriori.

Similarly, Domhoff proposed the neurocognitive theory of dreaming, which postulates that dreaming is a potent form of mind wandering, spontaneously induced by the activation of the DMN during sleep (G. W. Domhoff, 2011, 2018). In this framework, dreaming per se does not have any adaptive value and only reflects background mental activity. This theory is based on the observations of DMN associations with dream recall (see section *Dreams and neurophysiology*), the progressive development of the DMN in parallel with children dream reports (Sándor et al., 2014; Ruby, 2023), and the similarities between mind wandering and dreaming (Fox et al., 2013).

However, several other theories challenge this view as it can hardly explain some of the specific and elaborated characteristics of dreaming.



## Memory consolidation

The role of sleep in memory consolidation has been consistently demonstrated, with different types of memories being more or less specific to a sleep stage (Rauchs et al., 2004, 2005). According to the dual process hypothesis, NREM sleep and its neural features are associated with the consolidation of hippocampus-dependent declarative memories (e.g., Tucker et al., 2006), while REM sleep may consolidate more effectively procedural (e.g., Plihal & Born, 1997) and emotional (Werner et al., 2021; Hutchison & Rathore, 2015; see also Wislowska et al., 2013) memories. This hypothesis may however be too simplistic to account for the variability of the results (Ackermann & Rasch, 2014), as REM and NREM sleep may play different but complementary roles in memory consolidation (Ambrosini & Giuditta, 2001; Ficca et al., 2000; Stickgold et al., 2000; Tamminen et al., 2017).

Based on the contribution of sleep to memory processes, several authors have argued for a specific role of dreaming in memory consolidation (e.g., De Koninck et al., 1996; Wamsley et al., 2010). A few studies with important limitations (Plailly et al., 2019) suggest that memories incorporated into dreams may be indeed better consolidated than those not incorporated into dreams (Hudachek & Wamsley, 2023; Schredl, 2017; Plailly et al., 2019). Among these studies, Schoch et al. (2019) identified associations between dream incorporation and consolidation only for NREM dreams and not for REM dreams, suggesting different roles for different sleep stages and potentially explaining part of the inconsistencies between the existing results (Plailly et al., 2019).

The low rate of incorporation of memories to consolidate in recalled dreams, as well as the potentially metaphorical or symbolic representation of memories in dream content, tend to decrease the number of observations and thus the statistical power in the previously presented studies and to underestimate real incorporation in dream content, which make this hypothesis difficult to test properly (Plailly et al., 2019).

It should be noted that sleep has also been associated with targeted forgetting (Saletin et al., 2011; Andrillon et al., 2017). While there is no evidence for dream-related forgetting, dreams may have the potential to update some aspects of our memories, as will be described in the next section.

## Emotion regulation

Emotional regulation refers to the process of managing and modulating the intensity of memory-related emotions. As for memory consolidation, both REM sleep (e.g., Spoormaker et al., 2012) and NREM sleep (e.g., Arzi et al., 2014) are known to play a role in emotion regulation (Vandekerckhove & Wang, 2017; Palmer & Alfano, 2017; Meneo et al., 2023; Sollenberger et al., 2023), notably thanks to sleep deprivation studies. For instance, one such study demonstrated that sleep-deprived people had increased limbic and behavioural reactivity to pleasant stimuli (Gujar et al., 2011).

Several studies have also showed a continuity between wake emotions and dream content (Schredl, 2000a; Valli et al., 2005; Bulkeley & Kahan, 2008; Schredl & Reinhard, 2010) as predicted by the *continuity hypothesis of dreaming*, which states that dreams reflect waking-life experiences and thoughts (Schredl & Hofmann, 2003). The recent pandemic and lockdowns similarly induced emotional dreams and pandemic-related dream content (Ruby, 2021; Gorgoni et al., 2021; Mota et al., 2020; Remedios et al., 2023; Scarpelli et al., 2023). The relation between sleep and emotion regulation, coupled with the emotional nature of dreams (see section *General dream characteristics*), has therefore led several researchers to test for the involvement of dreaming in emotion regulation processes. Rosalind Cartwright and coll. (1991; 1998; 1998) were the first to investigate the relation between dreaming and emotion regulation. They identified that individuals who dreamt about their ex-partners during a divorce experienced reduced depression levels one year later (Cartwright, 1991) and that depressed individuals who had negative dreams at the beginning of the night followed by more positive dreams showed better depression remission after one year (Cartwright, Young, et al., 1998), suggesting that dreams reflect emotion regulation processes. In a longitudinal years-long study, Pesant & Zadra (2006) also showed that dreams contained more negative than positive emotions when the self-reported wake emotional well-being was low. More recently, Vallat et al. (2017) evidenced that when a memory is incorporated in a dream, the dreamt version has an attenuated emotional intensity (i.e. less positive when positive memory, and less negative when negative memory; see Figure 6), which supports a role of dreaming in downscaling emotional load. An investigation of culture-specific threats and emotions also supported an adaptive role of dreaming in emotion regulation, where dreams would express these threats and fears (Samson et al., 2023). Neurophysiological evidence also related fear in dreams and brain reactivity to frightening stimuli during the post-dream wake (Sterpenich et al., 2019; see also Scarpelli et al., 2019). On a different note, observations that traumatised people who develop PTSD have more negative dreams than traumatised people who did not develop PTSD (Pigeon et al., 2021) and that ADHD children, who have a dysfunctional emotion regulation (Christiansen et al., 2019), have more negative dreams than healthy children (Schredl & Sartorius, 2010), suggest that a failure to properly process (transform, downscale, balance..) emotions during dreaming may have adverse consequences. Consistently, the neurocognitive

model of nightmares (Levin & Nielsen, 2007; Nielsen & Levin, 2007) postulates that nightmares are a sign of a failure of emotion regulation during sleep and dreaming. This hypothesis would explain why frequent nightmares are associated with an elevated risk of suicide (Tanskanen et al., 2001; Sandman et al., 2017).

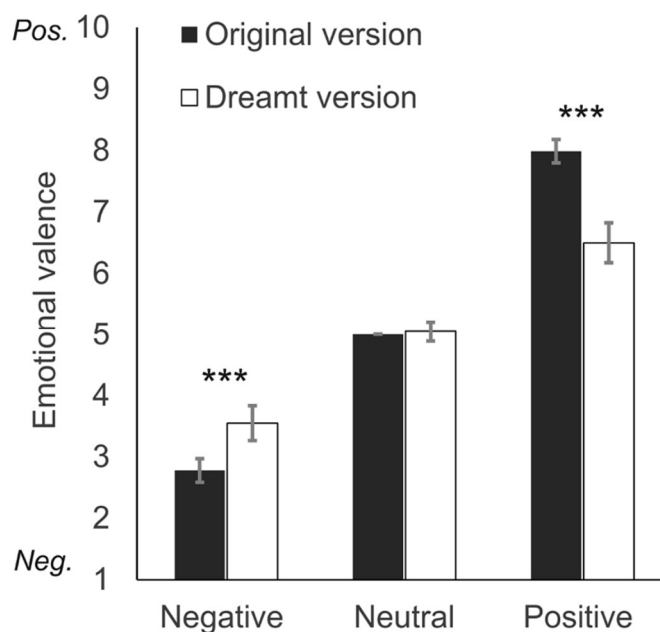


Figure 6 – Comparison of the emotional valence of the dreamt version (in white) and of the original version (in black) of the memory of waking-life events incorporated in dreams (from Vallat et al. 2017). Each waking-life event was scored on a 1-10 scale (1 negative, 10 positive), and each incorporation in dream content was scored on the same scale. The dreamt version of negative waking-life events was less negative than the original version, as the dreamt version of positive events which was also less positive; no difference was observed for neutral events. These results suggest a neutralisation of memories in dreams, supporting their role in emotion regulation. Error bars represent 95% confidence intervals; \*\*\*:  $p < 0.001$ .

Based on these results, several researchers proposed theories to explain the role of dreaming in emotion regulation. The basic idea of most of these theories relies on the integration of emotional memories among other, less emotional memories. Cartwright was the first to formulate such a role based on her previous studies (Cartwright, 1991; Cartwright, Young, et al., 1998; Cartwright, Lutten, et al., 1998): she suggested that dreaming could help in regulating emotions by embedding negative (and potentially positive) emotions into other waking-life elements, which would integrate them as a normal and less intense memory. Hartmann (1996; 2001; 2010) further suggested that this integration only affected the central image (i.e. the main element) of the dream. In this context, the dream would be an isolated place where the dreamer could make sense of the central image, explore it and integrate it in existing memory networks in order to reduce its emotional load. For him, this would mostly apply to REM sleep, which favours the hyper-connectivity (Cai et al., 2009; Martin et al., 2020) necessary for memory integration.

These models are consistent with several results showing a role of sleep in emotional regulation and with the model of memory consolidation and forgetting during sleep proposed by Walker (2009). Walker's model postulates that multiple iterations of sleep (and especially REM sleep) would lead to preservation of the core memory and the progressive attenuation of the associated affective tone (Figure 7)(Walker & Van Der Helm, 2009). Levin & Nielsen (2007) also proposed a neurocognitive model of emotion processing based on the integration of sub-elements of different memories during dreaming, and centered their theory on the expression of certain aspects of the recombined memories (for example fear). A failure to satisfyingly integrate emotions would lead to overexpressed emotions through nightmares. Perogamvros & Schwartz (2012) defended the Reward Activation Model (RAM) during sleep and dreams, which postulates that "memories with high emotional or motivational values for the individual are privileged to be reactivated during sleep" and therefore activate reward systems involved in memory consolidation. These memories would then be associated with elements from other memories to facilitate their processing. Malinowski & Horton (2015) attempted to integrate the previously cited theories and further suggested that dreams would mainly process salient events of the wake life so that they can be used as effectively as any neutral memory.

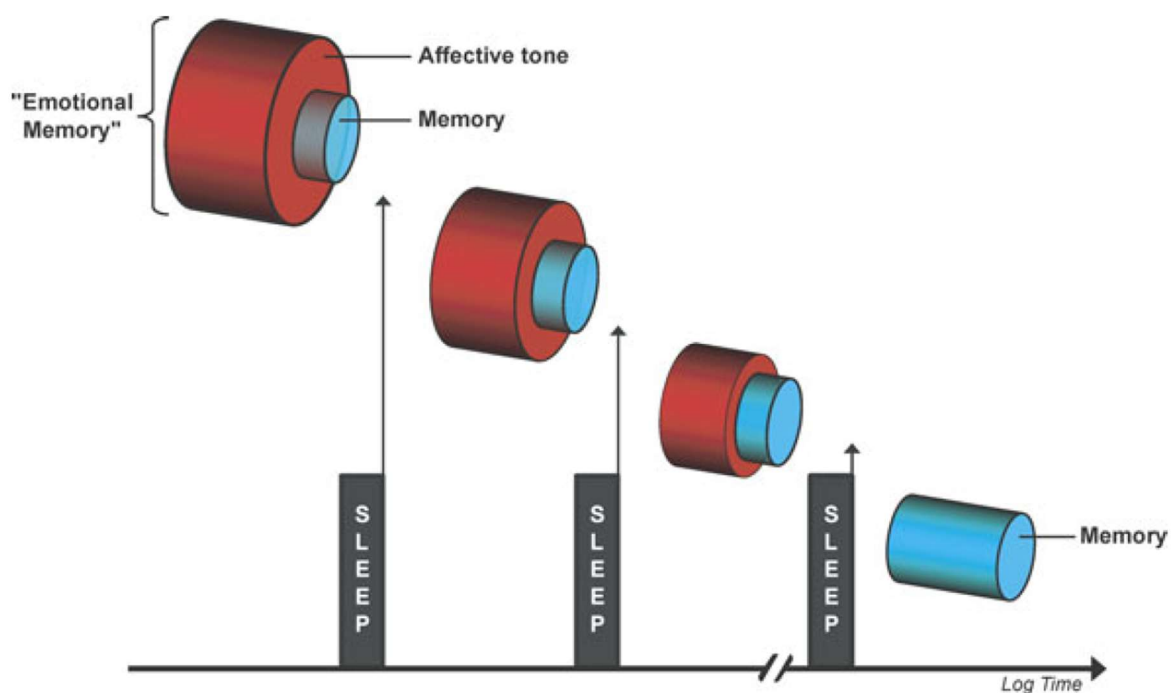


Figure 7 – Model of emotional memories processing during sleep (Walker 2009). Over multiple iterations of sleep (and especially REM sleep), the core of the memory (in blue) is strengthened while its affective cover (in red) is attenuated. This allows for a decoupling between the experience itself and its emotional aspects, leaving only the salient memory for future neural processes.

These theories are supported by emotion regulation processes observed during wake. For instance, Speer et al. (2021) showed that the reinterpretation of a negative memory with positive elements leads to long-lasting increased positive emotions and associated brain connectivity differences, similarly to what the presented-above theories suggest is happening during dreaming. Imagery Rehearsal Therapy (IRT) is based on the same approach, and consists in a transformation of nightmares into positive stories to rehearse which is associated with a reduction in nightmare frequency and negative intensity (Krakow & Zadra, 2010; Putois et al., 2019), with a high success rate (>70% according to Krakow & Zadra, 2010).

## A simulation mechanism for offline rehearsal

The extraordinary realism of dream experiences implies that a dream is a realistic and immersive offline world, in which many things are possible (e.g., flying or breathing underwater are not realistic). This observation led Annti Revonsuo and colleagues to propose the simulation theories of dreaming, which postulate that the evolutionary role of dreaming is “the simulation of waking events that were more important for survival and reproduction during human evolution” (Revonsuo & Valli, 2019). Such events include threats, as defended by the Threat Simulation Theory (TST; Revonsuo, 2000), and social interactions, as defended by the Social Simulation Theory (SST; Revonsuo et al., 2015).

The TST was first formulated by Revonsuo (2000), who proposed that dreaming was a realistic offline world in which threatening events could be rehearsed against without physical risks. Such risk-free rehearsal would improve chances to succeed when facing a similar threat in the post-sleep waking life. performance against future dangers. One illustrating example is the observation that students who dream of a test (i.e. a modern type of threat) the night before the test will have better results than the others (Arnulf et al., 2014). The TST was proposed after several observations. First, dreams had been mostly reported as more negative than positive (which is not as clear in recent studies with self-ratings, as defended in the section *General dream characteristics*), as if simulating negative events, and similarly, threatening dreams are even more threatening than equivalent real-life events (Valli et al., 2008), reinforcing the intensity of fear in dreaming. They also noted that being chased was a common dream theme, reported at least once by 80-90% of people (Nielsen et al., 2003; Yu, 2008), although it does not mean they occur frequently. In the framework of the TST, they also suggested that post-traumatic recurrent nightmares act as a rehearsal to be prepared for future similar situations, strengthening the evolutionary role of the threat in dreams (Valli et al., 2005).

While the TST focuses on events you have to survive against, the SST extends the TST to account for the social aspects of dreams, and therefore the usefulness of social networks to increase survivability (Revonsuo et al., 2015). In this framework, dreaming would be a training ground for socialisation, allowing to test social interactions or situations. It's inspired by previous theories considering the social component of dreaming, such as the Social Mapping Hypothesis of Brereton (2000), which integrates in the broader social brain hypothesis to propose the dream as showing virtual social scenarios, or the hypothesis of dreaming as a type of play (Humphrey, 2000; Bulkeley, 2004). The SST builds up on these theories and proposes to integrate them in the larger evolutionary framework of a world simulation.

# Dreams and neurophysiology

## Neural correlates of REM sleep

Early investigations of dreaming suggested it was specifically associated with REM sleep because of the higher likelihood to remember a dream after an awakening from REM sleep than from NREM sleep. This hypothesis was tempting as REM characteristics corresponded to some aspects of dreaming: eye movements may have reflected the scanning of dream images, the absence of muscular tone during REM sleep could prevent any potential dream movement... This hypothesis has since then been disproved (Solms, 2000), as several authors noticed actual dream reports after NREM awakenings (Foulkes, 1962; see also Nielsen, 2000 for a review), even in absence of previous REM sleep (Noreika et al., 2009; Oudiette et al., 2012). The diversity of NREM dream experiences may originate in the heterogeneity of NREM sleep (Bréchet et al., 2020), which may also explain why dreaming has been preferentially associated to REM sleep for a long time. Nonetheless, the idea that dreams were specific to REM sleep led to several neuroimaging studies of REM sleep to investigate the neural correlates of dreaming (Dang-Vu et al., 2009).

Among these studies (Maquet et al., 1996; Braun et al., 1997; for reviews, see Schwartz & Maquet, 2002; and Desseilles et al., 2011), PET investigations showed that regional cerebral blood flow was decreased during REM sleep in some regions (like the DLPFC) and increased in several others, like the occipital, temporal, anterior cingulate and motor cortices, and the limbic regions (see Figure 8).

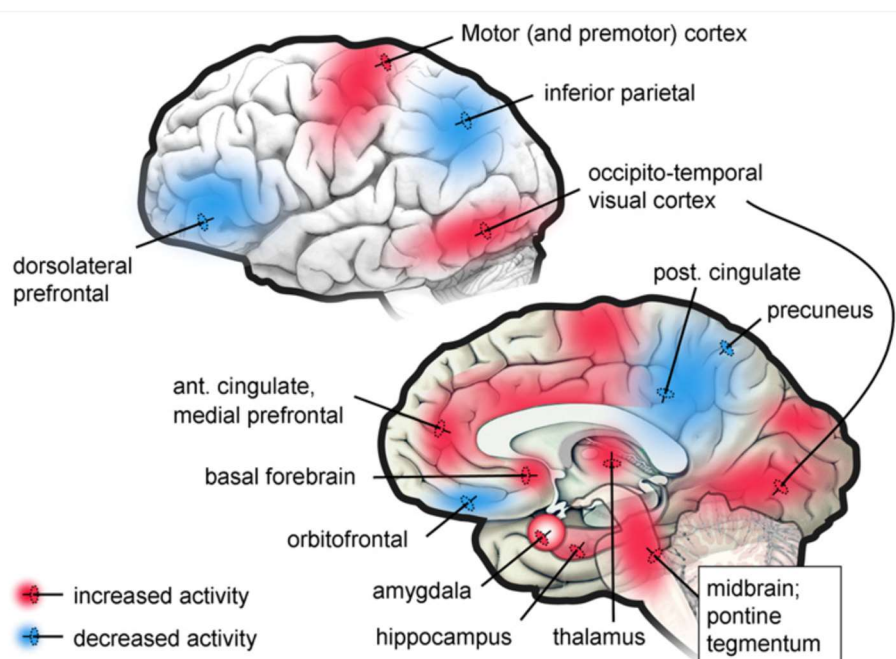


Figure 8 – Functional neuroanatomy of REM sleep compared to wake and/or non-REM sleep in PET studies (figure from Desseilles et al. 2011). Increased activity is indicated in red, and decreased activity in blue.

Following the REM sleep hypothesis of dreaming, several of these studies proposed that REM sleep specificities in brain functional organisation might explain the features of dream reports (e.g., Schwartz & Maquet, 2002). For example, increased occipital cortex activity during REM sleep could account for the predominance of visual elements in dreams (e.g., Lovati et al., 2014; Plailly et al., 2019). Moreover, the heightened hippocampal activity, a region associated with memory encoding and retrieval, could explain the presence of familiar places and characters in dreams. More generally, the involvement of limbic structures may explain the often-reported presence of emotional elements in dreams (Vallat, Chatard, et al., 2017). Conversely, decreased dorsolateral prefrontal cortex activity during REM sleep was proposed to contribute to the lack of consistency and logical reasoning in dream narratives (Hobson et al., 2011).

However, it should be remembered that dreaming is not exclusive to REM sleep and can occur during other sleep stages. Some NREM dream reports even closely resemble those from post-REM awakenings (Martin et al., 2020; Oudiette et al., 2012). This raises the question of how to reconcile the phenomenological aspects of dream reports with the distinct neurophysiological characteristics of NREM and REM sleep (Ruby, 2011).

## Neural activity preceding an awakening with a dream memory

In order to explore the cerebral underpinnings of dreaming regardless of the sleep stage, several researchers compared the cerebral activity between the sleep preceding a dream report and the sleep not followed by a dream report. This paradigm relies on the hypothesis that all dreams are remembered and that the absence of a dream memory is the consequence of the fact that no dream has been produced (Ruby, 2020), therefore not considering the case D in the Figure 9 below.



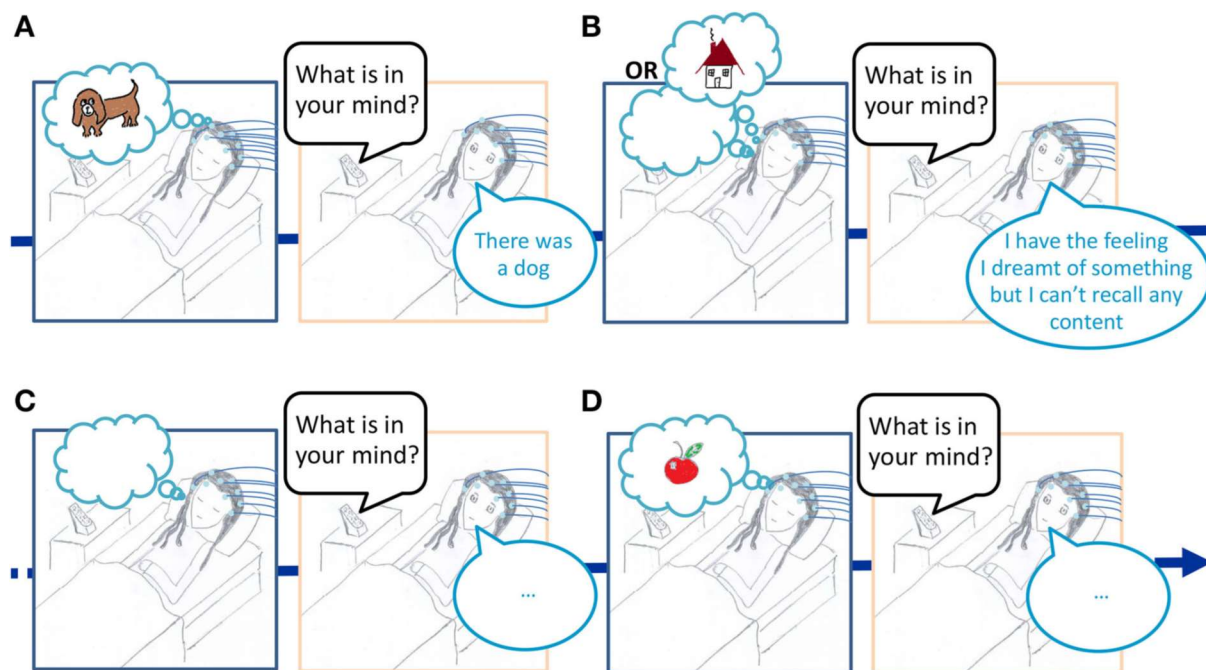


Figure 9 – Illustration of the serial-awakening paradigm (from Ruby, 2020). In a lab setting, a participant cerebral activity is recorded (e.g. with EEG scalp electrodes) during their sleep. They are awakened several times and asked to report what was in their mind just before awakening. The cerebral activity can then be classified as “preceding a dream report” (A), “preceding a white dream report” (B), or “preceding no dream report” (C and D). The cerebral activity from the cases “preceding a dream report” and “preceding no dream report” are then compared.

Spectral power analyses using this approach lead to the various and inconsistent results reported in Table 2 (Ruby, 2020). The role of beta, alpha and theta oscillations was reported in only a few studies. The decrease of delta power was more often replicated, although a large number of studies could not identify this effect. Additionally, the studies that did report an effect observed it in variable brain regions: in posterior regions in REM and NREM (Siclari et al., 2017), in left frontal and temporo-parietal regions in NREM sleep (Scarpelli et al., 2017), in frontal regions in NREM sleep (Chellappa et al., 2011), in right frontal regions in NREM sleep and in mostly temporoparietal regions in REM sleep (Esposito et al., 2004), in the midcingulate cortex in REM and NREM sleep (Perogamvros et al., 2017). More recently, Wong et al. (2020) further tested whether the brain activity preceding a dream report differed from an absence of dream report, in a multi-step blinded and severely controlled analysis, but could not find any association between dream recall and EEG spectral power.

With similar methodology, Horikawa et al. (2013; 2017) proposed similarities between visual perception at wake and during sleep onset imagery based on neural decoding of visual regions to determine dream content. Their decoding methods however were limited to categories of images, in only a few subjects, and have not been applied to periods of sleep longer than a few minutes of N1 sleep.

It should be noted that this approach generally does not address two key methodological issues. First, as there is no neurophysiological marker of dreaming, it is not

clear whether the dream actually occurred in the few minutes before awakening or long before, with its content persisting in memory until the awakening. Secondly, we can't be sure whether not recalling a dream means the person was not dreaming or simply did not remember it. If unremembered dreams preceded awakenings in those studies, it may have blurred the results to some extent, which may explain why so many inconsistent results have been reported by studies using this paradigm (Table 2).

Study	N	$\delta$ (0.5-4Hz)	$\theta$ (4-7Hz)	$\alpha$ (8-12Hz)	$\beta$ (>13Hz)
<i>REM sleep</i>					
Moffitt, 1982	8	=	=	=	=
Lehmann et al., 1981	-	↘	↘	↘	=
Wollman and Antrobus, 1987	30	=	=	=	=
Rochlen et al., 1998	17	=	=	=	↗
Germain et al., 1999	41	=	=	↗	↗
Takeuchi et al., 2003	8	=	=	↘	=
Esposito et al., 2004	11	↘	=	↘	=
Marzano et al., 2011	30	=	↗	=	=
Chellappa et al., 2011	17	=	=	↗↘*	↗
Scarpelli et al., 2015	6	=	↗	=	=
Siclari et al., 2017	46	↘	=	=	=
<i>Non-REM sleep</i>					
Moffitt, 1982	8	↘	=	=	=
Williamson et al., 1986	6	=	=	=	=
Morel et al., 1991	40	=	=	=	=
Takeuchi et al., 2003	8	=	=	↗	=
Wittmann et al., 2004	6	=	=	=	=
Esposito et al., 2004	8	↘	=	↘	=
Marzano et al., 2011	35	=	=	↘	=
Chellappa et al., 2011	17	↘	=	=	↘
Scarpelli et al., 2017	14	↘	=	=	=
Siclari et al., 2017	46	↘	=	=	=

Table 2 - Review of the studies that investigated EEG spectral power before an awakening with compared to without dream recall (from Ruby 2020). Red arrows indicate an increase in EEG spectral power, and blue arrows a decrease, when subjects recall a dream compared to no recall. =: no significant EEG spectral power difference between recall and no recall. \*: higher occipital alpha and lower frontal alpha.

## Neural correlates of lucid dreaming

For a long time considered a fantasy, the existence of lucid dreams, where the dreamer is aware of dreaming while dreaming and can sometimes control the dream environment and scenario, has been evidenced in 1980 by Stephen LaBerge (1980). As eyes can be moved and controlled by the lucid dreamer during REM sleep, the dreamer can be instructed to do a pre-determined sequence of eye movements to let experimenters know when they are lucid. Lucid dreams have been observed nearly exclusively in REM sleep, and only a few cases of NREM lucid dreaming have been reported so far (Stumbrys & Erlacher, 2012).

Lucid dreaming is a modified state of dreaming (Vallat & Ruby, 2019), as self-awareness is increased and may impact the dream scenario. Comparisons between REM sleep with and without lucid dreaming showed that regions normally deactivated during REM sleep and involved in self-awareness showed an increased activation during lucid dreaming (notably the prefrontal and occipito-temporal cortices, Dresler et al., 2012). Similarly, frequent lucid dreamers have increased resting-state brain connectivity between the prefrontal and temporoparietal cortices (Baird et al., 2018). Overall, these considerations imply that studies using lucid dreaming, with the unique population of frequent lucid dreamers, may misrepresent normal dreaming.

Despite these differences, lucid dreams remain a form of dreaming, with realistic simulated perceptions (LaBerge et al., 2018) and incomplete control over the dream content and scenario. Therefore, pre-determined eye-signaling allows for time-locked analyses of brain activity in relation to pre-determined actions, granting the opportunity for repeatable tests of neural activity during dreaming. One of the most remarkable endeavor showed that dreamt hand movements in lucid dreams are associated with activity in the hand area of the motor cortex (EEG: Erlacher et al., 2003; fMRI: Dresler et al., 2011), in line with previous studies which had shown increased EMG activity in the limbs moved in a lucid dream (LaBerge et al., 1981; Fenwick et al., 1984).

In conclusion, current studies of lucid dreaming suggest that dreaming is a real experience at the cerebral level, since the brain shows a similar activity while doing something awake and in a lucid dream. However, this is true only if lucid dreaming neural correlates adequately reflect the neural correlates of dreaming, which is not necessarily the case as detailed earlier. Results obtained with lucid dreaming are fascinating but should therefore be interpreted appropriately when considering normal dreaming.

## Brain lesions and dream recall alterations

Few neuropsychological studies investigated the effect of brain lesions on dream report frequency and content. The research of Solms was especially influential, as it involved studying the dream memories of 361 patients with neurological conditions (Solms, 1997). In this study he identified brain regions associated with partial or global cessation of dreaming, also called Charcot-Wilbrand syndrome.

Occipitotemporal lesions lead to a loss of visual imagery (the Charcot variant of the Charcot-Wilbrand syndrome) and were associated with similar impairments at wake, suggesting sleep and wake perception share at least some common neural bases. Global cessation of dreaming (the Wilbrand variant of the Charcot-Wilbrand syndrome) was most often accompanied by posterior lesions, in or near the temporoparietal junction (TPJ), and prefrontal lesions in the white matter of the medial prefrontal cortex and/or the head of the caudal nucleus (MPFC; second analysis of Solms data by Yu, 2001). As these lesions were not associated with any long-term memory impairment, language disorder or amnesia, Solms hypothesised that these regions were necessary for dream production rather than for dream recall. More recent studies (detailed in the next section) confirmed and extended these results by supporting an involvement of these regions in dream recall and/or production in healthy subjects (e.g., Eichenlaub, Nicolas, et al., 2014; Vallat et al., 2018, 2022).

As a final note, the amygdala, which is strongly activated in REM sleep (Maquet et al., 1996) and to a lesser extent in NREM sleep (Nofzinger et al., 2002) does not appear to be necessary for dream production (Blake et al., 2019).

## Cerebral correlates of high dream recall frequency

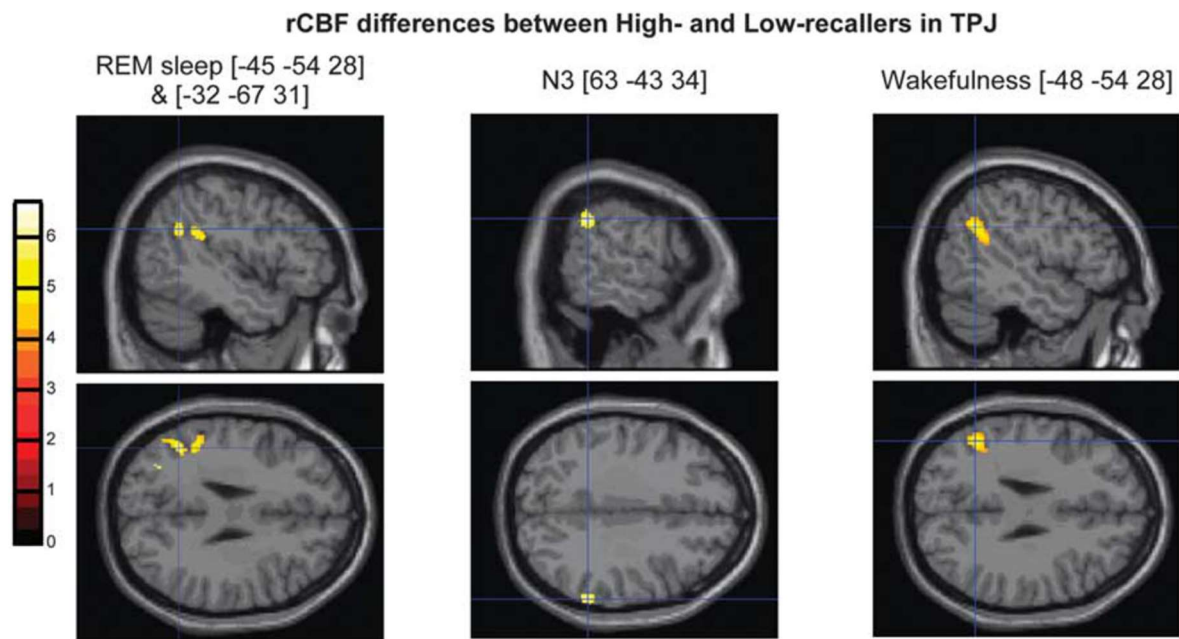
Studies comparing people with a low and a high DRF (LR vs HR) have been often designed to identify trait factors associated with DRF (see for instance studies of personality traits in section *Trait factors*) but more rarely to investigate potential neurophysiological trait differences between LR and HR.

First, brain reactivity differences between LR and HR were identified after salient and randomly presented stimuli in several studies. The rare novel stimuli in an oddball paradigm (first names randomly presented among pure tones) led to a longer decrease in posterior alpha power in HR than in LR during wake but not in REM sleep (Ruby et al., 2013), to a larger P3a during wake and N2 sleep, and to larger late responses in all vigilance states (Eichenlaub, Bertrand, et al., 2014), pointing to a higher brain reactivity and increased late complex cognitive processes in HR compared to LR. Similar findings were recently obtained by Ruby

et al. (2022), who identified increased bottom-up-related ERPs after to-be-ignored distracting sounds in HR compared to LR, supporting the increased distractibility of HR. They also found increased late ERPs after targets (similarly to the increased late ERPs after first names in HR vs LR found in Eichenlaub, Bertrand, et al., 2014), and a larger preparatory CNV after cue presentation in HR vs LR, i.e. HR showed increased markers of top-down attention. The authors interpreted these results by hypothesising that HR have increased bottom-up and top-down attention as compared to LR (see section *Factors of variability in dream recall frequency*). Likewise, another team recently associated DRF to the brain reactivity to emotional and neutral voices, both during wake and NREM sleep (Moyné et al., 2022). DRF correlated with the amplitude of early ERPs after emotional (but not neutral) stimuli during NREM, as well as with sigma and beta power, which are often associated with the processing of emotional stimuli. Overall, these results suggest an increased brain reactivity of HR compared to LR and are coherent with the observed increased intra-sleep awakening duration (Eichenlaub, Bertrand, et al., 2014) and longer arousals observed in HR (Vallat, Lajnef, et al., 2017).

Secondly, HR and LR manifest brain activity differences even while resting during wake and sleep. Regional cerebral blood flow was shown in a PET study to be higher in HR than in LR in REM sleep, N3 sleep and wake in the TPJ (Figure 10), and in REM sleep and in wake in the MPFC (Eichenlaub, Nicolas, et al., 2014). Similarly, resting brain functional connectivity is higher in HR than in LR within the DMN at wake, especially between the MPFC and the TPJ (Vallat et al., 2022). Using the same data, an increase in functional connectivity was observed especially just after awakening within the DMN and between the DMN and memory regions (right PFC, angular gyrus; Vallat et al., 2020).

Finally, these differences may have structural origins, as one MRI study showed increased white matter density in the MPFC of HR compared to LR (Vallat et al., 2018). As this region is involved in mind-reading, i.e. in thoughts attribution to characters (Legrand & Ruby, 2009), and based on the previous observation of increased cerebral blood flow in the MPFC during sleep in HR (Eichenlaub, Nicolas, et al., 2014), the authors proposed that this region is involved in dream production rather than in dream recall. This affirmation is further supported by neuropsychology studies (Solms, 1997; Yu, 2001) detailed in the section *Brain lesions and dream recall alterations*.



*Figure 10 – Differences between LR and HR in regional cerebral blood flow (rCBF) measured with positron emission tomography (PET) in the TPJ during REM sleep, N3 sleep, and wakefulness (from Eichenlaub et al. 2014). The sagittal and axial sections of the MRI show the specific regions with higher rCBF.*

These studies provide convincing evidence that dream recall frequency depends on neurophysiological traits objectivable both during wake and sleep. Although most of these studies focused on comparing two extreme profiles of DRF (HR and LR), the identified neurophysiological traits likely show a linear association with DRF. This hypothesis is supported by the results of Moyne et al. (2022), who found correlations between electrophysiological values and DRF, without a binary classification LR vs HR.

Overall, and in line with previous studies, the Default Mode Network appears to be at the core of explaining trait differences in DRF. Its involvement in waking and sleep mentation (Perogamvros et al., 2017) may contribute to both production and recall of dreams.

## Dreaming in epilepsy

### Epilepsy: definitions

Epilepsy is a neurological disorder defined by the International League Against Epilepsy (ILAE) and the International Bureau for Epilepsy (IBE) as an “enduring predisposition to generate epileptic seizures”, which are transient symptoms resulting from “abnormal excessive or synchronous neuronal activity in the brain” (Fisher et al., 2005). Epilepsy can result from developmental factors or be acquired, and it can manifest as focal seizures (originating in a single area of the brain), generalised seizures (affecting both hemispheres simultaneously), or a combination of these (Beghi, 2019). Epileptic seizures can manifest as various symptoms, depending on the brain regions involved in the epileptic discharge; however, they are stereotyped in a given patient. Overall, this condition encompasses a broad spectrum of neurobiological, cognitive, psychological, and social consequences stemming from its chronic nature and underlying causes, making it a complex and multifaceted disorder which concerns 7.6 persons out of 1000 (Fiest et al., 2017).

### Relationship Between Epilepsy and Dreaming: Current Knowledge, Hypotheses, and Perspectives



# Relationship Between Epilepsy and Dreaming: Current Knowledge, Hypotheses, and Perspectives

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The interactions between epilepsy and sleep are numerous and the impact of epilepsy on cognition is well documented. Epilepsy is therefore likely to influence dreaming as one sleep-related cognitive activity. The frequency of dream recall is indeed decreased in patients with epilepsy, especially in those with primary generalized seizures. The content of dreams is also disturbed in epilepsy patients, being more negative and with more familiar settings. While several confounding factors (anti-seizure medications, depression and anxiety disorders, cognitive impairment) may partly account for these changes, some observations suggest an effect of seizures themselves on dreams. Indeed, the incorporation of seizure symptoms in dream content has been described, concomitant or not with a focal epileptic discharge during sleep, suggesting that epilepsy might directly or indirectly interfere with dreaming. These observations, together with current knowledge on dream neurophysiology and the links between epilepsy and sleep, suggest that epilepsy may impact not only wake- but also sleep-related cognition.

**Keywords:** sleep, epilepsy, seizures, memory, dream, emotion

## INTRODUCTION

Epilepsy is a neurological disease characterized by an “enduring predisposition to generate epileptic seizures,” defined as “transient occurrence of signs and/or symptoms due to abnormal excessive or synchronous neuronal activity in the brain” (Fisher et al., 2005). Epilepsy is not only characterized by seizures, but it is further complicated by significant comorbidities such as cognitive impairment and psychiatric disorders (Fisher et al., 2005; Keezer et al., 2016). The interactions between epilepsy and sleep are numerous, including the comorbidity between epilepsy and sleep disorders, the activating effect of sleep on seizures and interictal epileptic activity, and the disturbance of sleep macro- and microstructure by these abnormalities (Bazil, 2000; Van Golde et al., 2011; Peter-Derex et al., 2020; Bergmann et al., 2021). Thus, epilepsy is likely to have an impact on sleep-related cognitive activity (e.g., memory consolidation, stimuli perception/integration, dreaming).

The cognitive processes at work during dreaming currently remain imperfectly understood. According to the phenomenology of dream reports, they comprise at least sensory and associative



processes, short and long term memory processes, executive and emotional processes, mind-reading, and consciousness: in other words nearly all the cognitive processes used during wakefulness (Nir and Tononi, 2010; Kahan and Laberge, 2011; Ruby, 2011, 2020; Windt et al., 2016).

Epilepsy is prone to interfere with these mechanisms in different ways. Seizures may influence dream content with possible incorporation of symptoms of diurnal or nocturnal seizures, especially when these latter occur during sleep when a dream is unfolding. Epilepsy may also modulate the ability to encode or remember dreams. Such ability is likely to be altered notably by the dysfunction of brain regions critical for the formation/recall of dream memories [medial prefrontal cortex (MPFC) and temporo-parieto-occipital junction (TPOJ)] (Solms, 2000, 2011; Eichenlaub et al., 2014b; Vallat et al., 2020) due to epileptic activity or due to the underlying neurological condition. On the contrary, it could also be promoted by increased wake after sleep onset observed in epilepsy patients (Koulack and Goodenough, 1976; Eichenlaub et al., 2014a; Vallat et al., 2017b; Sudbrack-Oliveira et al., 2019). Conversely, symptoms of daytime seizures may sometimes resemble dreaming experiences in some aspects, such as the oneiric atmosphere associated with a feeling of strangeness and familiarity, the so-called “dreamy state” (Jackson and Colman, 1898; Bancaud et al., 1994; Vignal et al., 2007), or by the feeling of experiencing or remembering a previous dream evoked during a seizure, the so-called “*déjà-rêvé*” (Curot et al., 2018).

In this review, we propose to discuss existing knowledge on the links between dreaming and epilepsy. In particular, we (i) provide a summary of the current understanding of the neurophysiological basis of dreaming, (ii) present the close interactions between epilepsy and sleep suggesting that epileptic activity might interfere with dreaming processes, and describe the potential relationship between seizures and dreams, both for sleep- and wake-related seizures; (iii) provide a synthesis of existing knowledge on the specificities of dreams in epilepsy patients and discuss these data in light of what is known about the determinants of dream recall and dream content in healthy subjects; and (iv) propose a perspective on the possible implications of dream disturbances in epilepsy, current research gaps and potential future developments.

## NEUROPHYSIOLOGY OF DREAMING

The definition of dreaming is still under debate (Pagel et al., 2001) but it is admitted that dreaming can be considered as a cognitive activity involving “mental imagery that consists of sensory hallucinations, emotions, story-like or dramatic progressions, and bizarreness” during sleep (Nielsen, 2000). Up to now, the brain mechanism at work during dreaming remains poorly understood due to methodological, technological and theoretical locks (Ruby, 2020). Indeed, except in specific situations, most often non-physiological [rapid-eye-movement (REM) sleep behavior disorders, lucid dreaming], only dream reports can be studied and not the dream experience itself (Guenole and Nicolas, 2010). Keeping these

restrictions in mind, we present below a summary of the current knowledge and concepts regarding the neurophysiology of dreaming.

## Models of the Neurophysiological Basis of Dreaming

Based on neuropsychological, electrophysiological and functional neuroimaging studies, two main models have been proposed. A “two-generator model” [one in REM and one in non-REM (NREM) sleep] or “activation-synthesis hypothesis” posits that brain mentation during sleep would vary along three dimensions: (i) activation, which depends on the brainstem reticular activating system; (ii) input, which refers to the processing of exteroceptive or interoceptive stimuli and depends on the input-output gating and the level of activation of the sensorimotor cortex; and (iii) modulation, which refers to the neuromodulatory balance (shift from noradrenergic and serotonergic tone in waking to cholinergic tone in REM sleep) and is involved in regulation of conscious state function and insight. These dimensions would behave differently according to vigilance states, which would explain quantitative and qualitative differences in dream reports between REM and NREM sleep (Hobson et al., 2000; Fosse et al., 2001). By contrast, a “one-generator model” proposes that dreaming would be under the control of a “trans-state” cortical and dopaminergic “dream on” mechanism involving the ventro-mesial frontal region and the TPOJ (Solms, 2000, 2011). This model would explain (1) why dreams occur not only in REM, but also in NREM sleep [50% in average and up to 90% of awakenings in NREM sleep are followed by dream reports, some of which are undistinguishable from REM dream reports (Cavallero et al., 1992; Cicogna et al., 1998; Nielsen, 2000; Wittmann et al., 2004), especially in the morning light NREM due to a circadian effect on dream recall (Cicogna et al., 1998; Chellappa and Cajochen, 2013)], (2) the increase in dream recall with increasing dopamine. It also suggests that dreaming might be facilitated in other situations such as epileptic activity and toxic/metabolic conditions (Solms, 2000, 2011).

## Experimental Results on the Neurophysiological Basis of Dreaming and Dream Recall

Several studies have demonstrated the involvement of specific brain structures in dream recall and/or production. The MPFC whose acute lesions result in a cessation of dream reports would play a central role in dreaming (Solms, 2000; Eichenlaub et al., 2014b; Vallat et al., 2018, 2020). The MPFC is part of the mesocortical dopaminergic pathways (Lena et al., 2005; Solms, 2011) and of the limbic system, which is particularly active during the “dreaming + REM sleep” state and may account for the emotional and mentalizing features of dreams (Maquet et al., 1996, 2005; Eichenlaub et al., 2014b). The TPOJ, which plays an important role in mental imagery, episodic memory and perspective taking, is also considered as a key generator of dreams (Maquet et al., 2005; Solms, 2011; Eichenlaub et al., 2014b; Vallat et al., 2020) with occipital

areas being involved in the visual component of dreams (Solms, 2011). The dorsolateral prefrontal cortex (dlPFC), would rather be deactivated during dreaming, except during lucid dreaming (Dresler et al., 2012; Vallat and Ruby, 2019), accounting for the alteration of executive functions during dreaming (Maquet et al., 1996; Muzur et al., 2002; Ruby, 2011) and its reactivation would help recalling dream content at awakening (Vallat et al., 2020). It is however important to keep in mind that the memory system involved in the dreaming process may be partly distinct from the one at work during wakefulness. Indeed, dream memories and episodic memories of diurnal experiences are very rarely confused even if similar in content, and dreams can be reported in amnesic patients even with bi-hippocampal lesions (Torda, 1969). Interestingly, in contrast with the preceding results, Fell et al. (2006) findings suggested that the rhinal-hippocampal connectivity would subserve the incorporation of episodic memory content in dream content and would participate in dream recall (Fell et al., 2006).

Some other studies have investigated the neurophysiological correlates of dream recall by analyzing the brain activity preceding (or following) an awakening associated with a dream recall (Ruby, 2020). Several features have been associated with dream recall, such as a decrease in slow wave activity in posterior regions (see Ruby, 2020, for a review), local frontal activation (Siclari et al., 2018), and changes in brain functional connectivity (Nieminen et al., 2016) in the sleep just preceding awakening. Other works have suggested that brain patterns of activity, with local increase in high frequency activity recorded with high density EEG or local increase in the BOLD signal (fMRI), might be associated with specific dream contents (Horikawa et al., 2013; Siclari et al., 2017). Finally, our team (CRNL) and other colleagues have emphasized the role of awakenings in dream recall whose frequency/duration and efficiency (in terms of memory encoding) would depend on a specific activity notably in the default mode network during sleep and at awakening (Eichenlaub et al., 2014a,b; Vallat et al., 2017b, 2020; Van Wyk et al., 2019). According to these works and to the “arousal-retrieval” model (Koulack and Goodenough, 1976), dream recall would require an awakening when the short-term memory of the dream experience is still “alive” and would depend on the brain’s ability to return to a cognitive functioning closer to the waking state (Schredl et al., 2003; Ruby et al., 2021). This hypothesis which gives an important role to short-term memory in dream recall, is coherent with results showing that short-term memory [involving the prefrontal cortex, (Nee and Jonides, 2008)] is at least partially preserved in N2 and REM sleep, even if dlPFC possible deactivation during sleep may diminish its capacity and duration (Daltrozzo et al., 2012).

## EPILEPTIC SEIZURES AND DREAMS

Epilepsy is prone to interfere in many ways with the processes involved in dreaming, especially as sleep has a strong activating effect on epileptic activity.

## Epilepsy and Sleep Interactions

Epilepsy results from the development of a neuronal hyperexcitability, due to a pathogenetic injury of various causes, which leads to recurrent focal or generalized seizures (Devinsky et al., 2018). Epilepsy and sleep interact in multiple ways (Malow, 2007; Grigg-Damberger and Foldvary-Schaefer, 2021; Moore et al., 2021). On the one hand, sleep has a modulating effect on epileptic activity; some epilepsy syndromes are characterized by seizures occurring almost exclusively during sleep, or by a major activation of inter-ictal epileptiform discharges during sleep, especially NREM sleep (Frauscher and Gotman, 2019; Nobili et al., 2020). This activating effect of NREM sleep on epilepsy is modulated by the depth of sleep: lighter stages of NREM sleep promote seizures, whereas deeper stages associated with high amplitude slow waves are more likely to enhance inter-ictal epileptiform discharges (Minecan et al., 2002; Frauscher et al., 2015). Conversely, REM sleep (particularly the phasic REM sleep microstate) has an inhibitory influence on epileptic activity potentially linked to neuronal desynchronization mediated by cholinergic neurotransmission (Ng and Pavlova, 2013; Frauscher et al., 2016). Although very rare, epileptic seizures can nonetheless be observed during REM sleep (Minecan et al., 2002; Peter-Derex et al., 2020). Chronobiological factors also influence the occurrence of seizures (Karoly et al., 2021). On the other hand, epilepsy has a disrupting effect on sleep macro- and micro-architecture. It is associated with an increase in wake after sleep onset (Sudbrack-Oliveira et al., 2019; Peter-Derex et al., 2020) but also with a micro-structural fragmentation of sleep, linked to both ictal and inter-ictal epileptic activity (Malow et al., 2000; Peter-Derex et al., 2020). Recently, it has been proposed that epileptic activity might disrupt NREM sleep oscillations (slow waves, spindles, ripples) underlying sleep-related memory consolidation processes, which may have a deleterious effect on patients’ cognition (Gélinas et al., 2016; Lambert et al., 2020; Lambert et al., 2021). In view of the aforementioned evidence that dreams are far from being restricted to REM sleep but also typically occur during light NREM sleep, precisely the stage associated with seizure activation (Minecan et al., 2002), one can expect that nocturnal epileptic activity might have an impact on dreaming processes. This would be more specifically the case for focal seizures. Indeed, epilepsy-induced local dysfunction of the MPFC, the TPO junction, the dlPFC and maybe temporo-mesial structures, could theoretically impact the dreaming process in a quantitative or a qualitative way.

## Focal Seizures and Dreams

The impact of seizures occurring during sleep and their impact on ongoing cognitive processes is still poorly understood. In the same way that stimuli during sleep are likely to be incorporated into dreams, especially if they have a specific intensity, i.e., just below the awakening threshold or a particular meaning for the sleeper (Dement and Wolpert, 1958; Berger, 1963; Koulack, 1969), symptoms related to an epileptic discharge could in theory be incorporated into dream content (this would represent a protective mechanism for sleep according to Freud). This

is supported by some clinical observations of patients with nocturnal temporal seizures, reporting that they were having a seizure in their dreams (or reporting subjective feelings associated with seizures as a component of their dream) (Epstein and Hill, 1966; Vercueil, 2005). Very seldom case reports, however, have provided evidence on video-EEG recordings of a concomitant epileptic discharge during sleep (see **Box 1**). Interestingly, the few documented cases suggest that epilepsy may influence dreaming both in REM sleep (Epstein and Hill, 1966) and NREM sleep (personal case). According to Solms, focal epileptic discharges could also act as intrinsic triggers for the activation of the MPFC yielding an increase in mesocortical dopaminergic activity thought to be involved in limbic structures activation during dreaming (Solms, 2011). Thus, a link between nightmares and nocturnal ictal activity has been suggested (Solms, 1997). This association was explored in a study of 20 patients with temporal lobe epilepsy (TLE) and parasomnia, among which 14 were suffering from recurrent nightmares; dream content included reminiscences of daytime seizures, such as “*déjà vu*” experiences with intense negative emotions, or feelings of unexplained sense of dread and fear. Interestingly, episodes that could be documented on a video-EEG recording were associated with an ictal discharge; moreover, parasomnia had started coincidentally or after seizure onset and a remission was observed after therapy optimization (Silvestri and Bromfield, 2004).

Interestingly, previously experienced dreams can also be a component of the subjective cognitive content of a diurnal seizure. It may happen notably during temporal lobe seizures, and is referred to as “*déjà-rêvé*” (Curot et al., 2018). According to the authors, this phenomenon actually includes three distinct entities: (i) the recollection of a specific and detailed dream with a specific date, which is an episodic-like memory; (ii) the reminiscence of a vague dream or elements of dream(s), which is more familiarity-like; (iii) or a “*feeling like dreaming*” which is a feeling that resembles what happens in dreams. The first two phenomena are mainly elicited by the electric brain stimulation of the medial temporal lobe whereas the “*feeling like dreaming*”

state has less anatomical specificity (Curot et al., 2018). The fact that these evoked memories are unambiguously identified as dream-related raises questions about the neuronal systems involved in dream and diurnal experiences memory; indeed, out of any pathological context, dream memories are rarely confused with semantic or episodic memories from waking life. This suggests that, at the time of encoding or consolidation of the dream memory, a “*dream tag*” would be either inserted within the memory or that the dream-memory system would be partly distinct from the waking-memory system. Such a dichotomization at the early stages of memory formation would ensure that memories from waking life are not confused with dream memories, which appears to be crucial from an adaptive point of view.

## MEMORY OF DREAMS IN EPILEPSY

### Dreams in Epilepsy Patients

Beyond the observation of a direct association between a single seizure and a particular dream, few studies have specifically investigated dreaming in epilepsy; in general, a mild decrease in dream recall frequency (DRF) is reported in epilepsy patients (Bonanni et al., 2002; Bentes et al., 2011).

### Dream Recall in Epilepsy Patients

DRF, assessed by a dream diary filled in at home during 60 days, was shown to be higher in patients with focal impaired awareness seizures due to temporal lobe epilepsy (TLE) than in patients with primary generalized seizures (daily DRF:  $0.55 \pm 0.30$  vs.  $0.25 \pm 0.23$ , with 85% vs. 61.9% of patients with at least one dream/week, respectively) (Bonanni et al., 2002). Using dream diaries in 52 drug-resistant TLE patients undergoing prolonged video-EEG recordings, another group observed that 71% of patients reported dreams but their DRF was lower than the one of healthy controls completing diaries at home ( $0.34 \pm 0.33$  vs.  $0.78 \pm 0.57$  dream/subject/day) (Bentes et al., 2011). In patients with focal impaired awareness seizures, DRF was found to be higher for REM vs. NREM awakenings, in a higher proportion than is usually observed in healthy individuals, suggesting a specific impairment of NREM sleep dream recall in patients; to note, length and structural organization of dreams reported after REM and NREM awakening did not differ (Cipolli et al., 2004).

### Dream Content in Epilepsy Patients

In a study of Paiva et al. (2011) dream reports in epilepsy patients were shorter and dream content differed from that of control subjects, with a higher proportion of familiar characters and settings, and a lower proportion of success and sexuality. Coherently, in another study of patients experiencing nightmares, short and poorly detailed dream reports have been observed (Silvestri and Bromfield, 2004). Interestingly, some differences between patients were identified according to the laterality of the epilepsy with higher DRF, more aggression, and less animals as well as self-negative expressions in left vs. right TLE (Paiva et al., 2011). Increased vividness and emotionality have also been reported in dreams of epilepsy

**BOX 1** | Examples of clinical cases suggesting an influence of epileptic activity on dreaming.

1. *Concomitant scalp EEG recording was available in the case reported by Epstein and Hill in 1966; in this case, right temporal epileptic rhythmic discharges were observed in the EEG during REM sleep and the patient, who had been awakened by the staff, could report a dream including some of her diurnal seizure symptoms (typical epigastric feeling) within the dream scenario (Epstein and Hill, 1966).*
2. *A 36-year old patient suffering from non-lesional frontal sleep-related hypermotor epilepsy was explored with video-EEG recording. He was interviewed at awakening after an hypermotor seizure which had occurred during late night N2 sleep stage, at 6:30 am. The patient did not report having a seizure, but described being awakened by a nightmare in which he was violently struggling against attackers. Presumably, the hyperkinetic ictal automatisms had been perceived during sleep, and incorporated into the oneiric narrative, suggesting that not only sensory or cognitive experience, but also motor symptoms may become part of the dream scenery (personal case).*

patients (Gruen et al., 1997). However, complaints of nightmares are only encountered in a small number of patients (Khatami et al., 2006). Finally, some specificities linked to the intrusion of ictal symptoms in dream reports of epilepsy patient have been reported (Epstein, 1964). This observation can be explained by the incorporation of nocturnal epileptic-related symptoms into dreams or by the continuity hypothesis of dreaming. Indeed, in the general population, dream content is strongly influenced by the dreamer's waking life (Schredl and Hofmann, 2003) and especially by recent and/or emotional events (Vallat et al., 2017a). Interestingly, typical dreams that are widespread in the general population (Schredl et al., 2004) can be very similar to epileptic auras, suggesting the involvement of common brain networks in the two phenomena; this has been described for auras resembling frightening dreams (death, falls, drowning...) or dreams with body image alteration such as the losing-tooth dream (Epstein, 1964, 1967, 2002).

## Factors Involved in Dream Memory in Epilepsy Patients

Data on the effect of the epileptic focus side are conflicting. Some authors reported no influence of epilepsy laterality on DRF (Bonanni et al., 2002; Cipolli et al., 2004) whereas others found lower dream recall in case of right vs. left epileptic focus (Paiva et al., 2011). The presence of a detectable lesion was not found to be associated with DRF, but a higher global cognitive functioning and abstractive abilities were associated with higher DRF and longer dream reports (Bonanni et al., 2002; Cipolli et al., 2004). In the same line, frontal dysfunction in TLE was reported to influence dream content regarding animal content and misfortune (Paiva et al., 2011). Finally, no relationship was found between DRF and the presence of diurnal seizures mentioned on a seizure diary (Bonanni et al., 2002) nor with seizure frequency recorded with video-EEG (Bentes et al., 2011). However, it is important to note that the completeness of the seizure count may have been limited by the subjective report of seizures and by scalp EEG exploration, as some deep-seated brief discharges remain undetectable by surface recordings and, during the night, may manifest only by an arousal (Malow et al., 2000; Peter-Derex et al., 2020).

To our knowledge, the possible relationship between sleep macro- and microstructure, epileptic activity and dream memory in epilepsy patients has never been investigated. The most consistent finding regarding sleep architecture in epilepsy is an increase in wake after sleep onset (Sudbrack-Oliveira et al., 2019), which could be expected to increase DRF (Koulack and Goodenough, 1976). However, no data are available regarding the characteristics of awakenings in epilepsy, although the length and number of awakenings in N2 NREM stage are critical factors for dream recall (Vallat et al., 2017b; Van Wyk et al., 2019). Importantly, long enough intra-sleep awakenings may facilitate dream recall if the content of working memory is not empty (Koulack and Goodenough, 1976). It can be hypothesized that the increased epileptic activity during NREM sleep might alter working memory notably by diminishing its capacity or erasing its content, which could explain the particular decrease

in DRF observed upon NREM sleep awakenings in epilepsy patient (Cipolli et al., 2004). Impaired working memory during wakefulness, frequent in epilepsy patients, could also diminish or suppress dream recall at awakening (Arski et al., 2020). REM sleep dreaming would be expected to be less impaired than NREM dreaming in epilepsy patients, given that ictal and inter-ictal epileptic activity is less frequent in REM than in NREM sleep. However some authors reported a decreased REM sleep duration and an increased REM sleep latency in epilepsy patient, particularly in case of nocturnal seizures (Bazil et al., 2000; Scarlatelli-Lima et al., 2016; Mekky et al., 2017). This reduction of REM sleep could participate in the reduced DRF in epilepsy patients. Additionally, changes in density, duration and frequency of sawtooth waves have been reported in TLE patients (Vega-Bermudez et al., 2005); such REM sleep micro-architectural disturbances may also interfere with dreaming processes, given the suspected role of sawtooth waves in driving multifocal fast activities which could be associated with dream content (Siclari et al., 2017; Bernardi et al., 2019; Frauscher et al., 2020).

Several other factors may be involved in a decreased dream recall ability in epilepsy patients, notably anxiety, depression, cognitive disorders and anti-seizure medications which may have an impact on both sleep structure (including arousability) and cognition/dreaming (Bonnet et al., 1979; Kwan and Brodie, 2001; Loring and Meador, 2001; Jain and Glauser, 2014; Keezer et al., 2016; Nicolas and Ruby, 2020). Finally, trait factors that have been identified to covary with DRF and dream content in healthy subjects such as interest in dreams (Schredl and Göritz, 2017), openness to experience (Schredl et al., 2003; Schredl and Göritz, 2017), creativity (Brand et al., 2011), thin personality boundaries (Hartmann, 1989; Schredl et al., 2003), and absorption (Schredl et al., 2003) have not been specifically investigated in epilepsy patients.

## DISCUSSION AND PERSPECTIVE: CURRENT RESEARCH GAPS AND POTENTIAL FUTURE DEVELOPMENTS IN THE FIELD

Despite the major theoretical interest in the study of dreams as a key component of the sleeping brain's cognitive activity, few studies have investigated the interactions between dreams and epilepsy. This gap is even more striking as sleep is known to be particularly disrupted in epilepsy and crucial for cognition (Diekelmann and Born, 2010). Most studies on this topic have explored dream recall and dream content in patients with epilepsy (Bonanni et al., 2002; Cipolli et al., 2004; Bentes et al., 2011; Paiva et al., 2011). They have found a moderate decrease in DRF, potentially linked to disturbed sleep with less REM sleep, to impairment of certain cognitive functions and to anti-seizure medications (Bonanni et al., 2002; Bentes et al., 2011). They have also highlighted some characteristics of dream content, being more negative and with more familiar settings, which can be related to patients' traits or life (altered mood, negative

waking life emotions) (Paiva et al., 2011). These results are interesting because they show that epilepsy influences cognition not only during wakefulness but also during sleep, and because they provide information about the cognitive and psychic state of the patients. Although dream function remains a matter of debate, the role of dreams in the regulation of emotions and in the consolidation of memory has been widely emphasized (Malinowski and Horton, 2015; Vallat et al., 2017a; Plailly et al., 2019; Scarpelli et al., 2019). Other theories propose that dreams may act as virtual reality training (to notably improve social and defensive skills) to prepare for waking life challenges (Valli et al., 2005; Hobson, 2009; Hobson et al., 2014; Tuominen et al., 2019) or that they may prevent the brain from overfitting waking experiences by allowing generalization of learned neural representations aiming to ensure a better adaptation to real-world life (Wagner et al., 2004; Hoel, 2021). Altered dreaming processes may thus have consequences on epilepsy patients' ability to adapt to waking life demands.

Very few projects have addressed the issue of "dreams and epilepsy" from a neurophysiological point of view. Many confounding factors make the study of dream and epilepsy interaction challenging. Longitudinal studies which aim at specifically identifying epileptic activity-related dream modulation would allow to overcome the many biases (underlying epileptogenic condition, comorbidities, treatments) of studies comparing patients and healthy subjects (Putois et al., 2020). A first step could be to more systematically question the epileptic patients explored with video-EEG about their dreams, especially after nocturnal seizures. The use of

intracranial EEG investigation may avoid the underestimation of epileptic activity resulting from patients reports or scalp recordings, especially in medial frontal and temporo-parietal epilepsy. Collecting dream narratives in such epilepsy patients, following provoked awakenings after seizures or outside seizures, would allow to assess the direct influence of focal epileptic discharges on dreaming. The occurrence of focal seizures during sleep provides a model of acute transient and spatially limited brain dysfunction that can disrupt or hijack oscillatory interactions within and between networks involved in cognition and notably memory formation (Mendes et al., 2019; Arski et al., 2020). Investigating the effect on dream recall and dream content of epileptic discharges involving the MPFC and/or the TPOJ—but also of other networks engaged in working memory—would advance our understanding of the neurophysiology of dreaming.

As a conclusion, studying the structure of sleep and dream experiences in epilepsy would not only allow to better understand the impact of epilepsy on sleep-associated cognitive functions, but also to explore the neurophysiological substrates of sleep-related cognitive processes from which dreams arise.

## AUTHOR CONTRIBUTIONS

AC, PR, and LP-D: drafting the manuscript. BF and AV: critical revision of the manuscript. AC, BF, AV, PR, and LP-D: final approval of the version to be published. All authors contributed to the article and approved the submitted version.

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# Objectives and hypotheses

## Open questions

As presented in the introduction, our understanding of various aspects of dreaming has improved over time, but dreaming remains a complex and enigmatic phenomenon, with many aspects that are still poorly understood. Despite decades of research, fundamental questions about the nature and function of dreams remain unanswered. For example, why do we dream, and what purpose do dreams serve, if any? In a related fashion, the mechanisms that govern dream content generation and the factors that influence dream recall remain incompletely understood. Currently, the impossibility to access the dream experience and the necessity to rely on dream reports is one of the major obstacles to dream research. Because of this obstacle, researchers cannot image a dreaming brain and a brain sleeping without dreaming and therefore identify the cerebral correlates of dreaming (Ruby, 2020). The dream research community has thus to find tricks and be witty to find alternative ways to address the cognitive and cerebral correlates of dreaming.

The goal of the current thesis is to address several of these questions, with parallel investigations using rare methodologies in the field of dream research. We first investigated the cognitive (Study 1a) and cerebral profiles (Study 1b, 1c) of HR and LR in a cognitively demanding task involving short-term memory under attentional distraction. Magnetoencephalography (MEG) recordings were acquired during the task to identify brain regions contributing to behavioural differences between LR and HR. We also investigated the possible influence of epilepsy (characterised by transient abnormal focal brain activity) on dream content and frequency. As the relationship between epilepsy and dreaming has been scarcely studied (de la Chapelle et al., 2021), the study 2a aimed at evaluating systematically dream habits (DRF and epilepsy-related content) in a large epileptic population. In the study 2b, we investigated how ictal and interictal activity contributed to dream recall and dream content thanks to intracerebral recordings conducted in drug-resistant epilepsy patients. Finally, we tested the emotion regulation hypothesis of dreaming by investigating how dreams evolved during the mourning process and by testing the possible coevolution of dreams and the mourning process in the first year after the death of a relative (Study 3). In this prospective study, we evaluated the emotional content of dreams in recently bereaved individuals who kept a dream diary for one year.

## Study 1: Role of Memory and Attention on Dream Recall Frequency

Among factors involved in DRF, the roles of cognitive abilities such as attention and memory are unclear and require further investigation. Understanding how attention and memory abilities influence DRF can provide valuable insight into the processes leading to dream formation and/or dream recall, as detailed in the section *Cognitive abilities*. More specifically, according to the arousal-retrieval model of dream recall, the dream memory stored in short-term memory during sleep should be transferred to long-term memory when awakening. Therefore, having a large STM store should lead to a recall of more dream details, leading to a more likely recall of the dream and a higher DRF. However, the current literature provides mixed results for this hypothesis. Regarding attention, several studies point toward increased bottom-up and top-down attention processes in HR compared to LR at the neurophysiological level (Eichenlaub, Bertrand, et al., 2014; Ruby et al., 2013, 2022) but failed to evidence any corresponding behavioural difference (Ruby et al., 2022). The authors therefore proposed that HR had a different attentional profile, where their elevated distractibility was compensated by their increased top-down processes toward the ongoing task, leading to normal performance. Under this hypothesis, behavioural differences between LR and HR should be observed if a challenging task, recruiting all attentional resources.

In the study 1a, we used a paradigm called MEMAT to compare the short-term auditory memory and attentional abilities of LR and HR (Blain, Talamini, et al., 2022). This paradigm consists in an auditory memory task where two melodies have to be compared (DMST, delayed-match-to-sample task), with additional auditory to-be-ignored stimuli. The use of an easy and a difficult memory task, combined with easy- or hard-to-ignore distractors, allows to test how these two variables individually and in combination affect performance. As HR have increased components associated with bottom-up and top-down attentional processes (Ruby et al., 2022), we supposed that HR would have better performance than LR in this task. Moreover, as the MEMAT paradigm is especially challenging for everyone except musicians (Blain, Talamini, et al., 2022), we expected the attentional balance of the HR to crumble under hard-to-ignore distractors compared to LR. Because of the unconvincing link identified so far between short-term memory abilities during wake and DRF, we did not expect the memory difficulty to show a differential effect in the two groups.

As the study 1a was conducted with concurrent magnetoencephalography (MEG) recordings, we investigated the neural correlates of the behavioural data of the study 1a in the studies 1b (across all subjects) and 1c (in LR and HR separately). These two studies use highly similar methodologies and are therefore both presented in this thesis, although only the study 1c relates to dreaming. As MEG has a high signal-to-noise ratio and shows very good temporal and good spatial resolution, these studies enable the investigation of the cerebral correlates of MEMAT with unprecedented detail and precision. This is even more important that memory differences between LR and HR have never been investigated with any neurophysiology

method, despite numerous behavioural studies. Regarding attention, several EEG studies showed a higher brain reactivity in HR during sleep and wake, but behavioural differences between LR and HR never accompanied these studies. Moreover, as MEG signals are less distorted by the skull and scalp than EEG, source reconstruction of the signal is more reliable and allows investigating more localised brain regions.

## Study 2: Dreaming in Epilepsy

In order to better understand dream recall and content, the investigation of dreaming in epileptic patients is promising, as described in the section *Dreaming in epilepsy* (de la Chapelle et al., 2021). This approach is all the more important that few dream studies were conducted in this population (de la Chapelle et al., 2021).

In a first study (2a), we investigated the role of several parameters directly (symptoms, seizure frequency, location for focal epilepsies, epilepsy duration, treatments) and indirectly related to epilepsy (psychological comorbidities, sleep quality) on DRF in a large population of epileptic patients (N=83, with ongoing inclusions). This project, which is still ongoing, allowed us to test the influence of a large array of factors (including epilepsy-related) on the dream recall frequency in this population.

In a second study (2b), the sleep of 24 drug-resistant epileptic patients was assessed with combined SEEG (StereoElectroEncephaloGraphy, which consists in intra-cerebral recordings performed in the context of pre-surgical evaluation; see section Methods below) and PSG (PolySomnoGraphy) to better understand the relationship between DRF/dream content, recorded epileptic activity, and sleep fragmentation. Thanks to this study, for which inclusions were recently completed, we started to test for the role of specific sleep parameters and to assess the influence on both DRF and dream content of sleep-related focal epileptic activity in all explored brain regions including deep areas.

Based on the existing literature, these two studies will allow us to test for several hypotheses. The first study will first allow to assess the general characteristics of patients with epilepsy regarding dreaming, especially parameters that were identified in our review (de la Chapelle et al., 2021). It will also allow us to assess the relevance of asking for dreams when clinically evaluating patients with epilepsy, considering dreaming as a marker of sleep-related cognitive functioning prone to provide information on possible focal brain dysfunction. In the second study, as epileptic seizures temporarily disrupt brain activity, sometimes leading to blanking/absence, dream memories stored during sleep may also be cleared after a seizure, preventing dream recall, especially in regions associated with dream recall (MPFC, TPJ; Solms, 1997; Eichenlaub, Nicolas, et al., 2014; Vallat et al., 2018, 2020, 2022) or short-term memory (e.g., DLPFC; Barbey et al., 2013). This would induce decreased dream recall or at

least less complex and shorter dreams in nights with seizures. However, as epilepsy increases sleep fragmentation (Peter-Derex et al., 2020), the increased intra-sleep wakefulness compared to healthy people may increase dream recall, as is the case in non-epileptic populations (Schredl et al., 2003; Eichenlaub, Bertrand, et al., 2014; Vallat, Lajnef, et al., 2017; van Wyk et al., 2019). While non-contradicting, these two effects may coexist and lead to variable profiles of DRF in epileptic patients. Finally, ictal and interictal activity (especially in the above-mentioned regions) might be capable not only of disrupting the function of the regions involved but also of triggering symptoms linked to the function of these regions, and might thus lead to epilepsy-related dream content, which we will be able to observe in the retrospective (2a) and in the prospective (2b) study.

### Study 3: Dreaming during the mourning process

As presented in several sections of the introduction, there is ample evidence that dreaming reflects waking-life events, especially those associated with emotions and/or concerns. On the other hand, sleep is known to play a role in emotion regulation. These two observations are especially consistent with the growing body of evidence supporting a role of dreaming in emotion regulation processes. To further test this hypothesis, we prospectively investigated dream recall and content in a common and very negative moment of life (which can even become pathological), i.e. the first 15 months of mourning after the death of a close relative. Several previous studies conducted retrospective investigations of dreaming after the death of a relative and proposed associations between grief and some aspects of dream content during mourning. However, serious limitations (forgetting and transformation of dream memories with time and emotional regulation processes, lack of emotional regulation indicators when the dreams were recalled) limit the reliability of their results, which have been hardly replicated. To further test the link between dreaming and emotional regulation during mourning a prospective approach was necessary.

The study 3 consisted in a 1-year-long prospective study of dreaming in recently bereaved individuals. The study involved keeping a dream diary for the whole year of the study, where dreams related to the death (i.e., dreams of the deceased, DD) were the most important to report in addition to unrelated, positive dreams (i.e., flying dreams, FD), while other dreams (OD) were also requested but in a facultative way. Participants had to rate the positive and negative emotional intensity of each reported dream on a 0 to 10 scale. OD and FD were collected as control conditions since they were not supposed to co-evolve with the mourning process. Grief intensity was also measured at several time points to estimate the evolution of the mourning process. As grief is a complex association of emotions, in addition to the self-ratings of dream emotions by the participants, we also ran external ratings of dream

content regarding additional parameters involved in the mourning process. Our study therefore provides a unique opportunity to evaluate within subjects in time and between subjects the associations between several aspects of dreaming and mourning-related grief. Our main objectives were 1) to evaluate the factors affecting the mourning process and its evolution, 2) to compare the content and recall frequency of DD and FD/OD, notably their emotional aspect, and 3) to test a correlation between aspects of dream reports and the evolution of the mourning process.

## II. Methods

## Magnetoencephalography (MEG)

Magnetoencephalography (MEG) is a non-invasive functional neuroimaging technique which consists in detecting the magnetic fields generated by electrical currents in the brain to map the neuronal activity. The first MEG recording of brain activity dates back to 1968 (D. Cohen, 1968), with low-sensitivity copper coils to detect the magnetic currents and very noisy results. Better results were then obtained with magnetometers paired with a SQUID (superconducting quantum interference device; D. Cohen, 1972). Nowadays, arrays of hundreds of SQUIDs are used to record MEG data; for instance, the data presented in this thesis contains 275 recorded channels. While the data obtained from MEG recordings has an excellent signal-to-noise ratio, the machine is cumbersome and necessitates constant and expensive cooling with liquid hydrogen (temperature around  $4\text{K} = -269^\circ\text{C}$ ). The development of different magnetometers (SERF magnetometer, Sander et al., 2012; Boto et al., 2018; OPM-MEG, Brookes et al., 2022) is promising regarding current immobility, costs, and technological limitations.

### Electric and magnetic brain signals

Neuronal activity transmission is based on the release of ions, which induces an electric current accompanied by a perpendicular magnetic field (Figure 11). Because of the way ions are released during the transmission of an action potential along the axon axis, the generated magnetic field cancels out and cannot be measured. On the contrary, synaptic transmission generates a measurable but weak magnetic field (Mason et al., 2013). As for electric currents in EEG, this magnetic field is cancelled out by other synapses in different orientations, which is why only groups of neurons with the same orientation (therefore reinforcing their magnetic field) can be detected. Most of brain MEG recordings therefore measure the activity of the parallel pyramidal cells of the cortex.

Despite this, the order of magnitude of these signals is 10 to 100 femtoTesla ( $\text{fT} = 10^{-15}\text{ T}$ ), more than 1 billion times smaller than the Earth magnetic field ( $10^{-5}\text{ T}$ ) which would in normal circumstances completely hide the brain magnetic activity. Because of this, MEG recordings must be conducted in a magnetically-shielded room.

Contrary to EEG signals (i.e. electric), magnetic fields are not distorted when passing through the head, but also decay faster. This means that MEG recordings have an excellent temporal resolution and a better spatial resolution than EEG, but only if the relative position of the sensors and of the brain is stable. As the MEG system is massive and cannot be moved, this implies that the head is maintained as stable as possible. Custom helmets or foam padding are therefore generally used to fix the participant's head, or head coils can be placed on the participant's head to monitor its position and adjust the recordings if necessary.

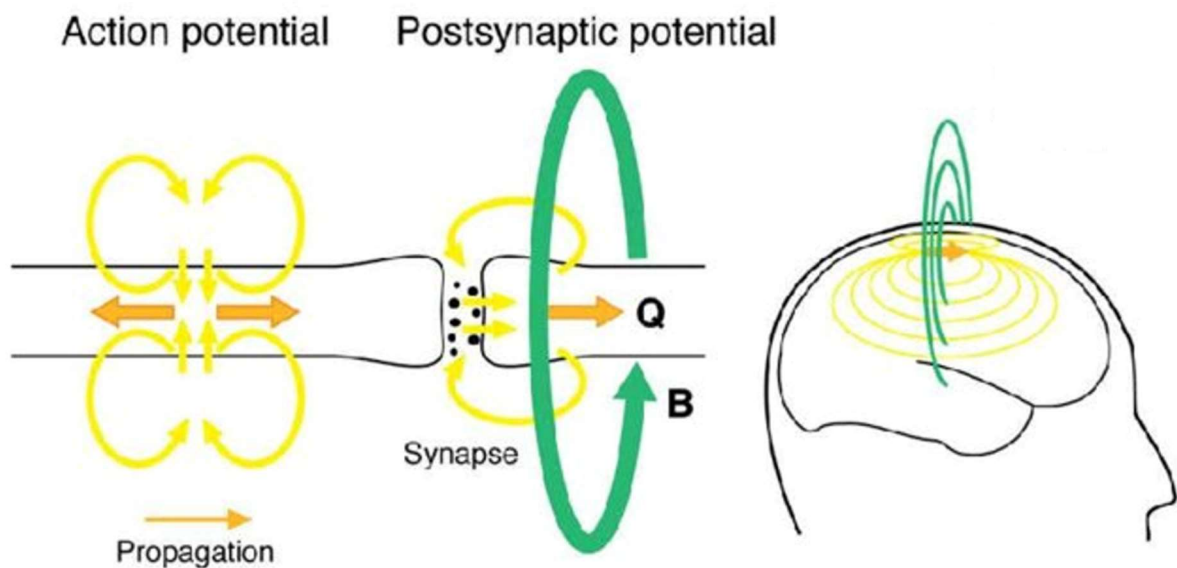


Figure 11 – Magnetic and electric activity in the brain. Neuronal activity induces an ionic current (orange arrows,  $Q$ ) accompanied by electric current flow (yellow arrows and circles) and a perpendicular magnetic activity (green arrow and circle,  $B$ ) (adapted from Mason et al. 2013).

## Sensor signals and source reconstruction

As magnetic fields decay at a faster rate than electric currents for a same distance, the large majority of the detected signal originates from superficial cortical areas. However, more and more source reconstruction algorithms allow to bypass this limit by inferring the origins of the measured signals in the brain (e.g., Attal & Schwartz, 2013; Dumas et al., 2013).

Source reconstruction is however not an easy problem. First, we must understand and model how neural activity within the brain will translate to the activity at the sensor level, a problem also known as the *forward problem*. This information (electromagnetic conductivity through the skull, organisation of the brain materials...) is necessary to propose solutions to the *inverse problem*, which consists in estimating the neural sources of brain activity within the brain's volume based on the measurements of magnetic fields recorded at the sensor level. Solving the inverse problem is complex and ill-posed because multiple combinations of source configurations can produce the same MEG sensor measurements. To address this challenge, various methods and algorithms have been developed in MEG source reconstruction, either by considering each brain region as a single dipole (“equivalent dipole” modelling) or as a continuity of dipoles (“distributed” modelling), the latter being more computationally intensive. As this factor is not as limiting nowadays, distributed modelling methods are more



widely used, such as minimum-norm estimation and beamforming methods. Minimum-norm estimation is a distributed modelling method that estimates the spatial distribution of neural sources across the entire brain volume, treating it as a continuous source space. It seeks to find a solution that minimizes the overall source strength, distributing it smoothly throughout the brain. In contrast, beamforming is a technique that only considers the signal from close regions in a grid-like organisation and suppresses interferences from other areas, which can be more adapted due to the decaying nature of the magnetic fields.

The sensor and the reconstructed source signals can afterwards be analysed with similar methods as EEG signals. For instance, Event-Related Fields (ERF; the equivalent of Event-Related Potentials for magnetic rather than electric signals) consist in averaging several signals time-locked to the same event. This methodology allows to reduce the signal-to-noise ratio, which is already low in the case of MEG. MEG is also perfectly adequate for functional connectivity analyses, thanks to its very good temporal and spatial precisions and source reconstruction methods for deeper brain structures.

## MEG in sleep and dreams studies

The respective constraints of sleep studies (electrodes for PSG, recordings in an unusual lab environment, relative immobility...) and of MEG studies (costs, availability, complete immobility, discomfort...) combine and limit severely the use of MEG for sleep and dreams studies. Nevertheless, the benefits of MEG measurements compared to traditional PSG recordings have led to many MEG-based sleep studies although with smaller sample sizes (e.g., Jourde et al., 2023).

Dream research employing MEG methods is even scarcer, except for the study 1c presented in this thesis. For instance, no MEG study was conducted regarding the difference between dreamless sleep and sleep leading to a dream recall to confirm the absence of EEG correlates of dreaming (Ruby, 2020).

# Intracerebral encephalography (iEEG)

## Electroencephalography

Electroencephalography (EEG) is a non-invasive neuroimaging technique that measures the electrical activity of the brain by recording the fluctuations in voltage at the scalp's surface. Multiple electrodes (sensors) are generally placed on the scalp, in the international standardised 10-20 system to improve reproducibility of the findings.

One of the primary advantages of EEG measurements is their high temporal resolution, which allows capturing rapid changes in brain activity with millisecond precision. However, EEG has limitations in terms of spatial resolution, as the signals are influenced by the intervening skull and scalp tissues, making it less accurate for precisely localising deep brain sources. To address this limitation, EEG can be combined with other neuroimaging techniques like fMRI and MEG to provide complementary information about brain activity. Alternatively, in rare conditions, electrode placement can be invasive, such as with intracranial recordings in humans.

## Intracranial recordings (iEEG)

Intracranial electroencephalography (iEEG) is a specialised neuroimaging technique that involves the placement of electrodes directly within (depth electrodes, SEEG, stereoelectroencephalography) or on the surface of the brain (ECoG, electrocorticography) to record neural electric activity. As this implies a surgical procedure, with its inherent risks, iEEG is only used in patient with drug resistant epilepsy, with the purpose of localising the seizure onset zone whose resection could enable epilepsy to be cured. iEEG signal is usually recorded continuously in hospital during 1 to 2 weeks, in order to capture enough seizures to study and understand the epileptic network. During the hospital stay of such patients, iEEG recordings can be also used for research purpose and research protocols can be conducted with the approval of the patient, of the physician in charge, and of an ethics committee. To note, such protocols allow to study epilepsy but also normal brain activity, as some electrodes turn out to be located outside the epileptic network.

In addition to the very good temporal resolution of EEG, iEEG provides excellent spatial resolution along the electrodes array, as they are as close as possible to the source. Moreover, SEEG presents the unique advantage of recording the brain activity in deep brain regions such as the medial part of the hemisphere and the hippocampus. The signal to noise ratio is much better, allowing for the detection of low-voltage, high-frequency components (such as ripples) that are partially blocked by the skull and therefore not detected by scalp EEG. These advantages are however limited to the implantation site (sampling bias, as in

average 10 to 15 electrodes with 10-15 channels are implanted per patient). In addition, contrary to typical EEG, there is no standardised placement of iEEG electrodes as the implantation scheme is adapted to the medical requirements of each patient. This bias can be overcome by the analysis of a high number of patients, using dedicated softwares such as BrainTV (Lachaux et al., 2007) or HiBoP (2020/2023) which were developed for this purpose.

## iEEG in sleep and dream research

While iEEG provides formidable advantages over traditional EEG, several disadvantages must be considered when conducting any research. First, the use of iEEG only in clinical populations implies that findings may only apply to these clinical populations, and extending the findings to healthy populations can be delicate. The patients are also in a hospital setting for days to weeks, and are monitored during their whole stay, which affects their routine as well as their mental and physical state. Furthermore, the intrusive electrodes are generally protected by a cumbersome headcap which can affect their behaviours.

Despite these limits, iEEG has been widely used to study sleep in drug-resistant epileptic patients, as this method presents several advantages over classical EEG in this specific population which needs the intracranial measures anyway for clinical reasons. The findings of these studies, which show a bidirectional relation between epilepsy and sleep, are detailed in our earlier review (see section *Dreaming in epilepsy*).

To our knowledge, only one study investigated dreaming with intracranial recordings. Thanks to SEEG measurements in deep brain structures, Fell et al. (2006) proposed a role for the rhino-hippocampal connectivity in dream recall, although their results were obtained in a small sample (6 recallers vs 6 non-recallers) of epileptic patients, and dream recall was assessed with a single awakening (instead of 2 weeks as suggested by Schredl & Fulda, 2005). Furthermore, their analysis did not consider other factors influencing dream recall such as the medical treatment (Nicolas & Ruby, 2020) or the epileptic activity which can influence the sleep architecture (Peter-Derex et al., 2020). This article illustrates the difficulties of conducting a rigorous analysis using iEEG data and of generalising these results to a healthy population. The advantages of iEEG however make it a powerful tool which deserves further consideration in this field, especially its ability to test anatomical hypotheses.

### III. Experimental results

# Study 1 – Dreaming, Attention, and Memory

Study 1a -  
*Dream recall frequency is associated with attention rather than with  
working memory abilities*

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# DREAM RECALL FREQUENCY IS ASSOCIATED WITH ATTENTION RATHER THAN WITH WORKING MEMORY ABILITIES

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## **Abstract**

Several factors influencing dream recall frequency (DRF) have been identified, but some remain poorly understood. One way to study DRF is to compare cognitive processes in low and high dream recallers (LR and HR). According to the arousal-retrieval model, long-term memory encoding of a dream requires wakefulness while its multisensory short-term memory is still alive. Previous studies showed contradictory results concerning short-term memory differences between LR and HR. It has also been found that extreme dream recall frequencies are associated with different electrophysiological traits related to attentional processes. However, to date, there is no evidence for attentional differences between LR and HR at the behavioural level. To further investigate attention and working memory in HR and LR, we used a newly-developed challenging paradigm, called MEMAT: it allows to study selective attention and working memory interaction, during memory encoding of non-verbal auditory stimuli. We manipulated the difficulties of the distractor to ignore and of the memory task. The performance of the two groups were not differentially impacted by working memory load. However, HR were slower and less accurate in presence of hard, rather than easy, to-ignore distractor, while LR were much less impacted by the distractor difficulty. Therefore, we show behavioural evidence towards less resistance to hard-to-ignore distractors in HR. Using a challenging task, we show for the first time attentional differences between HR and LR at the behavioural level. The impact of auditory attention and working memory on dream recall is discussed.

### *Keywords*

Dreaming; Dream recall; Short-Term Memory; Non-verbal; Memory encoding; Attentional Filter; Audition

## **Introduction**

The experimental research on dream reports since the end of 19th century improved significantly our understanding of dreaming (for reviews and state of the art see Nir & Tononi, 2010; Ruby, 2011; Scarpelli et al, 2021; Schredl, 2018). Yet the definition of dreaming is currently still debated (Montangero, 2018; Pagel et al., 2001; Ruby, 2020; Solms, 2000; Windt et al., 2016) and several questions remain unanswered (e.g., why and how interest in dreams leads to a rapid increase in DRF). Most researchers consider dreaming as a subjective experience that occurs during sleep and that can be recalled and reported during wakefulness (e.g., Guénolé & Nicolas, 2010; Ruby, 2020; Windt et al., 2016). Dream recall frequency (DRF) varies within subject across time but also between subjects. In average, in a representative sample of the population, DRF is around 1 dream recall per week, with a large dispersion (Schredl & Reinhard, 2008). Some only remember a few dreams a year, while others recall dreams every morning with many details (Nielsen, 2012; Vallat et al. 2018). In order to better understand the origin of the within and between-subject differences in DRF, several studies awakened dreamers in different contexts and times of the night and/or compared persons with a high dream recall frequency (HR) to persons with a low dream recall frequency (LR), using various tasks and questionnaires (for a review, see Schredl, 2018). State and trait factors were identified (Schredl & Montasser, 1996) and the results of these studies yielded several models of dream recall (see Table 1) such as the state-shift hypothesis (Koukkou & Lehmann, 1983), the life-style hypothesis (Schonbar, 1965), the interference hypothesis (Cohen & Wolfe, 1973), the salience hypothesis (Cohen & MacNeilage, 1974), and the arousal-retrieval model (Koulack & Goodenough, 1976). According to this last model, recently updated and complexified (Schredl, 2018; Vallat, 2017), the encoding of a dream into long-term memory requires wakefulness while its multisensory short-term memory is still alive.



Reference	Hypothesis name	Hypothesis description
<b>Schonbar 1965</b>	Life-style hypothesis	<i>Dream recall frequency would be a consequence of lifestyle, which includes personality and motivations. The “inner-acceptant” lifestyle (efficient access to one’s inner world, and a sense of control over one’s life) would be associated with a higher DRF than the “inner-rejectant” lifestyle.</i>
<b>Cohen &amp; Wolfe 1973</b>	Interference hypothesis	<i>Distractions at awakening (thoughts, actions/movements, or stimuli) would increase the chances of dream recall failure.</i>
<b>Cohen &amp; MacNeilage 1974</b>	Saliency hypothesis	<i>Dreams with a more salient content would be easier to remember.</i>
<b>Koulack &amp; Goodenough 1976</b>	Arousal-retrieval model	<i>The transfer from short-term memory to long-term memory would require wakefulness. In other words, for dreams to be recalled, an awakening would have to happen when the dream is still encoded into short-term memory.</i>
<b>Koukkou &amp; Lehmann 1983</b>	Functional state-shift hypothesis	<i>Dream recall would be more likely if a dream happens during a functional state similar to wakefulness</i>

*Table 1. Hypotheses explaining dream recall success/failure. These hypotheses are not incompatible between each other; for example, Koulack & Goodenough (1976) agreed with the interference hypothesis.*

This hypothesis fits with results showing that 1) repeatedly waking up participants increases their DRF, 2) HR demonstrate more intra-sleep wakefulness than LR (Eichenlaub, Bertrand, et al., 2014; Koulack & Goodenough, 1976; Schredl et al., 2003; Vallat et al., 2017, 2020). Interestingly, an EEG study from our lab linked intra-sleep wakefulness to brain reactivity and more specifically to electrophysiological markers of attention orientation (Eichenlaub, Nicolas, et al., 2014). The P3a, an Event-Related Potential following novel stimuli (salient, rare, and randomly presented) and considered as a marker of involuntary attention orientation (Polich, 2007) was found larger in HR as compared to LR, during both wakefulness and sleep (Eichenlaub et al., 2014). It was also confirmed that the larger the brain response to sensory stimuli during sleep, the higher the probability that the stimulation leads to an awakening (Bastuji et al., 2008; Vallat et al., 2017). These results, obtained during passive listening, suggest that HR present a stronger attentional reactivity to salient and unexpected events. Such potential attentional differences between HR and LR could explain, at least partly, their difference in DRF. Increased bottom-up processes in HR could increase intra-sleep wakefulness which is known to facilitate dream recall.

To further investigate attentional abilities in LR and HR, these two groups were tested on a task specifically designed to assess bottom-up and top-down processes of attention: the Competitive Attention Task (CAT, Bidet-Caulet et al., 2015). During the CAT, participants are asked to detect as quickly and accurately as possible visually-cued monaural target sounds while in some trials an unexpected binaural task-irrelevant distracting sound pops up before the target sound. In this context, HR showed a larger Contingent Negative Variation (CNV) before the target and a greater P3a (also called early-P3) in response to distractors than LR, pointing towards enhanced recruitment of both top-down and bottom-up attention processes (Ruby et al., 2021). However, these electrophysiological differences between groups were not associated with significant differences in behavioral performance. These results suggest that HR might compensate the enhanced bottom-up responses to distracting sounds by increasing the recruitment of top-down processes. In this way, HR could preserve the balance between top-down and bottom-up attention, probably at a higher energy/cognitive cost (increased brain response amplitude). If this interpretation is correct, HR should present difficulties in maintaining the attentional balance in a more challenging context, where differences in attentional performance might thus arise between HR and LR. One way to test this hypothesis is to use a highly demanding task, which may prevent HR from compensating and result in larger behavioural differences between LR and HR.

In the arousal-retrieval model, short-term memory plays a central role in dream recall (i.e., the model states that if an awakening arises when a dream is in short-term memory, and if the awakening process does not erase short-term memory content, then, and only then, the dream memory can be transferred into long-term memory before its content vanishes). According to this model, one could consider the possibility that better short-term and/or long-term memory abilities could contribute to inter-individual dream recall differences. It is the reason why several studies investigated long and short-term memory in HR and LR during wakefulness (Belicki et al., 1978; Blagrove & Akehurst, 2000; Bloxham, 2018; Butler & Watson, 1985; Cohen, 1971; Cory et al., 1975; Eichenlaub, Nicolas, et al., 2014; Martinetti, 1983, 1985; Nakagawa et al., 2016; Schredl et al., 1995, 1997, 2009; Solms, 1997; Waterman, 1991). Results from studies focusing on long-term memory exclude a clear and large difference between HR and LR (e.g., Blagrove and Pace-Schott, 2010; Ruby 2011; Eichenlaub, Nicolas, et al., 2014). Regarding short-term and working memory, some studies found better performance in HR but results lacked consistency and were thus inconclusive (see Table 2). In studies focusing on narrative memory (participants read or listen to a text and then

immediately recall its content or answer questions about it), whatever the sensory modality (visual or auditory), no correlation was observed between DRF and memory performance (Cohen 1971; Bloxham 2018; Blagrove & Akehurst 2000). For more traditional working/short-term memory tests such as the digit span, HR showed repeatedly significantly better performance than LR when numbers were presented orally (Butler & Watson 1985; Martinetti 1983, 1985), but not when numbers were presented visually (corr. between DS & DRF,  $r=0.02$ , Nakagawa et al. 2016). Note that for a visuo-spatial version of the digit span, a significant correlation between performance and DRF was observed but with a very low correlation coefficient (Nakagawa et al. 2016). Investigations of visuo-spatial short-term memory (complex pictures or route recall) resulted in significantly better performance in HR than in LR in some studies (Solms 1997; Schredl et al. 1995) but this finding was not replicated in other studies (Schredl et al. 1997; Schredl 2009). Regarding visual short-term memory (immediate recall of presented numbers, items, text, pictures, or a short movie), most studies revealed no significant differences in performance between HR and LR (Cohen 1971; Cory et al. 1975; Belicki et al. 1978; Waterman 1991; Schredl et al. 1995, 1997; Solms 1997; Schredl 2009; Bloxham 2018; Nakagawa et al. 2016), except for 4 of them (Cory et al. 1975; Schredl 1995; Solms 1997; Nakagawa et al. 2016). Regarding auditory short-term memory, in studies with verbal stimuli, HR proved better than LR at the digit span except for patients (Butler & Watson 1985; Martinetti 1983, 1985; Solms 1997), but not at story recall (Cohen 1971; Blagrove & Akehurst 2000). Note that in nearly all the studies presented here, authors expected/hypothesized that HR would show better memory performance than LR. Remarkably, most studies investigating the memory of HR and LR focused on the visual modality, even though the auditory experience is as intense and frequent as the visual experience in dreams (e.g., Plailly et al., 2019). To our knowledge, no studies compared non-verbal auditory short-term/working memory in LR and HR so far.

Based on the literature reviewed above, participants with high vs. low DRF might be expected to differ more on their attentional abilities than on their short-term memory abilities. The hypothesized more fragile attentional balance between top-down and bottom-up processes in HR may be expected to fail in challenging tasks and lead to impaired performance under high cognitive demand and distraction. Here, we tested directly this hypothesis with a paradigm recently developed in our lab (Blain et al., 2021). This auditory task, called MEMAT (for MEMory and ATtention), has been designed to simultaneously assess short-term memory, attentional abilities, and their possible interactions. Participants have to encode and maintain in short-term memory a four-tone melody presented in one ear

while a distracting melody is presented in the other ear (2 levels of memory load and 2 levels of distractions are presented). Given the available results on working memory and DRF, we did not expect the groups to be differentially affected by the memory load in MEMAT. By contrast, we expected the group to differ in their ability to resist interference during the working memory task, i.e., we expected that HR would be more distracted/impaired than LR by the distracting sounds presented during the working memory task, especially when the distraction increases.

Reference	N	Type of short-term memory	Type of test	Results
Butler & Watson 1985	12	Auditory verbal	Digit Span	<b>HR &gt; LR</b> (corr. DS & DRF, $r=0.69$ )
Martinetti 1983	30	Auditory verbal	Digit Span	(13±3) <b>HR &gt; LR</b> (9±2)
Martinetti 1985	70	Auditory verbal	Digit Span	(14±2) <b>HR &gt; LR</b> (11±2)
Nakagawa et al. 2016	779	Visual verbal	Digit Span	=
		Visuo-spatial	Visuo-spatial Span	<b>HR &gt; LR</b> (corr. DS & DRF, $r=0.07$ )
Solms 1997*	361	Auditory verbal	Digit Span	=
		Visuo-spatial	Pictures recall	(14/36) <b>HR &gt; LR</b> (11/36)
Cohen 1971	?	Auditory verbal	Story recall	=
	20	Visual	Pictures recall	=
Belicki et al. 1978	44	Visual	Pictures recall	=
		? verbal	Words recall	=
Cory et al. 1975	100	Visual implicit	Pictures recall	(12/50) <b>HR &gt; LR</b> (10/50)
		Visual explicit	Pictures recall	(24/40) <b>HR &gt; LR</b> (21/40)
Schredl et al. 1995	50	Visual	Pictures recall	=
		Visuo-spatial	Route recall	<b>HR &gt; LR</b> (corr. test & DRF, $r=0.36$ )
		Visual	Movie recall	=
Schredl et al. 1997	51	Visual	Pictures recall	=
		Visuo-spatial	Route recall	=
Schredl 2009	444	Visual	Pictures recall	=
		Visuo-spatial	Route recall	=
		Visual	Movie recall	=
Waterman 1991	93+80	Visual	Movie recall	=
Bloxham 2018	57	Visual verbal	Story recall	=
Blagrove & Akehurst 2000	93	Auditory verbal	Story recall	=

*Table 2. Review of the literature about short-term and working memory in high and low dream recallers (HR and LR respectively). HR > LR, HR showed significantly better performance than LR (each group scores are between brackets), or a significant correlation between DRF and memory score was observed. corr., stands for “correlation between”. DRF, dream recall frequency. DS, digit span. =, no significant link between DRF and memory performance was observed. \* in this study the population tested is mainly patients with cerebral lesions.*

## **Methods**

The experimental protocol is adapted from the first MEMAT study (Blain et al., 2021). The main difference is that the current data are based on a much larger number of trials. The present behavioural data were indeed collected during MEG recordings (which will be described in a separate paper), which required a larger number of trials than the original behavioural-only study.

### *Participants*

Twenty-two non-musician participants (20 right-handed, 10 men and 12 women, aged 20-33 years) took part in the experiment. Participants were considered as non-musicians when they practiced less than 1 year of instrument or singing outside compulsory educative programs. Among them, 11 were low-frequency dream recallers (LR, less than 2 dreams recalled per month at awakening) and 11 high-frequency dream recallers (HR, more than 5 dreams recalled per week at awakening). These frequency ranges for LR and HR have been previously used in several related studies (Eichenlaub, Bertrand, et al., 2014; Eichenlaub, Nicolas, et al., 2014; Ruby et al., 2013; Vallat et al., 2017, 2020). The two groups were matched in terms of school education, age, laterality, and gender. Demographics are presented in Table 3.

All participants were free from neurological or psychiatric disorder and had normal hearing and normal vision. They gave their written informed consent to participate and received a small monetary compensation for their participation. Experimental procedures were approved by the appropriate local ethics committee.

Variable	LR		HR		Group comparison LR vs HR	
	mean	SD	mean	SD	BF <sub>10</sub>	error %
Sex	men: 6 women: 5		men: 5 women: 6		0.5	
Laterality	left-handed: 1 right-handed: 10		left-handed: 1 right-handed: 10		0.7	
Years of music education	0.4	0.5	0.1	0.3	0.8	4e-3
Years of school education	15.9	1.9	15.2	2.2	0.5	6e-3
Age	23.5	3.6	24.0	3.0	0.4	5e-3
Hours of sleep (per night)	7.5	1.1	8.0	0.7	0.6	9e-3
Dream recall frequency (per week)	0.12	0.2	5.8	0.9	<b>1.8e+11</b>	1.9e-15
PSQI	6.0	3.1	5.7	3.5	0.4	5e-3
STAI: state	31.9	10.3	34.2	9.8	0.4	5e-3
STAI: trait	35.7	9.9	42.3	10.3	0.9	4e-3
BFI: openness	3.7	0.6	3.8	0.8	0.4	5e-3
BFI: conscientiousness	3.8	0.7	3.4	0.7	0.6	8e-3
BFI: extraversion	3.4	0.8	3.2	0.7	0.5	5e-3
BFI: agreeableness	4.0	0.6	3.7	0.5	0.8	6e-3
BFI: neuroticism	2.2	0.8	2.9	0.7	1.7	1e-3
GAUT	24.6	12.7	28.1	11.1	0.4	5e-3

**Table 3. Demographic and questionnaire information for the two groups of participants.** Mean and standard deviation (SD) in each group. Comparisons between groups were carried out using Bayesian statistics (contingency table for gender and laterality, non-paired t-test otherwise), we report Bayesian Factors (BF<sub>10</sub>) for each comparison. **LR**: Low Recaller, **HR**: High Recaller. **PSQI**: Pittsburgh Sleep Quality Index; it assesses sleep quality with scores ranging from 0 to 21 (lower scores denote better sleep quality). **STAI**: State-Trait Anxiety Inventory; scores range between 20 and 80. **BFI**: Big Five Inventory; scores range between 0 and 4. **GAUT**: Guilford Alternative Use Test; the fluency score reported here refers to the mean number of uses proposed for a given object.

### Procedure

First, participants have to fill in neuropsychological and demographical tests and questionnaires. Then, they are installed in the MEG in a seated position, in a sound-attenuated, magnetically shielded recording room, at 50-cm distance from the screen. All stimuli are delivered using Presentation software (Neurobehavioural Systems, Albany, CA, USA). Sounds are delivered through air-conducting plastic ear tubes. They undergo a volume calibration so that the auditory stimuli are easy to hear (hearing threshold +60 dB). They then perform the main MEMAT task. They are instructed to answer as accurately as possible and to keep fixating the cross during the recordings. Prior to the actual task, they perform two

short training blocks (12 trials) for each memory load. Training melodies (S1, DIS, and S2) are specific to the training sessions. Finally, they perform the ten experimental blocks (48 trials each), 5 under each memory load (low or high). They are aware in advance of the difficulty of the memory task but not of the difficulty of the distractors, which is randomized within each block. The order of the blocks is randomized between participants. Trials last 9400 to 9800ms, leading to eight-minute-long blocks.

### *Neuropsychological tests and questionnaires*

All neuropsychological tests and questionnaires were performed before the main task. Participants were asked to fill in the State Trait Inventory Anxiety questionnaire about their anxiety state and trait (STAI; Spielberger, 1983), the Big Five Inventory questionnaire for personality traits (BFI; John et al., 1991), and the Pittsburgh questionnaire for sleep quality (PSQI; Buysse et al., 1988). The STAI is an assessment of anxiety as a situation-specific emotional state (STAI state: feelings of apprehension, tension, nervousness and worry that the subject experiences at a specific time) and anxiety as a personality trait (STAI trait: feelings of apprehension, tension, nervousness and worry that the subject usually experiences). The BFI designates a descriptive model of personality in five central traits. They also had to perform a creativity test in which they had to invent possible alternative use for a chair, a teacup, or a pen in a free monologous way during 2 minutes for each object; it measures a level of divergent thinking, exploring multiple answers using creativity (Guilford Alternative Use Task, GAUT) (Bonk, 1967). Neuropsychological data are summarized in Table 3.

### *Stimuli*

240 four-sound-long melodies were created thanks to combinations of eight-harmonic synthetic sounds from the C major scale, spanning four octaves between 65 and 1046Hz. The maximal interval between any two sounds of a melody is 7 semi-tones. Sounds are 250-ms long and the interval between sounds (offset to onset) is 250 milliseconds.

In each melody, there are no consecutive identical sounds. Every melody contains at least an ascending and a descending interval.

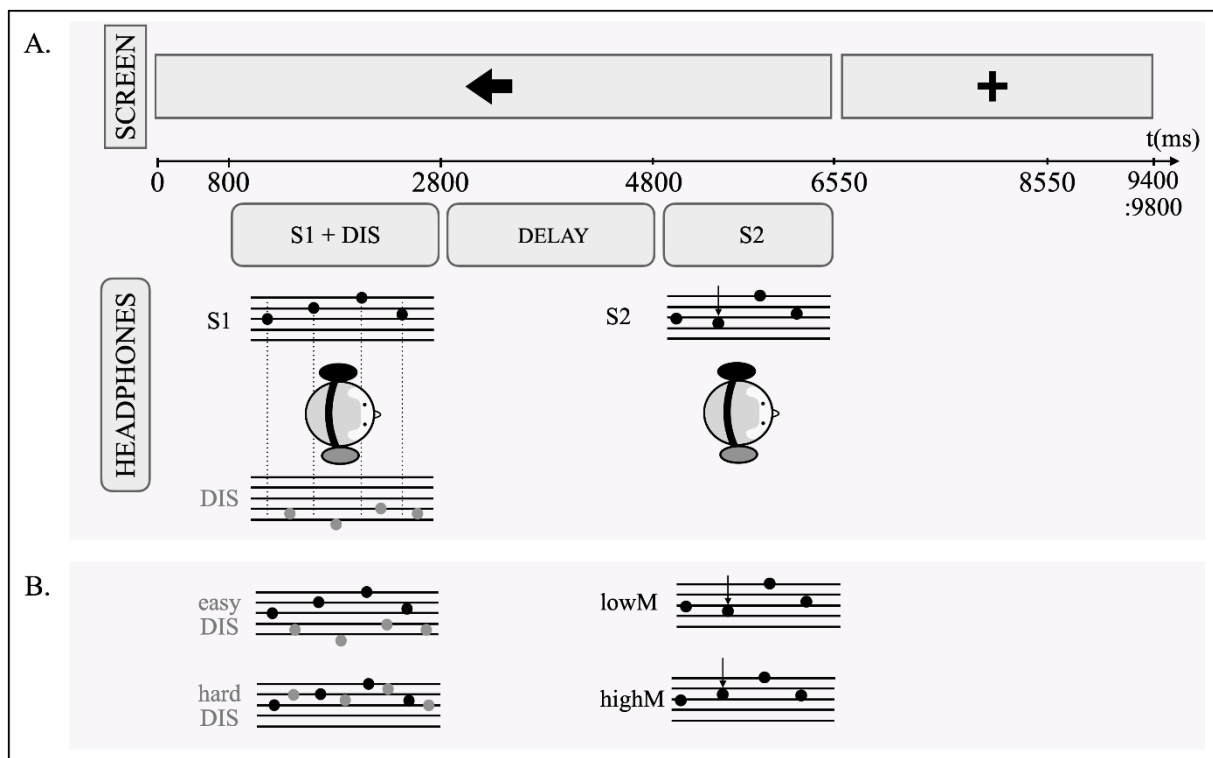
### *The MEMAT Paradigm*

#### Attention manipulation

The melody of interest (S1) and the distracting melody (DIS) melodies are played one in each ear. The tones of the two melodies are interleaved, thus not played simultaneously. S1 is played in the ear indicated by an arrow on the screen, and DIS is played in the other ear, each

tone one after the other. The first sound to be played is the first tone of S1, and the last tone to be played is the last tone of DIS (See Figure 1-A.).

The DIS melodies can be rather easy (easy DIS) or hard (hard DIS) to filter (see Figure 1-B.). An easy DIS melody is composed of sounds in a frequency range 6 to 7 semi-tones higher (or lower) than the corresponding S1 melody frequency range. A hard DIS melody frequency range is the same than the corresponding S1 melody frequency range. DIS melodies are constructed with the same rules as for the S1 melodies, as described above.



**Figure 1 - Trial design. A. Trial timeline.** The ear of interest is indicated at the beginning of each trial by an arrow on the screen. Participants have to encode the target melody presented in the ear of interest in memory (S1, black headphone), while filtering out an interleaved distracting melody presented in the other ear (DIS, grey headphone). After a silent retention delay, a second melody (S2) is presented in the ear of interest, and participants have to compare S1 and S2. **B. Examples of the different experimental conditions.** Distracting melodies can be either easy (easyDIS) or hard (hardDIS) to ignore, depending of their frequency proximity with the S1 melody. In trials where S2 differs from S1, the changed sound is 6 or 7 semi-tones different from the original one in the low difficulty memory task (lowM) vs. 1 or 2 semitones in the high difficulty memory task (highM).

### Memory task

For each trial (see Figure 1-A.), the participant is informed of the ear of interest by an arrow (all visual contents are seven-centimeter-wide black elements displayed individually at the center of a white screen). 800ms after the arrow presentation onset, S1 and DIS are played in the ear of interest and in the other ear, respectively. After a 2000-ms pause, the melody (S2)



to compare to S1 is played in the ear of interest. At the end of S2 presentation, the indicative arrow is replaced by a central cross. The participant has then 2000 ms to answer to the question “Is S2 identical or different from S1?”. When S2 differs from S1, only one sound out of four differs, and it can be either the second, third, or fourth one, never the first one which would be too salient. The answer period starts at the end of the S2 melody. At the end of the 2-second-long answering period, there is a pause jittered from 850ms to 1250ms before the start of the next trial.

In the low memory load task (low-M), when S2 differs from S1, one sound is replaced by another which is 5 to 6 semi-tones apart (within the C-major scale, ascending or descending) and induces a change in the melody contour. In the high memory load task (high-M), when S2 differs from S1, the changed sound differs from the original one only by 1 or 2 semi-tones (within the C-major scale) and does not induce a change in the melody contour (see Figure 1-B.).

#### Balancing – within blocks

Each block contains 48 trials. All the combinations of ear of interest (Left or Right), distractor difficulty (easy DIS or hard DIS), and associated answer (same or different) are equiprobable within block (6 trials/block each). For each combination with an expected answer “different”, the direction of the change is equiprobably ascending or descending in frequency (3 trials/block each). This within-block balancing allows to control for side, expected answer, and change direction.

#### Balancing – between blocks

For a given S1 melody, the expected answer, the direction of the change in S2 when different, the level of DIS difficulty, and the side of presentation are balanced across blocks. A given melody is used twice in each block.

Block order is balanced between subjects (Latin square). For half of the participants in each group, melodies S1 and DIS are inverted and become respectively DIS and S1. Association between one S1 melody and another DIS melody changes across participants, enabling us to limit the impact in the results from any unfortunate easy or difficult match.

### *Analysis*

All analysis were conducted using Bayesian statistics, which allow to test the similarity between measures and to estimate a degree of logical support or belief regarding specific results, as implemented in the JASP software (Marsman & Wagenmakers, 2017; Wagenmakers et al., 2018). We report Bayes Factor ( $BF_{10}$ ) as a relative measure of evidence (compared to the null model). To interpret the strength of evidence against the null model, we considered a BF between 1 and 3 as weak evidence, a BF between 3 and 10 as positive evidence, a BF between 10 and 100 as strong evidence and a BF higher than 100 as a decisive evidence (Lee & Wagenmakers, 2014). Similarly, to interpret the strength of evidence in favour of the null model, we considered a BF between 0.33 and 1 as weak evidence, a BF between 0.01 and 0.33 as positive evidence, a BF between 0.001 and 0.01 as strong evidence and a BF lower than 0.001 as a decisive evidence.

Additionally, we report for each factor and interaction the  $BF_{inclusion}$  that compares models that contain the effect to equivalent models stripped of the effect and was considered as a relative measure of evidence supporting the inclusion of a factor.

### Trial rejection

Trials in which participants gave no answer, several answers, or did answer at an inappropriate moment (*i.e.*, outside of the indicated period) are excluded from analysis. Average number ( $\pm$ SD) of trials excluded per participant is 4 trials ( $\pm$ 4) (out of 480).

### Measurements

Data were analysed using Signal Detection Theory measures.  $d'$  (d') is the difference between normalized "Hits" and normalized "False alarms". Hits are the proportion of correct "different" answer over all "different" trials, and False alarms are the proportion of incorrect "different" answer over all "same" trials. Criterion (c) indicates the response bias. Positive values indicate the tendency of answering "same" and negative values reflect the tendency of answering "different". Median Reaction Times (RTs) are computed out of correctly answered trials and correspond to the time between the end of the S2 and the button press.

### Group comparison

We compared demographics and neuropsychological data between groups thanks to Bayesian unpaired t-test and contingency tables (for sex and laterality only).

We compared results ( $d'$ , RT,  $c$ ) between groups thanks to Bayesian repeated-measure ANOVAs with MEMORYload (memory load, two levels: low, high), DISdiff (difficulty of the DIStractor, two levels: easyDIS, hardDIS) as within-participant factors, and GROUP (two levels: LR, HR) as a between-participant factor. Post-hoc comparisons for main effects or interactions were conducted using Bayesian t-tests.

As we planned to test the interaction between GROUP and DISdiff, we performed Bayesian paired t-tests between easyDIS and hardDIS conditions for each group, and Bayesian unpaired t-tests between LR and HR for each DISdiff level, for both  $d'$  and RT.

As we planned to test the interaction between GROUP and MEMORYload, we performed Bayesian paired t-tests between lowM and highM conditions for each group, and Bayesian independent t-tests between LR and HR for each MEMORYload level, for both  $d'$  and RT.

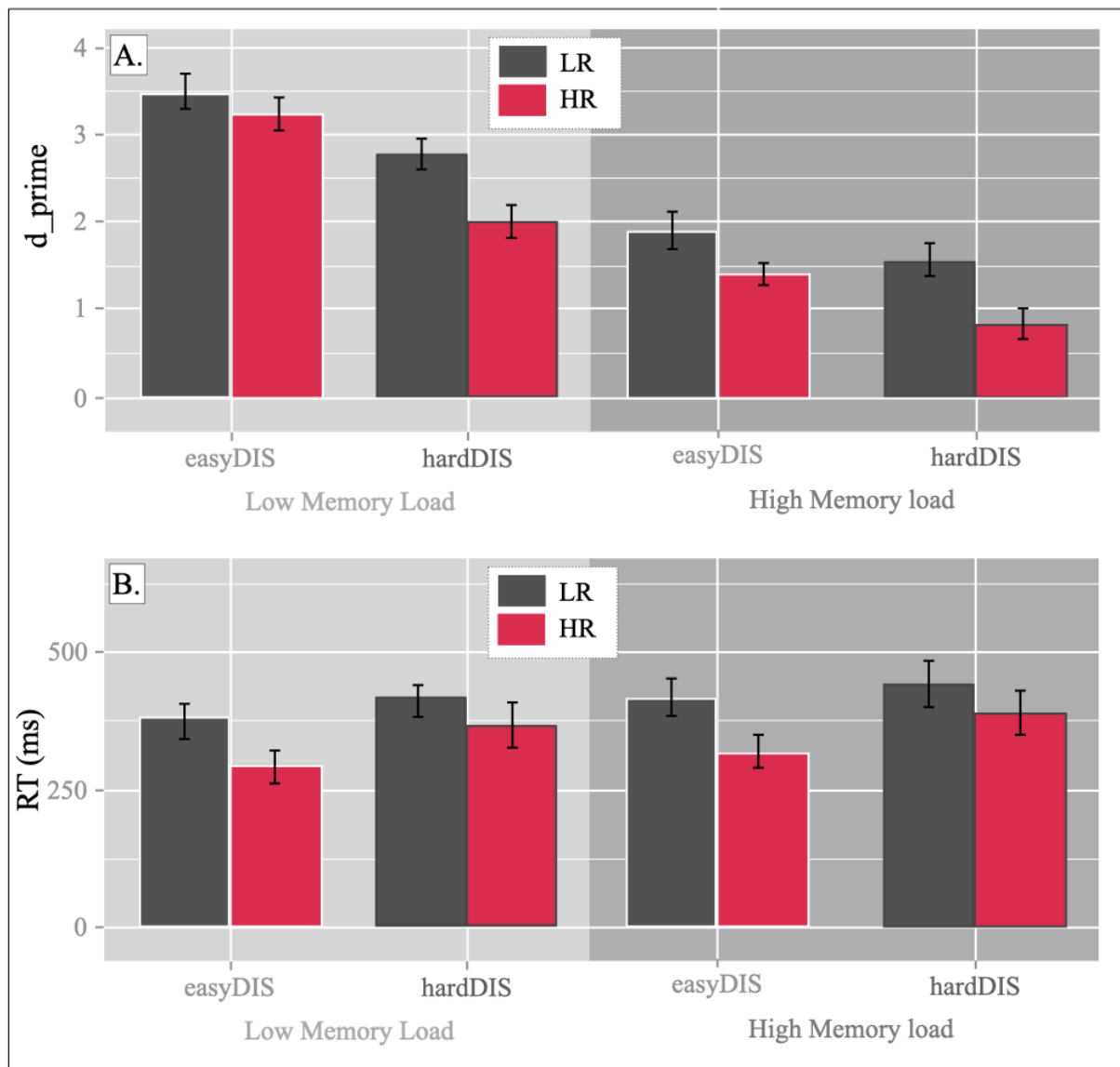
## Results

### *Demographics and neuropsychological data*

Bayesian t-tests confirm that the two groups were matched in school education, age, laterality, and gender ( $0.4 < \text{BF}_{10} < 0.8$ ; see Table 3). Also, as expected, there is decisive evidence ( $\text{BF}_{10} = 5.4e+7$ ) for a difference of dream recall frequency between groups. The evidence towards an absence or a presence of an effect of the GROUP for PSQI, STAI, BFI, and GAUT measures is weak ( $0.4 < \text{BF}_{10} < 1.7$ ; see Table 3).

### *MEMAT Behavioural results*

For  $d'$  (see Figure 2-A., Sup.Table 1), the best model explaining data in LR and HR is the model with the factors GROUP, MEMORYload, DISdiff, the interaction between MEMORYload and DISdiff, and the interaction between GROUP and DISdiff ( $\text{BF}_{10} = 3.3e+23$ ). There is decisive evidence for an effect of MEMORYload ( $\text{BF}_{\text{inclusion}} = 4.7e+20$ ) and DISdiff ( $\text{BF}_{\text{inclusion}} = 4.2e+7$ ), positive evidence for an effect of GROUP ( $\text{BF}_{\text{inclusion}} = 3.9$ ) and of the interaction between MEMORYload and DISdiff ( $\text{BF}_{\text{inclusion}} = 6.4$ ), and weak evidence for an effect of the interaction between GROUP and DISdiff ( $\text{BF}_{\text{inclusion}} = 1.6$ ) (see Sup.Table 2).  $d'$  are higher for LR compared to HR, for easy compared to hard distractors, and for low versus high memory load.



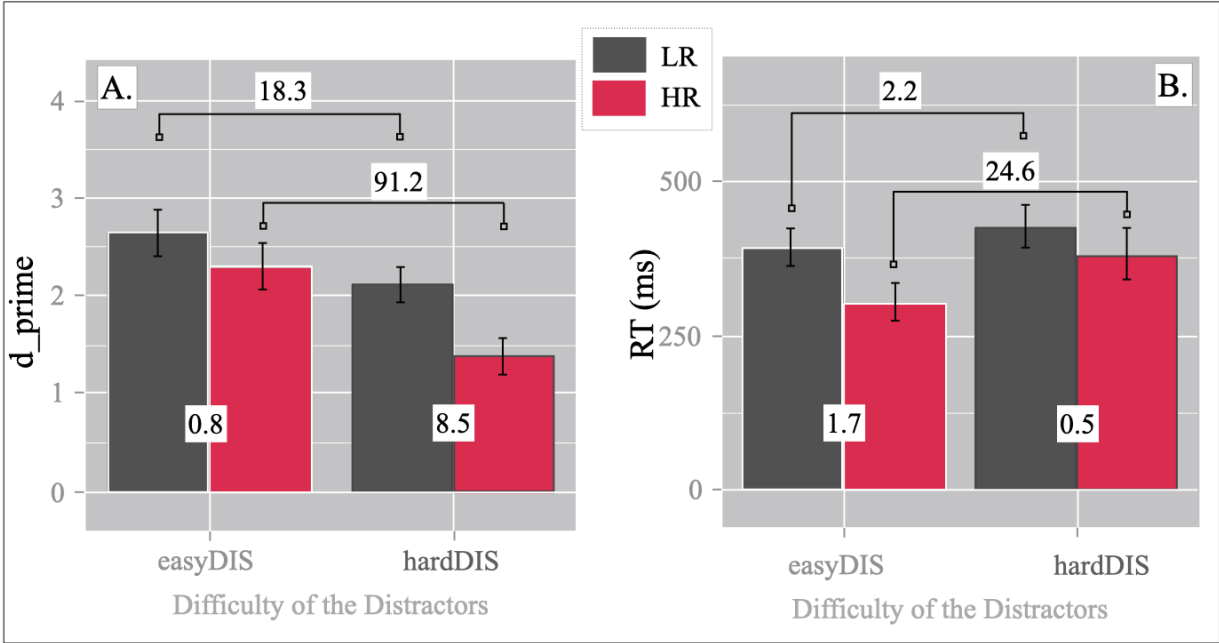
**Figure 2 - Behavioural results of low and high dream recallers.** Effects of the distractor difficulty and task load on  $d'$ -primes (A.) and RTs (B.) for each group separately. Error bars represent standard error of the mean.

These results are consistent with the results of a separate group of non-musicians tested with this same paradigm, yet with fewer trials (Blain et al., 2021): there is an effect of memory load and distractor difficulty upon  $d'$ , with better performance for low compared to high memory load, and better performance for easy- compared to hard-to-ignore distractors, and an effect of the interaction between memory load and distractor difficulty, with greater differences between easy- and hard-to-ignore distractors under low memory load than under high memory load. For more information about the interaction between DISdiff and MEMORYload, see Sup. Figures 1 and 2.

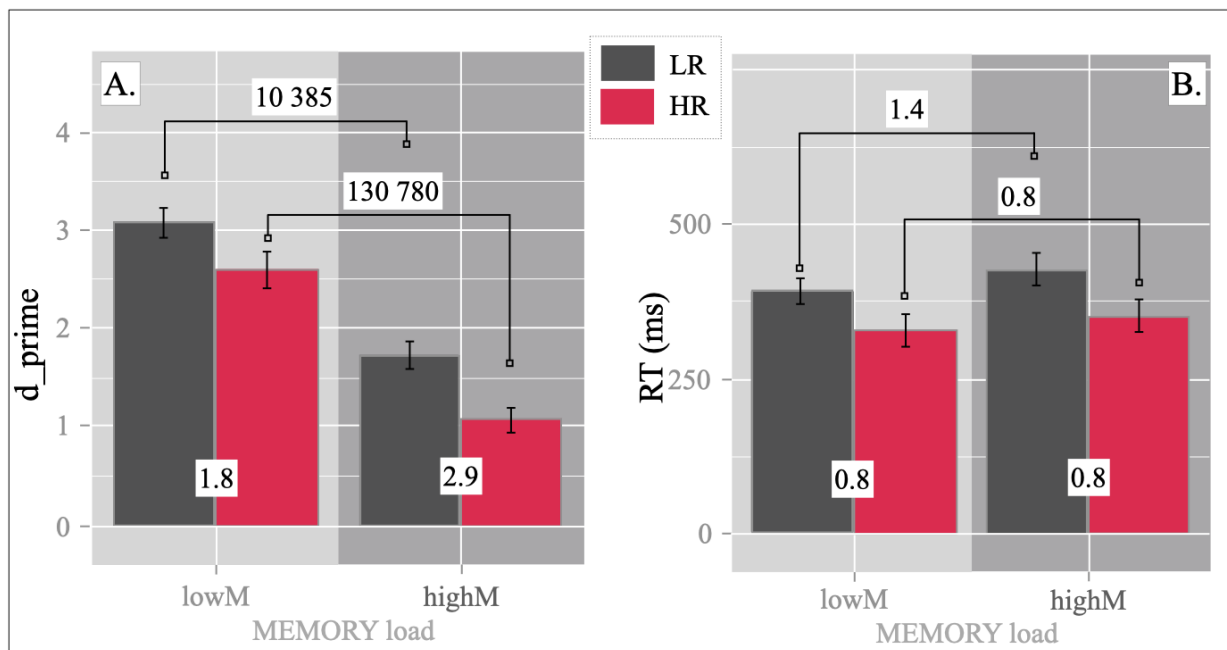
Concerning the planned investigation of the interaction between GROUP and DISdiff for  $d'$ , Bayesian t-tests reveal weak evidence for no difference between groups under easyDIS

( $BF_{10}=0.8$ ) and positive evidence for a difference between groups under hardDIS ( $BF_{10}=8.5$ ). They also reveal strong evidence for a difference between easyDIS and hardDIS in both groups (LR:  $BF_{10}=18.3$ ; HR:  $BF_{10}=91.2$ ).  $d'$  are higher in LR compared to HR, and this difference is higher under hardDIS than under easyDIS (see Figure 3-A.).

Concerning the planned investigation of the interaction between GROUP and MEMORYload for  $d'$ , t-tests reveal weak evidence for a difference between groups under lowM ( $BF_{10}=1.8$ ) and weak-to-positive evidence for a difference between groups under highM ( $BF_{10}=2.9$ ). They reveal decisive evidence for a difference between lowM and highM in both groups (LR:  $BF_{10}=10\ 385$ ; HR:  $BF_{10}=130\ 780$ ). There is only weak evidence, if any, of between-group differences regarding the impact of the memory load (see Figure 4-A.).



**Figure 3 – Effects of GROUP and DISdiff on  $d$ -primes (A.) and RTs (B.) for lowM and highM pooled together.** Numbers above the lines correspond to the  $BF_{10}$  resulting from paired Bayesian  $t$ -tests, while numbers on top of the bars correspond to the  $BF_{10}$  resulting from unpaired Bayesian  $t$ -tests.



**Figure 4 - Effects of GROUP and MEMORYload on d-primes (A.) and RTs (B.) for easyDIS and hardDIS pooled together.** Numbers above the lines correspond to the  $BF_{10}$  resulting from paired Bayesian t-tests, while numbers on top of the bars correspond to the  $BF_{10}$  resulting from unpaired Bayesian t-tests.

For the RTs, the best model explaining the results is the one with MEMORYload, DISdiff, GROUP and the interaction between GROUP and DISdiff ( $BF_{10}=110550.17$ ; see Figure 2-B. and Sup.Table 3). There is decisive evidence for a DISdiff effect ( $BF_{inclusion}=13121.84$ ), positive evidence for a MEMORYload effect ( $BF_{inclusion}=9.4$ ), and weak evidence for a GROUP ( $BF_{inclusion}=0.91$ ) and for the interaction between GROUP and DISdiff ( $BF_{inclusion}=2.7$ ) effects (see Sup.Table 4).

RTs are longer for hard DIS compared to easy DIS, they are longer for high- compared to low-memory load.

Concerning the planned investigation of the interaction between GROUP and DISdiff for RTs, t-tests reveal weak evidence for a difference between groups under easyDIS ( $BF_{10}=1.7$ ) and weak evidence for no difference between groups under hardDIS ( $BF_{10}=0.5$ ). They also reveal weak evidence for a difference between easyDIS and hardDIS in LR ( $BF_{10}=2.2$ ) and strong evidence for a difference between easyDIS and hardDIS in HR ( $BF_{10}=24.6$ ). RTs are higher under hardDIS than under easyDIS in HR but not in LR (see Figure 3-B.).

Concerning the planned investigation of the interaction between GROUP and MEMORYload for RTs, t-tests reveal weak evidence for no difference between groups under lowM ( $BF_{10}=0.8$ ) and under highM ( $BF_{10}=0.8$ ). They reveal weak evidence for no difference

between lowM and highM in both groups (LR:  $BF_{10}=1.4$ ; HR:  $BF_{10}=0.8$ ). There is no difference between groups, whatever the memory load, and no difference between memory loads, whatever the group (see Figure 4-A.).

For the criterion, in agreement with previous studies using delayed-matching-to-sample tests, there is weak to strong evidence for positive  $c$  values (see Sup.Table 5, especially in the difficult memory conditions, underlining that participants tended to miss differences between melodies.

The best model explaining criterion data (see Sup.Table 6) is composed of the factors MEMORYload, DISdiff, and the interaction between MEMORYload and DISdiff ( $BF_{10}=2.2e+12$ ). These results are consistent with the results of a separate group tested with this same paradigm, yet with fewer trials (Blain et al., 2021). However, the second-best model is very close to this best model, with a  $BF_{10}$  equals to  $1.0e+12$ . This second model is composed of factors MEMORYload, DISdiff, GROUP, and the interaction between MEMORYload and DISdiff. There is decisive evidence for an effect of MEMORYload ( $BF_{inclusion}=4.2e+10$ ) and DISdiff ( $BF_{inclusion}=3221.5$ ). There is weak evidence for an effect of the interaction between MEMORYload and DISdiff ( $BF_{inclusion}=2.5$ ) and weak evidence for no effect of the factor GROUP or of any interaction with the factor GROUP ( $BF_{10}<0.7$ , see Sup.Table 7).



## Discussion

In the MEMAT task, low dream recallers (LR) are more accurate ( $d'$ ) and tend to be slower to answer than high dream recallers (HR). Furthermore, both accuracy and reaction times are more impacted by the difficulty of the attentional filtering in HR compared to LR. In particular, there is a greater  $d'$  difference between groups in trials with hard-to-ignore distracting melodies in comparison with trials with easy-to-ignore melodies. The impact of working memory load is similar in the two groups, for both  $d'$  and RT.

### *Attention and Working Memory in HR and LR*

MEMAT is an auditory working memory task requiring an active attentional filtering of sounds. The difference of performance between groups can be due either to differences in short-term/working memory ability, or to differences in the capacity to filter out irrelevant and distracting elements. The difference of performance between LR and HR is not impacted by the memory load, and whatever the group, there is a similar difference between low and high memory load conditions. In other words, HR are not more impacted than LR by increasing the load in the short-term memory task.

The comparison between LR and HR performance under high memory load is close to lead to positive evidence towards a difference between the groups ( $BF_{10}=2.9$ , see Figure 4-A). However, this effect would go in favour of better auditory non-verbal short-term memory in LR than in HR, which is the opposite pattern of that observed in previous studies (Butler & Watson, 1985; Cory et al., 1975; Martinetti, 1983, 1985; Nakagawa et al., 2016; Schredl et al., 1995; Solms, 1997, see Table 1). Therefore, we cannot conclude towards a difference of auditory working memory between LR and HR.

In the MEMAT task, LR are less sensitive to the difficulty of the distractors than HR: HR performance is much more impacted by hard-to-ignore distractors than LR performance. Thanks to the MEMAT paradigm, and in particular because it is a challenging task, we show for the first time attentional differences between LR and HR at the behavioural level. Differences between LR and HR have been investigated for several cognitive processes (memory, verbal fluency, visual imagery, creativity, IQ, for reviews see Ruby 2011, Schredl 2018), but attention has been only scarcely explored so far. Contrary to the present results, a previous study using the Competitive Attention Task (Ruby et al., 2021) did not reveal any significant differences between groups at the behavioural level, while showing differences at the electrophysiological level. Namely, HR exhibited, compared to LR, (1) exacerbated bottom-up attention with a larger P3a to distractors, and (2) enhanced top-down facilitatory

attention processes, with a larger CNV and target-P3. In this previous study, the absence of behavioural effect could be explained by a compensatory strategy preserving the top-down/bottom-up balance: increased bottom-up processes would be compensated by enhanced top-down facilitatory attention processes. Such a compensation mechanism is, however, likely to fail when less cognitive resources are available to enhance top-down facilitatory attention (Bidet-Caulet et al. 2010). As a demanding task recruiting cognitive resources (Blain et al., 2021), MEMAT challenges this compensatory strategy and allows to reveal differences in behavioural performance between HR and LR. In other words, in the MEMAT task, a great amount of cognitive resources is devoted to the memory task, resulting in less cognitive resources available for the top-down attention mechanisms necessary to compensate for increased bottom-up processes in hard-to-ignore-distractor conditions.

We therefore here show a difference of cognitive trait between LR and HR, which is coherent with previously identified differences in neurophysiological trait between HR and LR (Ruby et al. 2013; Eichenlaub et al. 2014a,b; Vallat et al. 2017, 2020; Ruby et al. 2021). The analysis of the electrophysiological data collected together with the behavioural data reported here will help to specify on which attention-related components HR and LR differ in the MEMAT task. According to previous results, HR had both higher bottom-up processing and top-down control of attention (Eichenlaub et al., 2014; Ruby et al., 2021). In MEMAT, HR are more sensitive to hard-to-ignore distracting sounds. This could be either caused by 1) increased bottom-up processing (more resources are automatically devoted to process the surrounding environmental sounds), or 2) greater difficulties to inhibit the distracting sounds (insufficiently efficient top-down attention).

Under high memory load, cognitive resources are taken away from active inhibition of distractors (Blain et al., 2021). Following the second hypothesis above, one would expect that the lack of resources to inhibit the distracting sounds would lead to smaller difference between easy- and hard-to-ignore distractor in HR under high memory load compared to low memory load. Such an interaction between memory load and distractor filtering difficulty is observed in the data (Sup.Figure 2) but is not further modulated by the group factor (no triple interaction between group, DISdiff, and MEMORYload). The difference between LR and HR thus does not seem to be related to differences in the amount of available resources to inhibit distractors, but rather to increased bottom-up processing of irrelevant sounds in HR. This interpretation is in keeping with previous ERP findings of an increase in bottom-up processes in HR (Eichenlaub et al., 2014; Ruby et al., 2021).

## *Implication for the role of Short-Term Memory and Attention in Dream Recall*

### Short-Term memory

According to the arousal-retrieval model (Koulack & Goodenough, 1976), dreams can be recalled if still in short-term memory at awakening. This might lead to the hypothesis that higher short-term/working memory ability could be associated with higher DRF, especially for the main senses involved in dreaming, such as vision and audition (Plailly et al., 2019). Despite the difficulty of the MEMAT task, we found no differential impact of working memory load on performance in LR and HR, which adds to previous negative results in the auditory modality showing no short-term memory difference between HR and LR (Blagrove & Akehurst, 2000; Cohen, 1971; Solms, 1997; Table 1). There is also no conclusive evidence in the literature for an association between visual short-term memory ability and DRF. In other words, in the context of the existing literature, the results of this study suggest that short-term memory ability during wakefulness is not a determinant factor of dream recall frequency. Rather, the resistance of the short-term memory content to the sleep-wake transition could be a determinant parameter of DRF, and attention has many reasons to play a role in this ability.

### Bottom-Up and Top-down Attention

Enhanced bottom-up processes have been observed in HR in the present study and in previous ones (Eichenlaub, Bertrand, et al., 2014; Ruby et al., 2021; Vallat et al., 2017). Being more reactive to the environment can favor dream recall by inducing abrupt awakenings which are more associated with dream recall than gradual awakenings (Shapiro et al., 1963), and by yielding longer awakenings during sleep, which are necessary for the storage of short-term memory into long-term memory according to the arousal-retrieval model (Koulack & Goodenough 1976). This hypothesis is supported by several results in HR (Eichenlaub, 2014; Vallat et al., 2017) and notably by those showing an increase of dream recall rate in LR when they are woken up several times during the night (Eichenlaub, Bertrand, et al., 2014; Goodenough et al., 1959; Vallat et al., 2020). However, increased bottom-up attention in HR may also have an adverse effect on dream recall by increasing distraction and interference effects at awakening. Indeed, according to the interference hypothesis, distraction at awakening promotes the vanishing of the dream content in short term memory (Cohen & Wolfe 1973).

Though using the MEMAT task, the present study could not show differences in top-down processes between HR and LR, increased electrophysiological markers of top-down attention

have been observed in HR during another task recruiting attentional processes (Ruby et al., 2021). This increased recruitment of top-down attention could result from a strategy to compensate exacerbated bottom-up processes and to preserve the bottom-up/top-down attentional balance in HR. A similar compensatory strategy could also trigger an enhanced recruitment of top-down attention processes during sleep and/or at awakening in HR, increasing the focus of attention on dream content and strengthening its maintenance in short-term memory. This hypothesis is coherent with recent results (Vallat et al., 2020) showing an increased connectivity in HR at awakening in a network comprising the dorsolateral prefrontal cortex known to be involved in top-down attention and consciousness (e.g., Dresler et al., 2012; Legrand & Ruby, 2009; Voss et al., 2014; Bidet-Caulet et al., 2015; Corbetta & Shulman, 2002; Petersen & Posner, 2012). Interestingly, this hypothesis could explain why increased interest in dreams result in enhanced DRF (Ruby et al. 2021), both in a state (temporary) or in a trait manner (Cory et al., 1975; Schredl, 2002, 2004; Schredl et al., 2003) since interest and motivation have been linked to increased top-down attention (Bourgeois et al., 2016; Robinson et al., 2012).

### *Limitations*

The interpretation of the results could have been improved if we had added a short-term memory baseline condition without auditory distractors. With such a supplementary condition, we could have known if auditory short-term memory is significantly different between HR and LR in undisturbed conditions with the MEMAT paradigm. Unfortunately, the addition of such a condition made the experiment too long and was not feasible to simultaneously acquire MEG data of good quality.

To conclude, if LR and HR show performance in the normal range at the MEMAT task according to previous results (Blain et al. 2021), they appear to have different attentional traits: HR appear less resistant to irrelevant and hard-to-ignore sounds. This difference is most likely due to increased bottom-up attention and a more fragile balance between top-down and bottom-up processes in HR than LR (Ruby et al 2021). These traits may mostly promote dream recall but may also have adverse effects in case of external or internal distraction at awakening. Further studies will have to investigate more precisely the brain processes underlying these attentional differences. Importantly, these results open new avenues of research to understand better the links between dreaming, dream recall, and attention and how the modulation of one of these processes may causally modify the other ones.

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# Study 1 – Dreaming, Attention, and Memory

Study 1b -  
*Auditory selective attention during a working memory task  
with melodies: a MEG study*

Preprint on BioRxiv; submitted to *Human Brain Mapping*

## **Auditory selective attention during a working memory task with melodies: a MEG study**

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## Abstract

Working memory and attention are jointly needed in most everyday life tasks and activities. They have however mostly been studied separately. Here we investigate how auditory working memory and selective attention interact using a recently introduced paradigm (MEMAT) that combines a classic working memory paradigm, the delayed-matching-to-sample task, and selective attention, with distractors presented during the encoding phase. All stimuli are four-tone melodies. Twenty-two participants performed the MEMAT task during MEG recordings. We manipulate the difficulty of the memory task and of attentional filtering. *When memory task difficulty increases*, the amplitude of the CNV in anticipation of the melody to encode increases and the decrease in alpha power during encoding and maintenance in a left fronto-temporal network is reduced. *When attentional filtering difficulty increases*, the amplitude of the sustained evoked response during encoding increases, whereas the differential processing of relevant and irrelevant sounds in auditory areas is less pronounced, and frontal theta power during encoding and maintenance is higher. In the left auditory cortex, we could directly observe the result of the interaction between auditory memory and attention: the facilitation of relevant sound processing in the easy filtering condition was reduced when the memory task difficulty increased. This pattern mirrors the observed behavioral effects. Overall brain dynamics highlight reciprocal influences of working memory and selective attention processes, in keeping with shared cognitive resources between them.

**Keywords:** short-term memory, attentional filtering, auditory sequences, ERF, theta oscillations, alpha oscillations.

## Introduction

Attention and working memory are constantly at play in cognitive tasks and have been the subject of intense experimental work. Yet only a fraction of these studies examines the interplay between these two major cognitive processes. We focus here on auditory selective attention, working memory, and their interactions as revealed by brain imaging studies.

### *Auditory selective attention and working memory: brain networks*

Numerous studies have shown that auditory selective attention and working memory rely on distributed brain networks, encompassing auditory temporal areas, prefrontal, and parietal cortex. On the one hand, using fMRI or PET, auditory attention has been shown to enhance activation in the auditory cortices in the superior temporal gyri (e.g., O’Leary et al., 1997; Lipschutz et al., 2002; Petkov et al., 2004). Similarly to the visual modality, top-down auditory attention is found to be supported by the dorsal frontoparietal network of attention (dorsal attention network, DAN), including the frontal eye fields, the inferior and middle frontal gyri, the anterior cingulate cortices, and parietal regions, with greater activation in the right hemisphere (e.g., Lipschutz et al., 2002; Kawashima et al., 1999; Belin et al., 1998). However, in the case of auditory spatial selective attention (attention to left or right ear), activation of this DAN and of the auditory cortices is greater contralaterally to the to-be-attended side (e.g., Lipschutz et al., 2002; Tzourio et al., 1997; Alho et al., 1999). On the other hand, auditory working memory networks have also been studied with fMRI and PET, mostly using verbal stimuli (for a review see Buchsbaum & D’Esposito, 2019) but also with melodic (tonal) material (e.g., Zatorre et al., 1994; Schulze et al., 2011). During sound sequence encoding, these neuroimaging studies have shown that activity increases in auditory cortices and the prefrontal cortex, with a left-hemisphere bias especially in prefrontal areas for verbal stimuli (meta-analysis in Buchsbaum et al., 2011), and more bilateral activity patterns for tonal stimuli (Gaab et al., 2003; Albouy et al., 2019). The maintenance (rehearsal) of auditory information recruits prefrontal areas, especially in the left hemisphere for verbal stimuli (e.g., Buchsbaum et al., 2011; Albouy et al., 2019) and bilaterally for tonal stimuli (Albouy et al., 2019), but also other areas including the hippocampus (Kumar et al., 2016), premotor and motor areas (Koelsch et al., 2009; Schulze et al., 2011), cerebellum (Gaab et al., 2003), and the Sylvian-parietal-temporal (Spt) area for verbal rehearsal (meta-analysis in Buchsbaum et al., 2011). The Intra-Parietal Sulcus (IPS) is involved in tonal working memory, especially when manipulation of the stored information is requested (Foster & Zatorre, 2010a, 2010b).



Neuroimaging studies that directly compare the networks subtending selective attention and working memory are scarce, especially in the auditory modality. A notable exception is the study by Huang et al. (2013), where they manipulated the level of attentional interference and memory load in an auditory Continuous Performance Task. Both manipulations resulted in activity changes in a fronto-parietal network, which were largely overlapping, with however some regions being sensitive only to memory load (notably in the anterior dorsolateral prefrontal cortex) and others only to attentional interference (notably in the Inferior Frontal Cortex).

#### *Auditory selective attention and working memory: network dynamics*

The brain dynamics of auditory selective attention has been extensively investigated using non-invasive EEG and MEG and the dichotic paradigm introduced by Hillyard and collaborators (Hillyard et al., 1973). By comparing the evoked responses to the same sounds when task-relevant or irrelevant, attention has been shown to enhance transient responses as early as 20ms after sound onset (e.g., Hillyard et al., 1973; Woldorff et al., 1987; Woods et al., 1991; see Giard et al., 2000 for a review) and sustained responses (Picton et al., 1978; Bidet-Caulet et al., 2007). Importantly, recordings directly from the auditory cortices using intracortical EEG in epileptic patients have shown that auditory selective attention is supported by both an enhancement of evoked responses to relevant sounds and a suppression of evoked responses to irrelevant information, in primary and secondary auditory areas (Bidet-Caulet et al., 2007). It suggests that both facilitatory and inhibitory mechanisms are at play (see also Michie et al., 1993; Alho et al., 1987, 1994; Bidet-Caulet et al., 2010; Chait et al., 2010; Donald, 1987; Schroger & Eimer, 1997). They are modulated by task difficulty: on one hand, the difficulty of the task at hand (e.g., more difficult discrimination of to-be-attended sounds) seems to increase the brain responses to to-be-attended sounds while not affecting the brain responses to to-be-ignored sounds (Lange & Schnuerch, 2014). On the other hand, the difficulty of distractor filtering was found to reduce the processing of to-be-attended sounds (Alain & Woods, 1994; Alain et al., 1993; Ponjavic-Conte et al., 2013) or to increase the brain responses to to-be-ignored sounds (Melara et al., 2005). Alpha oscillations have also been found to be involved in top-down auditory attention. During anticipation and processing of a target sound, the power of alpha oscillations decreases in task-relevant auditory regions and increases in task-irrelevant occipital regions (Müller & Weisz, 2012; Weisz et al., 2014; Frey et al., 2014; Weise et al., 2016; ElShafei et al., 2018, 2020; Wöstmann et al., 2016), in line with an inhibitory role of the alpha rhythm (e.g., Klimesch et

al., 2007; Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Thut et al., 2006; Palva & Palva, 2011). Interestingly, distinct frequency peaks in the alpha band have been found for the power increase in the occipital regions (around 11 Hz) and the power decrease in the auditory regions (around 9 Hz) (ElShafei et al., 2018, 2020), emphasizing the importance of considering the alpha frequency peak in different brain regions (see also Haegens et al., 2014).

EEG and MEG studies of auditory working memory have revealed a modulation of evoked responses by memory load and specific oscillatory signatures of working memory processes in various frequency bands. The amplitude of the N1 evoked response is related to memory performance: the N1 is reduced (and delayed) during encoding of short melodies in participants with congenital amusia who have a specific deficit of pitch short-term memory (Albouy et al., 2013). When memory load increases, the amplitude of sustained evoked responses during the maintenance in memory increases, with a specific component recorded over frontal areas reflecting auditory maintenance, the Sustained Anterior Negativity (SAN, e.g., Lefebvre et al., 2013; Grimault et al., 2014). Sustained evoked responses are also observed during the encoding of sound sequences, showing an increase in amplitude when the difficulty of the memory task increases (Albouy et al., 2013), which is very similar to the effect of attention observed during sound sequence processing (Bidet-Calet et al., 2007). Oscillatory activities have been largely studied during working memory tasks, in particular during the maintenance period, when there is no actual stimulus presented. In a recent systematic review, Pavlov and Kotchoubey (2022) highlighted that the most consistent findings were an increase of frontal midline theta oscillations during both verbal and visuo-spatial working memory tasks, as well as an occipito-parietal alpha increase during verbal memory tasks. A majority of studies report that frontal theta oscillations increase with memory load, and these oscillations have been linked with the maintenance of items' order (e.g., Hsieh et al., 2011), through a coupling with higher-frequency (gamma) activity (Canolty et al., 2006; Lisman & Jensen, 2013). Regarding alpha oscillations, the occipito-parietal alpha power increases with increasing memory load during verbal short-term memory tasks (Obleser et al., 2012) and could reflect the inhibition of the task-irrelevant visual areas (Klimesch et al., 2007), to protect the memory traces. EEG and MEG studies of oscillatory activities during working memory for non-verbal auditory material are far less numerous than studies about verbal working memory. However, for example during a melody short-term memory task, an increase of alpha power in task-irrelevant regions, namely the left fronto-

temporal pathway and bilateral visual areas, has been observed (see Tillmann et al., 2016), suggesting similar principles of organization across auditory verbal and non-verbal domains.

### *Interactions between selective attention and working memory*

The studies reviewed above suggest: (1) largely overlapping brain networks involved in auditory selective attention and working memory, and (2) some similarities in how filtering out distractors and memory load impact on brain network dynamics. In particular, sustained evoked responses increase when selecting the relevant information in attention tasks and when memory load increases in working memory tasks. In both attention and working memory tasks, alpha oscillations increase in non-relevant brain areas. Some studies have tested more directly interactions between selective attention and working memory.

Such interactions have been studied extensively in the visual modality. One prominent finding is increased distraction effects at the behavioral and cerebral levels (increased responses to distractors) under high memory load in dual task-paradigms (one WM task and one attention task), in agreement with the Cognitive Load theory (de Fockert et al., 2001; Lavie et al., 2004; Lavie, 2005). However, in studies using single tasks (one WM task with attentional filtering of distractors), reduced distraction has been found under high memory load (Sörqvist, Stenfelt, et al., 2012; Sörqvist, Nörtl, et al., 2012; Sörqvist & Marsh, 2015). Similarly, in the few studies exploring the effect of memory load on auditory selective attention, inconsistent results have been found, with evidence for both enhanced (Bidet-Caulet et al., 2010) or reduced distraction effects (Bayramova et al., 2021; Berti & Schröger, 2003; SanMiguel et al., 2008) with increasing memory load. The other way around, auditory distraction stemming from irrelevant speech or non-speech sounds has been shown to impede on WM performance, mostly assessed with visually-presented verbal material (e.g., Salamé & Baddeley, 1989; review in Banbury et al., 2001). Interestingly, modulations of both memory load and attentional filtering were found to be reflected in activity patterns in the DAN using fMRI (Majerus et al., 2018).

Such studies either manipulated memory load and assessed its impact on distractors processing, or manipulated filtering difficulty and assessed its impact on memory processes. A joint investigation of both types of manipulation, together with neurophysiological measurements, would however be needed to further understand the interplay between working memory and selective attention.

### *The current study*

In the current study, to shed light on the links between selective attention and working memory networks, we take advantage of a newly designed paradigm, MEMAT (Blain, Talamini, et al., 2022), which allows to manipulate both selective attention and working memory processes during sound sequence encoding and rehearsal, using melodies (hence non-verbal auditory material). In MEMAT, participants perform a delayed-matching-to-sample task (DMST) using melodies presented in one (cued) ear. They have to indicate whether two consecutive sequences of four notes, separated by a two-second silent retention delay, are identical or not. During encoding of the first sequence, an interleaved to-be-ignored melody is presented in the other ear. The to-be-ignored melody can be more or less similar to the to-be-attended melody, hence allowing to manipulate the difficulty to filter out distractors (selective attention manipulation), and the memory task require more or less precision during encoding, depending on blocks, thus allowing to manipulate the memory load (see Blain, Talamini, et al., 2022). In previous reports (Blain, de la Chapelle, et al., 2022; Blain, Talamini, et al., 2022), we have shown that behavioral results obtained with the MEMAT paradigm are in favor of some shared cognitive resources between working memory and selective attention in the auditory non-verbal domain, which can be interpreted within the Cognitive Load theory framework (Lavie et al., 2004; Lavie, 2005), i.e., inhibition of distractors would be easier under low memory load. However the results also point to differences between working memory and selective attention processes, as revealed by slightly different patterns of results in various participants groups: on the one hand, musicians exhibit greatly enhanced working memory abilities for musical sequences but only limited advantages if any for selective attention compared to non-musicians (Blain, Talamini, et al., 2022), and on the other hand, participants with high dream recall frequency are more sensitive to the presence of difficult-to-filter-out distractors than participants with a low dream recall frequency, whereas the impact of the memory task difficulty manipulation was similar in these two participant groups (Blain, de la Chapelle, et al., 2022). These between-groups differences reveal that attention and working memory are differently sensitive to expertise effects (for the effect of musical expertise on auditory working memory see for example George & Coch, 2011; Talamini et al., 2016, 2017, 2022) and psychophysiological traits (for the effect of such traits on auditory attention, see Ruby et al., 2013; Eichenlaub, Bertrand, et al., 2014; Eichenlaub, Nicolas, et al., 2014; Vallat et al., 2020, 2022; Ruby et al., 2022). Overall, behavioral results obtained so far with the MEMAT paradigm revealed both shared and separated processes subtending auditory selective attention and working memory. Here we use MEG recordings during performance of MEMAT to tackle the interplay between selective

attention and working memory at the neurophysiological level, using non-verbal auditory sequences. Based on the literature reviewed above, we focus our investigation on both transient and sustained evoked responses, as well as on oscillatory activities in the theta and alpha range, in auditory, visual, and frontal areas.

## Methods

The experimental protocol is adapted from the recent behavioral-only MEMAT study (Blain, Talamini, et al., 2022). The main difference is that the current data is based on a much larger number of trials, to achieve a good signal-to-noise ratio in the MEG data analysis.

### *Participants*

Twenty-two non-musician participants (20 right-handed, 11 men and 11 women, aged 20-33 years, mean education level  $\pm$  standard deviation, SD:  $15.5 \pm 2.0$  years) participated in the experiment. Participants were considered as non-musicians when they practiced less than 1 year of instrument or singing outside compulsory educative programs (mean music education level  $\pm$  SD:  $0.4 \pm 0.7$  years). Note that these participants were selected to have low or high frequency of dream recall, in order to be able to study the relationship between dream recall frequency (DRF), attention, and short-term memory in analyses not presented here. Behavioral data collected in the present study were analyzed as a function of participants' DRF in Blain, de la Chapelle et al. (2022). Detailed neuropsychological testing and questionnaire data can be found in Blain, de la Chapelle et al. (2022). The present report focuses on MEG data combined from all participants.

All participants were free from neurological or psychiatric disorder and had normal hearing and normal vision. All subjects gave written informed consent to participate. Experimental procedures were approved by the appropriate regional ethics committee.

### *Stimuli*

240 four-sound-long melodies were created to be used as S1 melodies (see below) thanks to combinations of eight-harmonic synthetic sounds from the C major scale, spanning four octaves between 65 and 1046Hz. The maximal interval between any two sounds of a melody is 7 semi-tones. Sounds are 250-ms long and the interval between sounds (offset to onset) is 250 milliseconds. In each melody, there are no consecutive identical sounds. Every melody contains at least an ascending and a descending interval.

### *Paradigm*

#### Attention manipulation

The to-be-attended melody (S1) and the to-be-ignored melody (DIS) are played one in each ear. The tones of the two melodies are interleaved, thus not played simultaneously. S1 is played in the ear indicated by an arrow on the screen, and DIS is played in the other ear, each

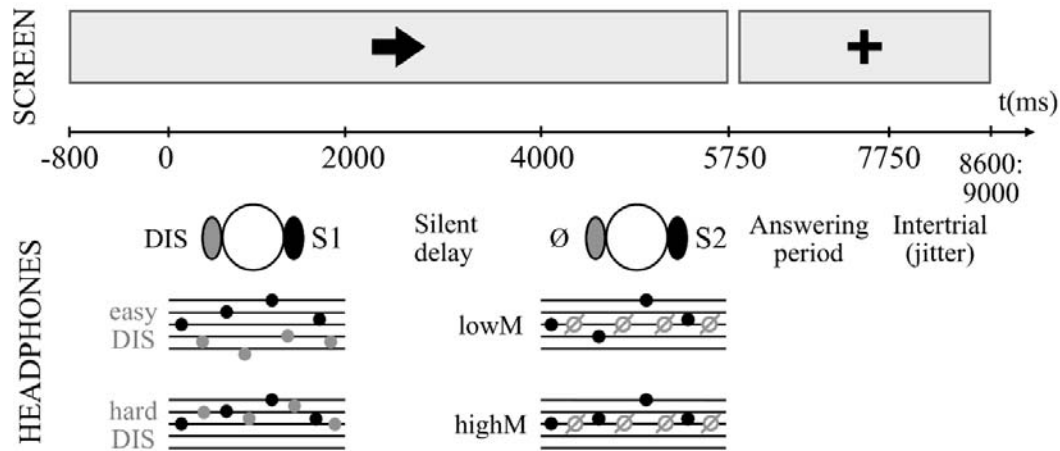
tone one after the other. The first sound to be played is the first tone of S1, and the last tone to be played is the last tone of DIS (see Figure 1).

The DIS melodies can be rather easy (easyDIS) or hard (hardDIS) to filter. An easyDIS melody is composed of sounds in a frequency range 6 to 7 semi-tones higher (or lower) than the corresponding S1 melody frequency range. A hardDIS melody frequency range is the same as the corresponding S1 melody frequency range. DIS melodies are constructed with the same rules as for the S1 melodies, as described above. Presentation of easy- and hard-to-ignore distractors is randomized within a given block therefore participants are not aware in advance of their difficulty.

### Memory task

For each trial (see Figure 1), the participant is informed of the ear of interest by an arrow (all visual contents are seven-centimeter-wide black elements displayed individually at the center of a white screen). 800ms after the arrow presentation onset, S1 and DIS are played in the ear of interest and in the other ear, respectively. After a 2000-ms pause, the melody (S2) to compare to S1 is played in the ear of interest. At the end of S2 presentation, the indicative arrow is replaced by a central fixation cross. The participant has then 2000 ms to answer the question “Is S2 identical or different from S1?” using two response buttons (index and middle fingers of the right hand for identical and different respectively). When S2 differs from S1, only one sound out of four differs, and it can be either the second, third, or fourth one, never the first one which would be too salient. The answer period starts at the end of the S2 melody. At the end of the 2-second-long answering period, there is a pause lasting randomly from 850 ms to 1250 ms before the start of the next trial.

In the low memory task (lowM), when S2 differs from S1, one sound is replaced by another which is 5 to 6 semi-tones apart (within the C-major scale, ascending or descending) and induces a change in the melody contour. In the high memory task (highM), when S2 differs from S1, the changed sound differs from the original one only by 1 or 2 semi-tones (within the C-major scale) and does not induce a change in the melody contour. The difficulty of the memory task (MEMdiff) is fixed within a block, participants are notified of this difficulty at the beginning of each block.



**Figure 1 – Trial design.** The same paradigm is described in Blain, de la Chapelle et al. (2022). The ear of interest is indicated by an arrow on the screen during the trial. The to-be-attended melody S1 played in this ear must be encoded in memory while a to-be-ignored melody DIS is played in the other ear, interleaved with S1 tones. After a 2s retention delay, a melody S2 is played in the ear of interest and participants indicate whether S1 and S2 are identical or different. The melody DIS can be either easy (easyDIS) or hard (hardDIS) to ignore based on their frequency similarity with S1. When S2 is different from S1, one note is changed of either 5-6 semi-tones, entailing a contour change in the melody (low difficulty memory task; lowM blocks) or 1-2 semi-tones without contour change (high difficulty memory task; highM blocks).



## Procedure

First, participants fill in neuropsychological and demographical tests and questionnaires. Then, they are installed in the MEG in a seated position, in a sound-attenuated, magnetically-shielded recording room, at 50-cm distance from the screen. All stimuli are delivered using Presentation software (Neurobehavioural Systems, Albany, CA, USA). Sounds are delivered through air-conducting plastic ear tubes. Detection thresholds for each ear are measured with an adaptive tracking procedure for A3 (220Hz, which is at the middle of the range of notes used). The auditory stimuli are subsequently presented at a comfortable listening level (60 dB SL). Then brain activity is recorded during a 5-min resting state period (eyes opened with a fixation cross provided to the participant). Participants then perform the main task. They are instructed to answer as accurately as possible with their right hand and to keep fixating the cross during the recordings. Prior to the actual task, they perform two short training blocks (12 trials) for each memory difficulty level. Training melodies (S1, DIS, and S2) are specific to the training sessions. Finally, they perform the ten experimental blocks (48 trials each), 5 under each memory difficulty (low or high). They are aware in advance of the difficulty of the memory task but not of the difficulty of the distractors, which is randomized within each block. The order of the blocks is randomized between participants. Trials last 9400 to 9800ms, leading to eight-minute-long blocks.

## Balancing – within blocks

Each of the ten blocks contains 48 trials. All the combinations of ear of interest (Left or Right), distractor difficulty (easyDIS or hardDIS), associated answer (same or different) are equiprobable within block (6 trials/block each). For each combination with an expected answer “different”, the direction of the change is equiprobably ascending or descending in frequency (3 trials/block each). This within-block balancing allows to control for side, expected answer, and change direction.

## Balancing – between blocks

The same S1 sequences are used in lowM and highM. For half of the participants in each group, melodies S1 and DIS are inverted and become respectively DIS and S1. Association between one S1 melody and another DIS melody changes across participants, enabling us to limit the impact in the results from any unfortunate easy or difficult match.

## *Behavioral Data*

### Trial rejection

Trials in which participants gave no answer, several answers, or did answer at an inappropriate moment (*i.e.*, outside of the indicated period) are excluded from analysis. Average number  $\pm$  SD of trials excluded per participant is 4 trials  $\pm$  4 (out of 480).

### Measurements

Data are analyzed using Signal Detection Theory measures.  $d'$  is the difference between normalized “Hits” and normalized “False alarms”. Hits are the proportion of correct “different” answer over all “different” trials, and False alarms are the proportion of incorrect “different” answer over all “same” trials. Criterion ( $c$ ) indicates the response bias. Positive values indicate the tendency of answering “same” and negative values reflect the tendency of answering “different”. Median Reaction Times (RTs) are computed out of correctly answered trials and correspond to the time between the end of the S2 and the button press.

### Statistical analyses for the behavioral data

All analyses are conducted using Bayesian statistics, which allow to test the similarity between measures and to estimate a degree of logical support or belief regarding specific results, as implemented in the JASP software (v0.16.3, JASP Team, 2022; Marsman & Wagenmakers, 2017; Wagenmakers et al., 2018; van den Bergh et al., 2022). We report Bayes Factor ( $BF_{10}$ ) as a relative measure of evidence (compared to the null model). To interpret the strength of evidence against the null model, we consider a BF between 1 and 3 as weak evidence, a BF between 3 and 10 as positive evidence, a BF between 10 and 100 as strong evidence, and a BF higher than 100 as a decisive evidence (Lee & Wagenmakers, 2014). Similarly, to interpret the strength of evidence in favor of the null model, we consider a BF between 0.33 and 1 as weak evidence, a BF between 0.01 and 0.33 as positive evidence, a BF between 0.001 and 0.01 as strong evidence and a BF lower than 0.001 as decisive evidence. For clarity, we report information about the best model only, unless several models account almost as well for the data (as assessed when comparing models to the best model). Additionally, we report the results of an analysis of effects that compares models that contain a given effect (of a factor or an interaction) to equivalent models stripped of the effect and was considered as a relative measure of evidence supporting the inclusion of a factor ( $BF_{inclusion}$ ).

$d'$ , criterion (c), and RTs are submitted to a Bayesian repeated-measure ANOVA with MEMdiff (difficulty of the task, two levels: lowM, highM), DISdiff (difficulty of the DIStractor, two levels: easyDIS, hardDIS) as within-participant factors. Post-hoc comparisons for main effects or interactions are conducted using Bayesian t-tests. Criteria (c) for the four conditions (2 levels of MEMdiff x 2 levels of DISdiff) are submitted to a Bayesian one-sample t-test comparison to zero.

### *Brain recordings*

MEG data are continuously recorded using a 275-channel whole-head axial gradiometer system (CTF-275 by VSM MedTech Inc., Vancouver, Canada) with a sampling rate of 600Hz and a 0.016-150Hz bandpass filter. Head movements are continuously monitored using 3 coils placed at the nasion and the two preauricular points.

For each participant, a T1-weighted 3D MRI is obtained using a 1.5T or 3T whole-body scanner (Magnetom Siemens Erlangen, Germany) after the MEG session. At the end of MEG session, locations of the nasion and the two preauricular points are marked using fiducials markers visible on the T1 acquisitions. The T1 images are used for reconstruction of individual head shapes to create forward models for the source reconstruction procedures.

### *Data pre-processing*

MEG data are pre-processed offline using the software package for electrophysiological analysis (ELAN Pack) developed at the Lyon Neuroscience Research Center (Aguera et al., 2011). A third-order spatial gradient noise cancellation is applied to the data. The recorded signal is rejected when head movements exceed the threshold of +/-1cm around the median position. Sensor jumps (> 10 picoTesla) are detected and corrected with custom software. Blinks, saccades, and heartbeats are removed from the signal thanks to an Independent Component Analysis (ICA), using eeglab MATLAB toolbox (Delorme & Makeig, 2004). This ICA is computed on band-pass filtered signal (0.5-45Hz). Eye-movements and heartbeat-related components are determined by visual inspection of component topographies and time courses and removed through an ICA inverse transformation applied to the non-filtered signal. The ICA-corrected signals are then band-stop-filtered between 47 and 53 Hz, 97 and 103 Hz, and 147 and 153 Hz (zero-phase shift Butterworth filter, order 3) to remove power-line artifacts. Data segments contaminated with any residual artifact are excluded using a threshold of 2.5 picoTesla. 92% ( $\pm 11$ ) of trials remain in the analyses after artifact rejection (resulting in 55 ( $\pm 6$ ) trials per presentation side of S1 and condition).

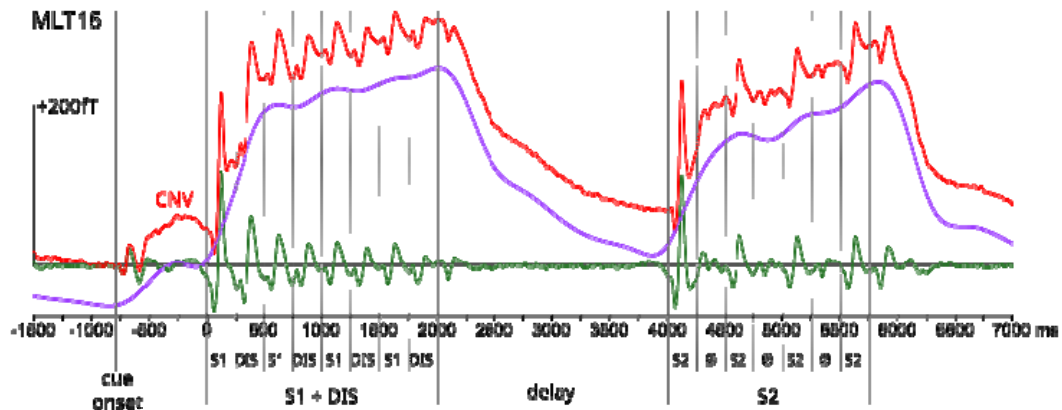
## ERF analyses

### ERF at sensor-level

For each participant and condition, event-related fields (ERFs) are obtained by averaging band-stopped ICA-corrected MEG data locked to the onset of S1 (time-window: -1500 to 7000 ms, averaging epochs thus start 250 ms prior to cue onset, see Figure 2). To study the Contingent Negative Variation (CNV) after the visual cue, in anticipation of the melody to encode, ERFs are filtered with a 30-Hz low-pass filter and baseline corrected to the mean amplitude of the 250-ms period before cue onset (-1050 to -800 ms before S1 onset). To study transient evoked responses to tones of S1/DIS melodies and sustained responses during S1/DIS melodies or the retention delay, ERFs are filtered with a 2-30-Hz band-pass filter and with a 2-Hz low-pass filter, respectively. ERFs are then baseline corrected to the mean amplitude of the -250 to 0 ms period before S1 onset (see Figure 2 and Table 1).

Because of saliency effects for the first note, we further separate the analysis of the first note and the following ones: on the one hand, ERFs are computed locked to the first note onset, and on the other hand, we compute the average of the ERFs locked to the second, third, and fourth notes of the melodies, with no further baseline correction, separately for S1 and DIS in both cases. We also compute the difference between S1 and DIS (average across notes 2, 3, 4).

Grand-average ERF is obtained by averaging the same computed ERF across all 22 participants.



**Figure 2 – Filters used for ERF analyses (grand-average ERF).** In red, a 30Hz low-pass filter was applied to preserve the CNV, between the onset of the visual cue (-800ms) and the onset of S1 (0ms), with a -1050 to -800 ms pre-cue baseline. In green, a 2-30Hz band-pass filter was applied to study the ERF to each S1 and DIS tone (between 0 and 2000ms), with a -250 to 0 ms pre-S1 baseline. In purple, a 2Hz low-pass filter was applied to highlight the sustained response during the S1/DIS melodies (0 to 2000ms) and the retention delay (2000 to 4000ms), with a -250 to 0 ms pre-S1 baseline.

### ERF source reconstruction

Segmentation of the individual T1-weighted MRIs is conducted using the FreeSurfer software package (Fischl, 2012; <http://surfer.nmr.mgh.harvard.edu>). Segmentation is visually inspected and then imported (15,002 vertices) in the Brainstorm toolbox (version 3.191209 (09-Dec-2019) on Matlab R2015a; Tadel et al., 2011; <http://neuroimage.usc.edu/brainstorm>) with which further source analyses are conducted. The white matter–grey matter boundary segmented by FreeSurfer is used as a source space for subsequent weighted minimum norm estimation. A noise covariance matrix is computed on resting state data, which has been preprocessed with the same pipeline as data collected during task performance. After coregistration between the individual anatomy and MEG sensors, the forward model is computed with the OpenMEEG software (Gramfort et al., 2010; <https://openmeeg.github.io/>). Cortical currents are estimated using a distributed model consisting of 15,002 current dipoles from the time series of the 275 gradiometer signals, using a linear inverse estimator (weighted minimum-norm current estimate, signal-to-noise ratio of 3, whitening PCA, depth weighting of 0.5). Sources orientations are constrained to be orthogonal to the grey-white matter boundary of the individual MRIs. The results are then projected on a standard brain model anatomy (ICBM152; 15,002 vertices) for group analysis purposes.

### ERF source analysis

ERF analyses are performed following five steps: (1) the main ERFs are identified at the sensor level, and time-windows of interest are defined for each ERF (see Table 1 for a list of ERFs studied and the associated time-windows); (2) at the source level, emergence of ERFs (all four conditions collapsed) is tested at the whole brain level using t-tests comparing signal amplitude (on average across the time-window of interest) to zero at each vertex (FDR-correction for multiple comparisons, corrected  $p < 0.05$ ); (3) regions of interest (ROIs) are drawn using Brainstorm based on these emergence tests with a procedure allowing to grow from a seed voxel to match the shape of the activation patch on the cortical surface; (4) ROI time-courses of activity are extracted for each participant, each condition, each presentation side; (5) mean amplitudes in time-windows of interest are computed for each participant, each condition, each presentation side; (6) Bayesian ANOVA (see Results and Table 1 for details about factors, and the Statistical methods for the behavioral data section above for details about Bayesian ANOVA) for each studied ROI and each time-window are performed (see Table 1 for ROIs and time-windows). Emergence of ERFs (step 2) is scrutinized for stimuli presented at left or right ear separately, and if similar patterns are observed, data are further

Event of interest	Filtering	Studied ERF	STATISTICS
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collapsed across stimulus presentation side for ROI definition (see Table 1). Emergence of ERFs is also assessed in the difference between S1 and DIS (notes 2, 3, 4).

			ROI [number of vertices]	Time-window for analysis (ms)	Factors tested	Main result
S1	lp 30Hz	CNV	left PP [32]	-400 to -200	Cued Side & MEMdiff	-
				-200 to 0		-
			right PP [40]	-400 to -200		-
				-200 to 0		highM > lowM after left cue
S1: note1	bp 2-30Hz	N1	left temporal [55]	90 to 140	MEMdiff	-
			right temporal [66]			-
			left frontal [54]			-
			right frontal [60]			-
DIS: note1	bp 2-30Hz	N1	left temporal [55]	100 to 150	MEMdiff & DISdiff	hardDIS > easyDIS
			right temporal [66]			-
			left frontal [54]			-
			right frontal [60]			-
S1 & DIS: notes 2,3,4	bp 2-30Hz	N1	left temporal [68]	100 to 150	Stimulus Type, MEMdiff & DISdiff	S1 > DIS; lowM & S1 only: easyDIS > hardDIS
			right temporal [65]			S1 > DIS; S1 only: easyDIS > hardDIS
			left frontal [27]			S1 > DIS
			right frontal [24]			S1 > DIS
S1 & DIS: notes 2,3,4		P2	left PP [46]	200 to 250	Stimulus Type, MEMdiff & DISdiff	DIS only: hardDIS > easyDIS
			right PP [44]			S1 > DIS; DIS only: hardDIS > easyDIS
S1 – DIS: notes 2,3,4	bp 2-30Hz	Late differential response	right temporal [78]	225 to 275	Stimulus_Side, MEMdiff, & DISdiff	easyDIS > hardDIS
S1	lp 2Hz	Sustained response	left PP [51]	500 to 2000	S1 side, DISdiff, & MEMdiff	hardDIS > easyDIS
			right PP [44]			hardDIS > easyDIS
			left PT [37]			-
			right PT [11]			-
			left PP [51]	2500 to 4000		-
			left PT [37]			-

**Table 1. Summary of the ERF analyses:** event and filtering used, studied ERF, ROI information, time-window used for statistical analysis, factors of the Bayesian repeated-measure ANOVA used, and results of the statistical analysis. For CNV and sustained responses, ROIs are defined based on activation from all stimuli between -400 and 0 ms and between 500 and 2000 ms respectively, whereas for N1, P2, and late responses, ROIs are defined based on activation from contralateral stimuli only

(see text for details). When computing the difference between S1 and DIS, both S1 and DIS stimuli are contralateral (i.e. they are taken from different trials). For N1 and P2 for notes 2, 3, 4, as activity is largely overlapping for S1 and DIS, the ROIs are drawn from the emergence test of S1. We report in the table only effects for which at least positive evidence (i.e.,  $BF_{10}$  or  $BF_{inclusion} > 3$ ) was observed (see text for the full results). “>” means larger ERF (in absolute value) in a given condition compared to another one. “-” means no positive or greater evidence for an effect. S1: to-be-attended melody, DIS: to-be-ignored melody; lp: low pass; bp: band-pass; PP: Planum Polare; PT: Planum Temporale; MEMdiff: memory task difficulty (lowM vs. highM); DISdiff: distractor filtering difficulty (easyDIS vs. hardDIS).

### *Time-Frequency analysis*

#### TF at sensor-level

To investigate the dynamics of theta and alpha power during the task, a time-frequency analysis is performed using the Fieldtrip toolbox (v20190626; Oostenveld et al., 2011) on Matlab R2017A. Time-frequency analysis is computed from -2500 to +8000ms relative to S1 onset, using Morlet wavelet decomposition with a width of four cycles per wavelet ( $m=7$ ; Tallon-Baudry & Bertrand, 1999), for frequencies from 4 to 20Hz, with steps of 1Hz and 50ms. For each single trial, the corresponding ERF is subtracted before wavelet decomposition to focus on induced (and not evoked) activity. The relative change in power is then obtained by subtracting then dividing each power value with the power in a pre-cue baseline period (-1800 to -1000 ms relative to S1 onset) in the corresponding frequency range. The main power modulations are identified at the sensor level for all conditions collapsed and used to define time-frequency windows of interest for source-level analyses.

#### TF: head model

For source reconstruction, the processing of the T1 MRI is performed using CTF software (CTF Systems Inc., VSM Medtech Inc., Vancouver, Canada). For each participant, an anatomically realistic single shell headmodel based on the cortical surface is generated from individual head shapes (Nolte, 2003) and imported in the Fieldtrip toolbox (v20190626; Oostenveld et al., 2011). Then, a grid with 0.5-cm resolution is normalized on a MNI template and morphed into the brain volume of each participant.

#### TF: whole brain source analyses

To elucidate the possible brain regions underlying the sensor-level modulations in the theta and alpha bands, we perform whole brain analysis on time-frequency windows of interest.

Several time-windows relative to S1 onset are chosen based on the protocol design: one during the cue presentation (-800:0ms); two during the presentation of S1 and DIS melodies



(400:1200ms & 1200:2000ms); and two during the delay (2400:3200ms & 3200:4000ms). Three different frequency bands (4 to 7Hz, 7 to 11Hz & 11 to 15 Hz) are chosen based on the observations at the sensor level and previous findings (ElShafei et al., 2018, 2020).

We use the frequency-domain adaptive spatial technique of Dynamical Imaging of Coherent Sources (DICS; Gross et al., 2001). For each participant, data from all conditions is concatenated, and the cross-spectral density (CSD) matrix (-2.5 to +7s, relative to S1 onset, lambda 5%) is calculated using the multitaper method with a target frequency of 9.5 (+/-5.5) Hz. Leadfields for all grid points along with the CSD matrix are used to compute a common spatial filter that is in turn used to estimate the spatial distribution of power for all time-frequency windows of interest.

Afterward, for left and right S1 presentation separately (irrespective of MEMdiff and DISdiff), power in each time-frequency window of interest is contrasted against the power in a corresponding baseline pre-cue window (-1800 to -1000 ms relative to S1 onset) for frequencies around 5.5 (+/- 1.5), 9 (+/- 2) and 13 (+/- 2) Hz using a nonparametric cluster-based permutation analysis (Maris & Oostenveld, 2007) across participants, controlling for multiple comparisons in the source space dimension.

### Reconstruction of source-level single-trial activity in ROIs

In order to get a time-frequency resolved estimation of source activity, we use an approach based on regions of interest (ROIs) and we reconstruct single trial activity at the level of ROIs using the linearly constrained minimum variance (LCMV) beamformer (Van Veen et al., 1997) in each subject.

Regions of interest (ROIs), in each hemisphere, are defined from the Brodmann atlas based on the group whole brain activation (see previous paragraph): the *auditory ROI (Aud)* is composed of Brodmann areas 22, 41, and 42, the *visual ROI (Vis)* is composed of Brodmann areas 17, 18, and 19, the *anterior prefrontal cortex ROI* is composed of Brodmann areas 9 and 10, the *Broca ROI* is composed of Brodmann areas 44 and 45, and the *dorso-lateral prefrontal (DLPFC) ROI* is composed of Brodmann area 46.

Spatial filters are constructed from the covariance matrix of the averaged single trials at sensor level (-2.5:7s, relative to S1 onset, 1-20Hz, lambda 5%) and the respective leadfield for all grid points. Then, spatial filters are multiplied by the sensor-level single-trial data, thus obtaining the time course activity of each voxel of interest within the defined ROIs. Single-trial activity is averaged across all voxels within each ROI in each hemisphere. For each ROI, the evoked response (i.e., the signal averaged across all trials) is subtracted from each trial.

### ROI peak frequency

To extract the frequency peak in each ROI (source-level activity reconstructed with LCMV, see previous paragraph), for each time-window of interest (-1800:-1000; -800:0; 400:1200; 1200:2000; 2400:3200; 3200:4000 ms), we compute the power spectral density using Fourier decomposition based on Hann windows and extract the rhythmic activity from the concurrent 1/f modulations of the signal using the Fitting oscillations and one-over-F (FOOOF) toolbox implemented in Fieldtrip (v20221004; Oostenveld et al., 2011; Donoghue et al., 2020), for all conditions collapsed. The resulting FFT of the baseline is subtracted from the resulting FFT of each following time-window.

The theta peak corresponds to the highest local maximum in the resulting spectrum between 3 and 7 Hz; while the peaks for alpha decrease and increase correspond to the lowest local minimum and highest local maximum between 7 and 15 Hz, respectively.

In each ROI, the group frequency range is then defined from the median peak frequency across subjects  $\pm$  1.5 Hz, averaged over time-windows, resulting in 4-7 Hz, 8-11 Hz and 9-12 Hz to be used in subsequent analyses for theta, low alpha and high alpha respectively.

### ROI statistical analysis

In each ROI, the time-frequency power is calculated for each trial using Morlet wavelet decomposition with a width of four cycles per wavelet ( $m = 7$ ) at frequencies between 4 and 15 Hz, in steps of 1 Hz and 50 ms. The relative change in power is then obtained by averaging single trial TF power in each condition (for each level of memory difficulty, distractor filtering difficulty, and side of S1 presentation) and by subtracting then dividing each averaged power value with the power in a pre-cue baseline period (-1800 to -1000 ms relative to S1 onset) in the corresponding frequency range.

For each frequency range (4-7 Hz, 9-12 Hz and 8-11 Hz) and each time-window of interest (-800:0; 400:1200; 1200-200; 2400:3200; 3200:4000 ms), the relative change in power is extracted in each subject and for each ROI of interest based on DICS analysis. To investigate the impact of the memory task and distractor difficulties, these averaged values are submitted to a Bayesian repeated-measure ANOVA with factors MEMdiff, DISdiff, and S1side, for each ROI and each corresponding time-frequency window (see Table 2). Post-hoc comparisons for main effects or interactions are conducted using Bayesian t-tests.

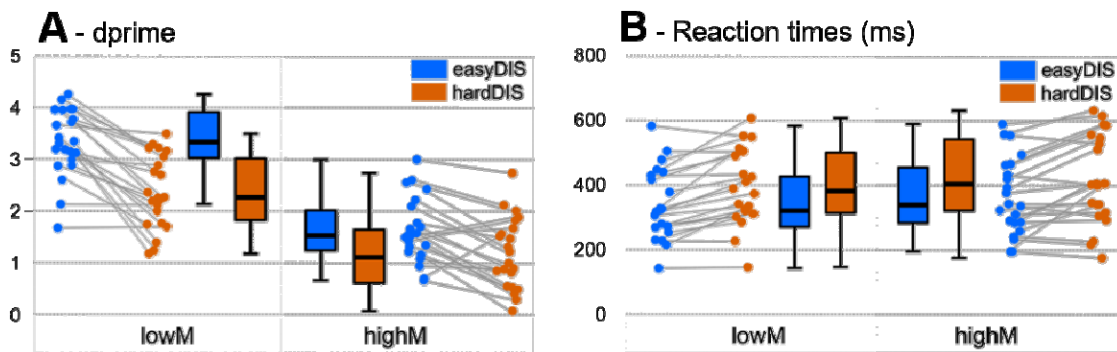
ROI	Brodmann areas	Hemisphere	Target frequency	STATISTICS				
				Cue	S1 + DIS presentation		Retention delay	
				-800:0 ms	400:1200 ms	1200:2000 ms	2400:3200 ms	3200:4000 ms
Anterior Prefrontal	9, 10	L	$\theta \nearrow$ 4-7 Hz	$\theta \nearrow \nearrow$ after left cue	-	$\theta \nearrow \nearrow$ in hardDIS	-	$\theta \nearrow \nearrow$ in hardDIS
		R		-	-	-	$\theta \nearrow \nearrow$ in hardDIS	
Auditory	22, 41, 42	L	$\alpha \searrow$ 8-11 Hz		$\alpha \searrow \searrow$ in lowM	-	-	-
		R			-			
Broca	44, 45	L	$\alpha \searrow$ 8-11 Hz		-	-	-	$\alpha \searrow \searrow$ in lowM
		R			-			
DLPFC	46	L	$\alpha \searrow$ 8-11 Hz		-	-	-	-
		R			-			
Visual	17, 18, 19	L	$\alpha \searrow$ 8-11 Hz	-				
		R		-				
		L	$\alpha \nearrow$ 9-12 Hz		-	-	-	-
		R			-			

**Table 2 – Summary of the TF analysis.** We report in the table only effects for which at least positive evidence (i.e.,  $BF_{10}$  or  $BF_{inclusion} > 3$ ) was observed with a Bayesian repeated-measure ANOVA with factors *S1side*, *DISdiff* (distractor filtering difficulty, *easyDIS* vs. *hardDIS*), and *MEMdiff* (memory task difficulty, *lowM* vs. *highM*; see text for the full results). Reported effects are relative to the opposite condition. “-” means no positive or greater evidence for an effect. Gray cells were not tested in accordance with the whole-brain source results.  $\nearrow$ : increase in power,  $\searrow$ : decrease in power.

## Results

### Behavioral results

For  $d'$  (Figure 3A), the best model explaining the data is the one with factors MEMdiff, DISdiff, and the interaction between MEMdiff and DISdiff ( $BF_{10}=2.3e+16$ ), in keeping with Blain, Talamini et al. (2022) and Blain, de la Chapelle et al. (2022). The analysis of effects across models reveals decisive evidence for MEMdiff ( $BF_{inclusion}=3.7e+10$ ), for DISdiff ( $BF_{inclusion}=6729.8$ ), and for the MEMdiff x DISdiff interaction ( $BF_{inclusion}=116.0$ ).  $d'$  is higher for easyDIS compared to hardDIS, and higher in lowM compared to highM. The difference between hardDIS and easyDIS is smaller in highM compared to lowM (or put differently, the difference between lowM and highM is smaller for hardDIS than easyDIS), as revealed by a post-hoc Bayesian t-test ( $BF_{10}=123.2$ ).



**Figure 3 – Behavioral results.** Effect of the difficulty of the task (lowM: low difficulty, highM: high difficulty) and of the difficulty of the distractor (easyDIS: easy to ignore, hardDIS: hard to ignore) on performance  $d'$  (A) and on reaction times (B). Whisker plots show the median $\pm$ quartile and the minimum/maximum values. Lines in the strip plots connect data from the same participant.

For the criterion (c), in agreement with previous studies using delayed-matching-to-sample tests, there is weak to decisive evidence for positive c values in all conditions, underlining that participants tended to miss differences between melodies (see Table S5 in Blain, de la Chapelle, et al., 2022). The best model explaining criterion results is the one with factors MEMdiff, DISdiff, and the interaction between MEMdiff and DISdiff ( $BF_{10}=4.4e+9$ ). There is decisive evidence for MEMdiff ( $BF_{inclusion}=1.4e+7$ ), strong evidence for DISdiff ( $BF_{inclusion}=73.7$ ), and positive evidence for the MEMdiff x DISdiff interaction ( $BF_{inclusion}=7.0$ ). Criterion is higher under highM compared to lowM and is higher for easyDIS compared to hardDIS. Post-hoc Bayesian paired-samples t-tests reveals strong evidence for a difference in criterion between easyDIS and hardDIS for lowM ( $BF_{10}=90.7$ ) but only weak evidence for such a difference in highM ( $BF_{10}=1.5$ ).

For RTs (see Figure 3B), the best model explaining results is the one with factors MEMdiff and DISdiff ( $BF_{10}=671.5$ ). The analysis of effects reveals decisive evidence for DISdiff ( $BF_{inclusion}=151.2$ ) and positive evidence for MEMdiff ( $BF_{inclusion}=4.6$ ). RTs are longer for hardDIS compared to easyDIS, and they are longer for highM compared to lowM.

### *Event-Related Fields Results*

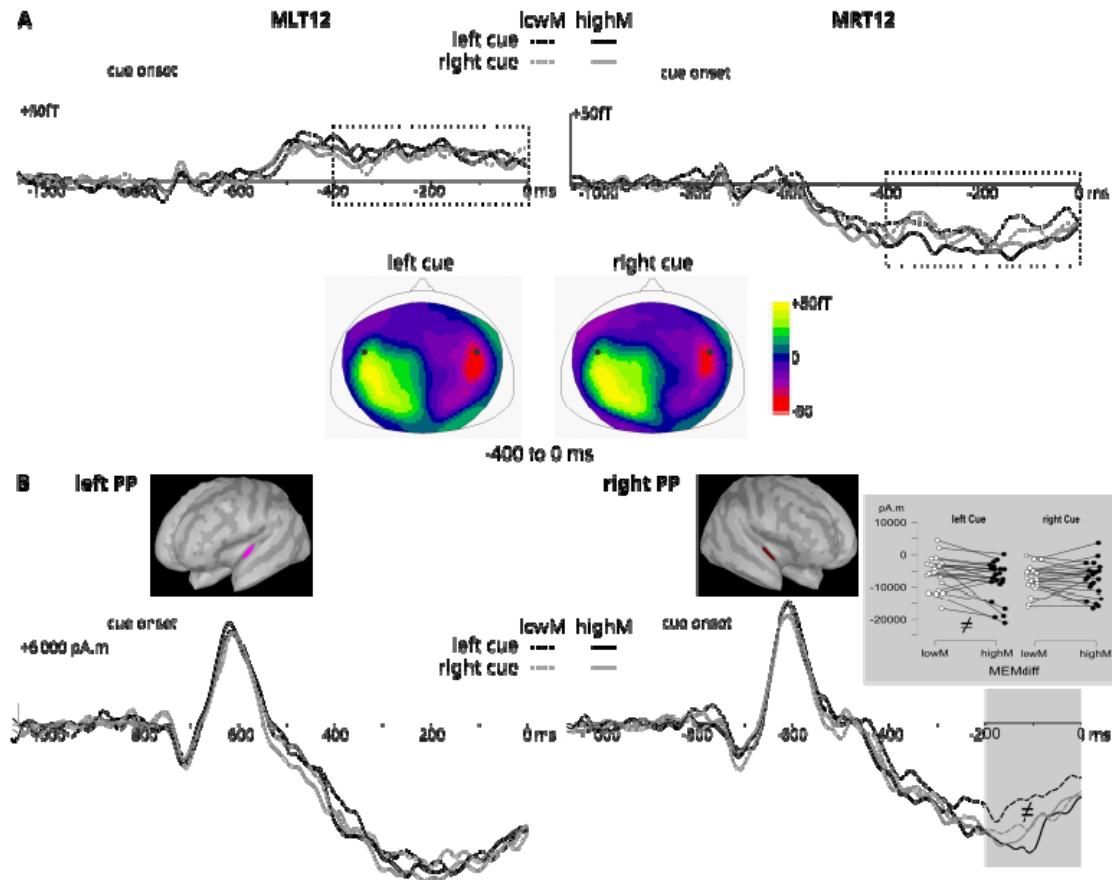
A summary of the main results obtained for ERF analyses is provided in Table 1.

### Contingent Negative Variation (CNV)

The time course and topographies at the sensor level of the CNV developing after the visual cue are shown in Figure 4A. Emergence tests at the source level (time window: -400 to 0 ms relative to S1 onset) reveal activity in temporal regions before S1 onset, extending bilaterally along the Planum Polare, irrespective of the cued ear. Activity in these temporal regions was examined with Bayesian repeated-measure ANOVAs with Cued Side and MEMdiff as factors, during early (-400 to -200 ms relative to S1 onset) and late (-200 to 0 ms relative to S1 onset) CNV (see Table 1).

In the right Planum Polare ROI (see Figure 4B), the best model explaining the data just before S1 presentation (time-window -200 to 0 ms relative to stimulus onset) is the model with the MEMdiff factor ( $BF_{10} = 1.2$ ), immediately followed by the full model including the interaction between Cued Side and MEMdiff ( $BF_{10} = 1.1$ ). Note that these models are thus almost as likely as the null model. The analysis of effects reveals weak evidence for the interaction between MEMdiff and Cued Side ( $BF_{inclusion} = 2.6$ ) and for MEMdiff ( $BF_{inclusion} = 1.2$ ). Post-hoc Bayesian paired-sample t-tests revealed positive evidence for a difference between lowM and highM with contralateral stimuli ( $BF_{10} = 3.7$ ) and for no difference between lowM and highM with ipsilateral stimuli ( $BF_{10} = 0.23$ ). When the left ear was cued, larger CNV amplitudes are thus observed in the right Planum Polare for the highM condition compared to lowM.

The best model explaining CNV amplitudes in the left and right Planum Polare ROIs between -400 to -200 ms prior to S1 onset, as well as in the left Planum Polare ROI between -200 and 0 ms prior to S1 onset, is the null model in all three cases ( $BF_{10}$  for all other models < 0.56).



**Figure 4 – Contingent Negative Variation (CNV).** (A) In the sensor space, time course of the ERF to the visual cue onset (arrow, -800ms relative to S1 onset), for each MEMdiff and Cued Side condition, at MLT12 and MRT12 (above the left and right temporal lobes, respectively). Topoplots show sensor data to left and right cues, over the time period of interest, indicated by the dotted rectangles (-400 to 0 ms). Black dots on topographies indicate corresponding sensor position. (B) In the source space, time course of the ERF to the visual cue onset, for each MEMdiff and Cued Side condition, in the corresponding ROI represented on the MNI template. The strip plot shows individual data averaged by condition in the gray period (-200 to 0 ms) showing positive or greater evidence (see Table 1 for time-windows and results). Lines connect data from the same participant. leftPP: left Planum Polare, right PP: right Planum Polare.

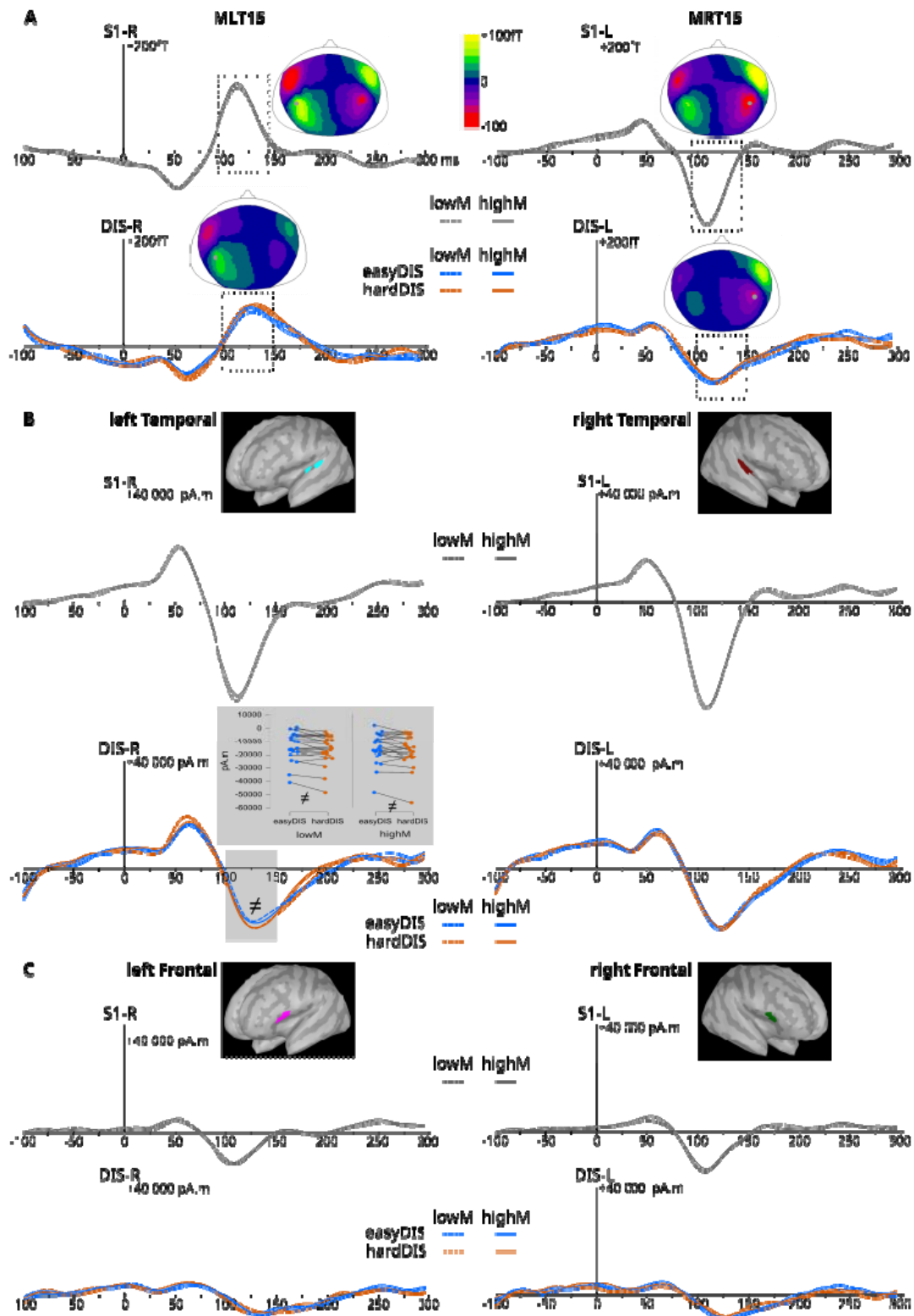
### Transient Evoked Responses: N1 to first tones of S1 and DIS

The time course of the transient evoked responses after each note in S1 and DIS melodies as recorded at the sensor level is shown in Figure 2. ERFs to the first notes of S1 and DIS are larger than ERFs to subsequent notes and are thus analyzed separately (see Figure 5). The first note of S1 and DIS evokes a large N1 response in contralateral temporal (Heschl Gyrus, HG, and around) and frontal (Inferior Frontal Gyrus, IFG) regions. Smaller responses with longer latencies are observed ipsilaterally. Therefore, the amplitude of the N1 is analyzed separately for each presentation side in the contra-lateral ROIs with Bayesian paired-value t-tests for the

first note of S1 (S1-L and S1-R separately), to assess the effect of the MEMdiff factor, and with Bayesian repeated-measure ANOVAs with MEMdiff and DISdiff as factors for the first note of DIS (DIS-L and DIS-R separately).

For the N1 elicited in response to the first presented tone (S1, time window 90-140 ms post S1 onset), no evidence is found for an effect of MEMdiff (all  $BF_{10} \leq 0.65$ ) in the four ROIs investigated (Table 1 and Figure 5B).

For the N1 elicited in response to the first to-be-ignored tone (DIS, time window 100-150 ms post DIS onset), the best model explaining the data in the left Temporal ROI (i.e., for DIS stimuli presented in the right ear) is the model with the DISdiff factor ( $BF_{10} = 3.6$ ), followed by the model with DISdiff and MEMdiff ( $BF_{10} = 2.2$ ), with the analysis of effects confirming only positive evidence for DISdiff ( $BF_{inclusion} = 3.7$ ). A larger N1 is observed in response to the first DIS tone in hardDIS compared to easyDIS. In the left IFG ROI, the best model explaining the data (N1 to the first DIS tone) is the full model including the interaction between MEMdiff and DISdiff ( $BF_{10} = 1.9$ ), however it is almost as likely as the null model and further Bayesian paired-value t-tests comparing N1 amplitudes across conditions reveal only weak evidence for differences between conditions, if any (all  $BF_{10} < 1.7$ ). In the right hemisphere ROIs (temporal and IFG), for DIS stimuli presented in the left ear, the best models explaining the N1 amplitudes are the null model (for all other models,  $BF_{10} < 0.9$ ).



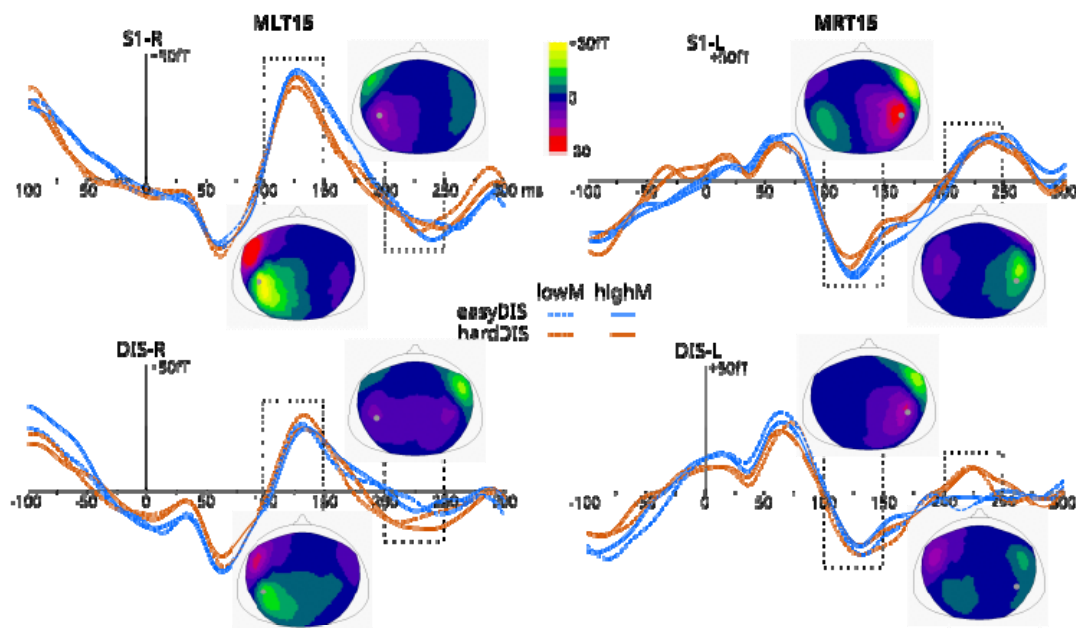
*Figure 5 – Transient evoked responses to the first tone. (A) In the sensor space, time course of the ERF to the first tone of the to-be-attended melody S1 and of the to-be-ignored melody DIS (tone onset at 0ms), for each DISdiff (DIS only) and MEMdiff condition (S1 and DIS), at MLT15 and MRT15 (above the left and right temporal lobes, respectively). Topoplots show sensor data over the time*



period of interest, indicated by the dotted rectangles (90 to 140 or 100 to 150 ms for S1 or DIS, respectively). Gray dots on topographies indicate corresponding sensor position. (B & C) In the source space, time course of the ERF to the first tone of S1 and DIS melodies, for each DISdiff (DIS only) and each MEMdiff condition, in the corresponding ROIs represented on the MNI template. The strip plot shows individual data averaged by condition in the gray period showing positive or greater evidence (see Table 1 for time-windows and results). Lines connect data from the same participant. Only contralateral tones are analyzed here: S1-R and DIS-R for left sensors and sources, and S1-L and DIS-L for right sensors and sources. S1-L or S1-R: S1 melodies presented to the left or right ear, respectively. DIS-L or DIS-R: DIS melodies presented to the left or right ear, respectively.

### Transient Evoked Responses: N1 to tones 2, 3, 4 (S1 and DIS)

Sensor-level ERFs for subsequent tones (S1 and DIS) are illustrated in Figure 6. Emergence tests reveal significant activity in contralateral temporal (HG and around) and frontal (IFG) regions at the latency of the N1 (100-150 ms post tone onset). Smaller responses with longer latencies are observed ipsilaterally. N1 amplitudes are analyzed in contralateral ROIs with Bayesian ANOVAs with StimulusType (S1 or DIS), MEMdiff, and DISdiff as factors (see Table 1 and Figure 7).



**Figure 6 – Transient evoked responses to the tones 2, 3 and 4 in the sensor space.** Time course of the averaged ERF to the tones 2, 3 and 4 of the to-be-attended melody S1 and of the to-be-ignored melody DIS (tone onset at 0ms), for each DISdiff and MEMdiff condition, at MLT15 and MRT15 (above the left and right temporal lobes, respectively). Topoplots show sensor data over the time periods of interest, indicated by the dotted rectangles (100 to 150 ms and 200 to 250 ms for N1 or P2 responses, respectively). Gray dots on topographies indicate corresponding sensor position. Only contralateral tones are studied here: S1-R and DIS-R for left sensors, and S1-L and DIS-L for right sensors. S1-L or S1-R: S1 melodies presented to the left or right ear, respectively. DIS-L or DIS-R: DIS melodies presented to the left or right ear, respectively.

In the left Temporal ROI, the best model explaining N1 amplitude is the full model, including the triple interaction between StimulusType, MEMdiff, and DISdiff ( $BF_{10} = 222797.5$ ). The analysis of effects reveals decisive evidence for StimulusType ( $BF_{inclusion} = 17470.0$ ), with larger N1 for S1 compared to DIS, and strong evidence for the triple interaction ( $BF_{inclusion} = 13.4$ ), which we further explore in separate analyses by Memory difficulty (for all other effects,  $BF_{inclusion} < 2.4$ ). *Under low Memory difficulty*, in a Bayesian ANOVA with StimulusType and DISdiff as factors, the best model explaining N1 amplitude is the full model including the StimulusType by DISdiff interaction ( $BF_{10} = 118659.4$ ). The analysis of effects reveals decisive evidence for StimulusType ( $BF_{inclusion} = 1692.7$ ) and for the StimulusType by DISdiff interaction ( $BF_{inclusion} = 108.4$ ), and weak evidence against DISdiff ( $BF_{inclusion} = 0.65$ ). Bayesian t-tests exploring this interaction reveal strong evidence for an effect of DISdiff on N1 amplitude for S1 ( $BF_{10} = 51.3$ , larger N1 amplitudes for the easyDIS condition), but weak evidence for an absence of effect of DISdiff on N1 amplitude for DIS ( $BF_{10} = 0.36$ ). *Under high Memory difficulty*, in a Bayesian ANOVA with StimulusType and DISdiff as factors, the best model explaining N1 amplitude is the model with only the StimulusType effect ( $BF_{10} = 104513.0$ ), followed by the model with StimulusType and DISdiff effects ( $BF_{10} = 56277.9$ ). The analysis of effects reveals decisive evidence for StimulusType ( $BF_{inclusion} = 103549.6$ ) but weak evidence against DISdiff ( $BF_{inclusion} = 0.54$ ).

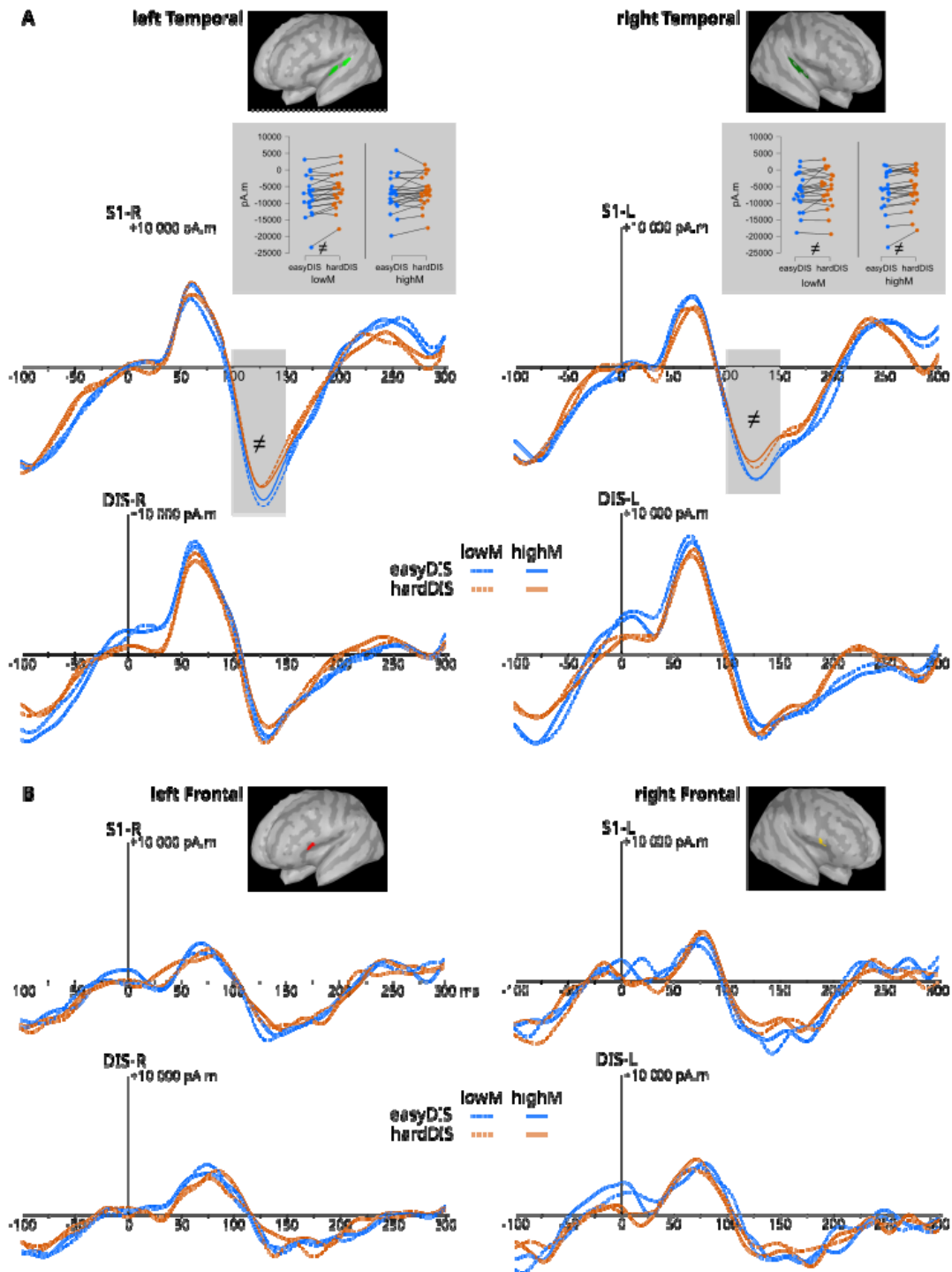
In the right Temporal ROI, the best model explaining N1 amplitude is the model with StimulusType, DISdiff, and the interaction between StimulusType and DISdiff ( $BF_{10} = 4173.9$ ), immediately followed by the model with the same effects and interaction and the effect of MEMdiff in addition ( $BF_{10} = 2399.1$ ). The analysis of effects reveals decisive evidence for the effect of StimulusType ( $BF_{inclusion} = 1520.4$ ), positive evidence for the interaction between StimulusType and DISdiff ( $BF_{inclusion} = 6.0$ ), and weak evidence for an absence of an effect of MEMdiff ( $BF_{inclusion} = 0.69$ ) and of DISdiff ( $BF_{inclusion} = 0.50$ ). Further post-hoc Bayesian t-test to explore the StimulusType-by-DISdiff interaction reveal that, for S1, there was positive evidence for larger N1 amplitude for easyDIS than for hardDIS ( $BF_{10} = 4.2$ ), whereas for DIS, there is weak evidence for no difference in N1 amplitude between easyDIS and hardDIS ( $BF_{10} = 0.63$ ).

In the left Frontal ROI, the best model explaining N1 amplitude is the model with only the effect of StimulusType ( $BF_{10} = 5266.8$ ). Other models have similar  $BF_{10}$ , but the analysis

of effects reveals only decisive evidence for StimulusType ( $BF_{\text{inclusion}} = 3088.3$ ; for all other effects and interactions,  $BF_{\text{inclusion}} < 2.1$ ).

In the right Frontal ROI, the best model explaining N1 amplitude is the model with StimulusType ( $BF_{10} = 22.3$ ), followed by the model with StimulusType, DISdiff, and the interaction between StimulusType and DISdiff ( $BF_{10} = 17.1$ ), the model with StimulusType and DISdiff ( $BF_{10} = 11.9$ ), and the model with StimulusType, MEMdiff and the interaction between StimulusType and MEMdiff ( $BF_{10} = 8.4$ ). The analysis of effects confirms strong evidence for the effect of StimulusType ( $BF_{\text{inclusion}} = 22.5$ ), and only weak evidence for the interactions between StimulusType and DISdiff ( $BF_{\text{inclusion}} = 1.4$ ) and between StimulusType and MEMdiff ( $BF_{\text{inclusion}} = 1.6$ ); there is weak to positive evidence against all other effects ( $BF_{\text{inclusion}} < 0.55$ ).

In the four ROIs, the N1 is larger for S1 than DIS, revealing efficient filtering. In the left temporal ROI, the N1 to S1 is larger in easyDIS than in hardDIS, under lowM only. In the right temporal ROI, the N1 to S1 is larger in easyDIS than in hardDIS, irrespective of the memory task difficulty.



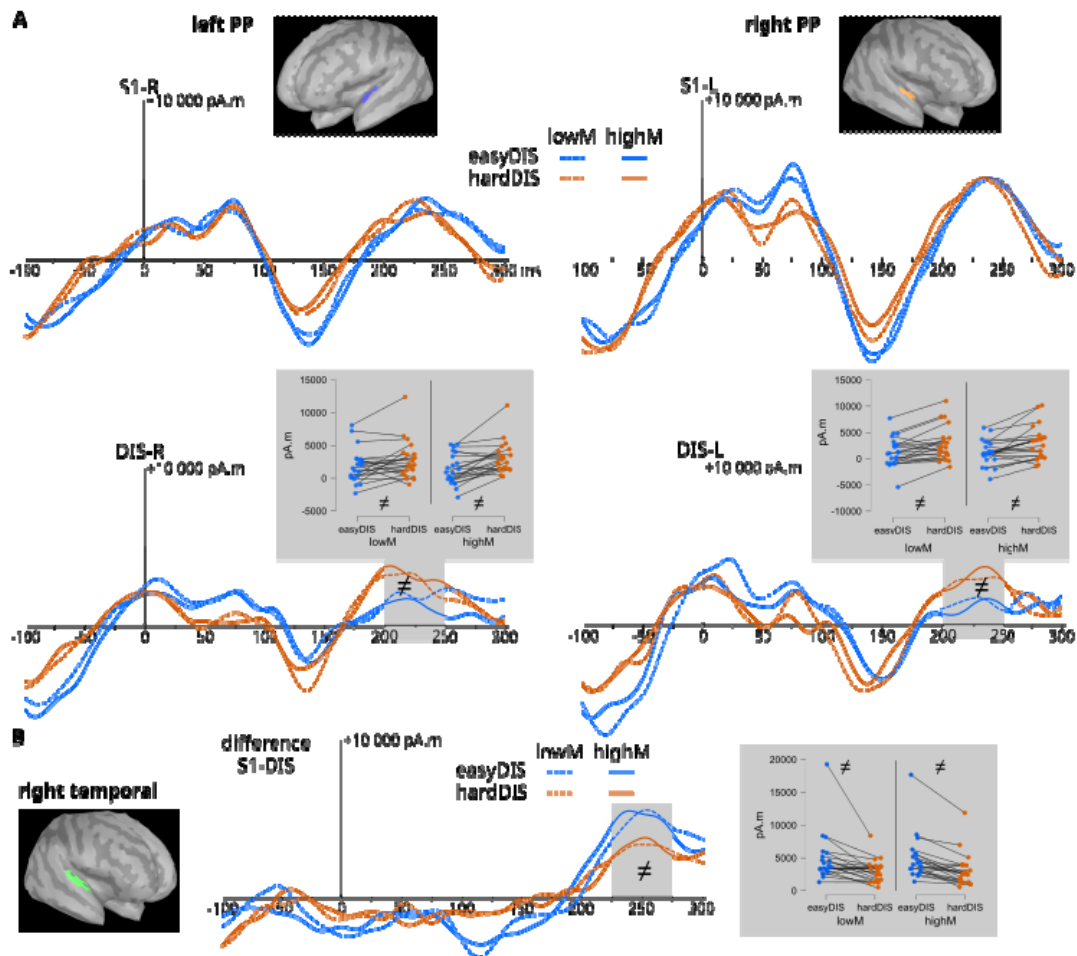
**Figure 7 – Transient evoked responses to the tones 2, 3 and 4 in the source space (NI ROIs).** Time course of the averaged ERF to the tones 2, 3 and 4 of the to-be-attended melody S1 and of the to-be-ignored melody DIS (tone onset at 0ms), for each DISdiff and MEMdiff condition (S1 and DIS), in the corresponding ROI represented on the MNI template. The strip plots show individual data averaged by condition in the gray periods showing positive or greater evidence (see Table 1 for time-windows and results). Lines connect data from the same participant. Only contralateral tones are analysed here: S1-R and DIS-R for left sources, and S1-L and DIS-L for right sources. S1-L or S1-R: S1 melodies presented to the left or right ear, respectively. DIS-L or DIS-R: DIS melodies presented to the left or right ear, respectively.

### Transient Evoked Responses: P2 to tones 2, 3, 4 (S1 and DIS)

Activity is observed in the contralateral Planum Polare in the P2 latency range (200-250 ms) for tone 2,3,4 (S1 and DIS). As for the N1, P2 amplitudes are analyzed with Bayesian repeated-measure ANOVAs with StimulusType, MEMdiff, and DISdiff as factors (see Table 1 and Figure 8).

In the left Planum Polare, the best model explaining P2 amplitude is the model with StimulusType, DISdiff, and the interaction between StimulusType and DISdiff ( $BF_{10} = 32.1$ ). The analysis of effects confirms positive evidence for the interaction between StimulusType and DISdiff ( $BF_{inclusion} = 5.6$ ) and for the effect of DISdiff ( $BF_{inclusion} = 5.0$ ), and weak evidence for the effect of StimulusType ( $BF_{inclusion} = 1.1$ ). Further post-hoc Bayesian t-test to explore the StimulusType-by-DISdiff interaction reveal that, for S1, there is positive evidence for no difference in P2 amplitude between easyDIS and hardDIS ( $BF_{10} = 0.23$ ), whereas for DIS, there is strong evidence for a larger P2 amplitude in hardDIS compared to easyDIS ( $BF_{10} = 22.8$ ).

In the right Planum Polare, the best model explaining P2 amplitude is the model with StimulusType, DISdiff, and the interaction between StimulusType and DISdiff ( $BF_{10} = 855.6$ ), followed by the model with StimulusType and DISdiff ( $BF_{10} = 732.2$ ). The analysis of effects confirms an effect of StimulusType with decisive evidence ( $BF_{inclusion} = 123.0$ ; P2 is larger for S1 than DIS), of DISdiff with positive evidence ( $BF_{inclusion} = 6.9$ ), and of the interaction between StimulusType and DISdiff with weak evidence ( $BF_{inclusion} = 1.2$ ). Further post-hoc Bayesian t-test to explore the StimulusType-by-DISdiff interaction reveal that, for S1, there is positive evidence for no difference in P2 amplitude between easyDIS and hardDIS ( $BF_{10} = 0.25$ ), whereas for DIS, there is strong evidence for a larger P2 amplitude in hardDIS compared to easyDIS ( $BF_{10} = 69.9$ ).



**Figure 8 – Transient evoked responses to the tones 2, 3 and 4 in the source space (P2 and late differential response ROIs).** (A) Time course of the averaged ERF to the tones 2, 3 and 4 of the to-be-attended melody S1 and of the to-be-ignored melody DIS (tone onset at 0ms), for each DISdiff and MEMdiff condition (S1 and DIS), in the corresponding ROI represented on the MNI template. (B) Time course of the difference (S1-DIS) between averaged ERF to the tones 2, 3 and 4 of the to-be-attended melody S1 and of the to-be-ignored melody DIS (tone onset at 0ms), for each DISdiff and MEMdiff condition, in the corresponding ROI represented on the MNI template. The strip plots show individual data averaged by condition in the gray periods showing positive or greater evidence (see Table 1 for time-windows and results). Lines connect data from the same participant. Only contralateral tones are analyzed here: S1-R and DIS-R for left sources, and S1-L and DIS-L for right sources. S1-L or S1-R: S1 melodies presented to the left or right ear, respectively. DIS-L or DIS-R: DIS melodies presented to the left or right ear, respectively. leftPP: left Planum Polare, right PP: right Planum Polare.

### Transient Evoked Responses: late differential response to tones 2, 3, 4 (S1 - DIS)

The ERF evoked by S1 and DIS not only differs during N1 and P2, as described above, but they also diverge later, between 225 and 275 ms, in right temporal areas around Heschl's gyrus, irrespective of stimulation side. This late differential response (S1 – DIS amplitude) is

examined with Bayesian repeated-measure ANOVAs with Stimulus\_Side, DISdiff, and MEMdiff as factors (see Table 1 and Figure 8).

In the right Temporal ROI, the best model explaining the late differential response (S1 – DIS amplitude) is the model with the factors Stimulus\_Side, DISdiff, and the interaction between Stimulus\_Side and DISdiff ( $BF_{10} = 91.2$ ), followed by the model with only the effect of DISdiff ( $BF_{10} = 75.5$ ) and the model with the effects of Stimulus\_Side and DISdiff ( $BF_{10} = 36.4$ ). The analysis of effects confirms strong evidence for DISdiff ( $BF_{inclusion} = 42.9$ ) and weak evidence for the interaction between Stimulus\_Side and DISdiff ( $BF_{inclusion} = 2.0$ ), while there is weak evidence against an effect of Stimulus\_Side ( $BF_{inclusion} = 0.49$ ). The difference between S1 and DIS ERF amplitude is larger for easyDIS than hardDIS.

### Sustained Evoked Responses

During S1 and DIS presentation, irrespective of S1 presentation side, emergence tests (time window 500-2000 ms after S1 onset) reveal activity in bilateral temporal areas, in two distinct clusters in the Planum Polare and the Planum Temporale. Activity in these temporal ROIs is examined with Bayesian repeated-measure ANOVAs with S1side, DISdiff, and MEMdiff as factors (see Table 1 and Figure 9).

In the left Planum Polare, the best model explaining results during presentation of S1 and DIS melodies is the one with the factors DISdiff and S1side ( $BF_{10} = 129061.0$ ), immediately followed by the model with only DISdiff ( $BF_{10} = 94853.0$ ), and several other models with similar evidence. The analysis of effects only reveals decisive evidence for the effect of DISdiff ( $BF_{inclusion} = 89087.1$ ) and weak evidence for the effect of S1side ( $BF_{inclusion} = 1.4$ ), whereas there is weak to positive evidence against all other effects ( $BF_{inclusion} < 0.63$ ). Sustained evoked responses in the left Planum Polare during S1 and DIS are larger in condition hardDIS compared to easyDIS.

In the right Planum Polare, the best model explaining sustained evoked response amplitudes during S1 and DIS is the one with only the factor DISdiff ( $BF_{10} = 207.1$ ). Other models explain almost as well the data, however the analysis of effects brings only decisive evidence for an effect of DISdiff in the right Planum Polare ( $BF_{inclusion} = 202.2$ ). As in the left hemisphere, response amplitudes are larger in condition hardDIS compared to easyDIS.

In the left Planum Temporale, the best model explaining sustained evoked response amplitude during S1 and DIS is the one with factors DISdiff, MEMdiff, S1side, and the interaction between DISdiff and MEMdiff ( $BF_{10} = 1.6$ ). Several other models, including the null model, explain almost as well the data. The analysis of effects only reveals weak

evidence for the effect of DISdiff ( $BF_{\text{inclusion}} = 1.9$ ) and S1side ( $BF_{\text{inclusion}} = 2.2$ ), with differences in the same direction as in the Planum Polare, and weak evidence for no effect of MEMdiff ( $BF_{\text{inclusion}} = 0.90$ ) and of the interaction between DISdiff and MEMdiff ( $BF_{\text{inclusion}} = 0.47$ ).

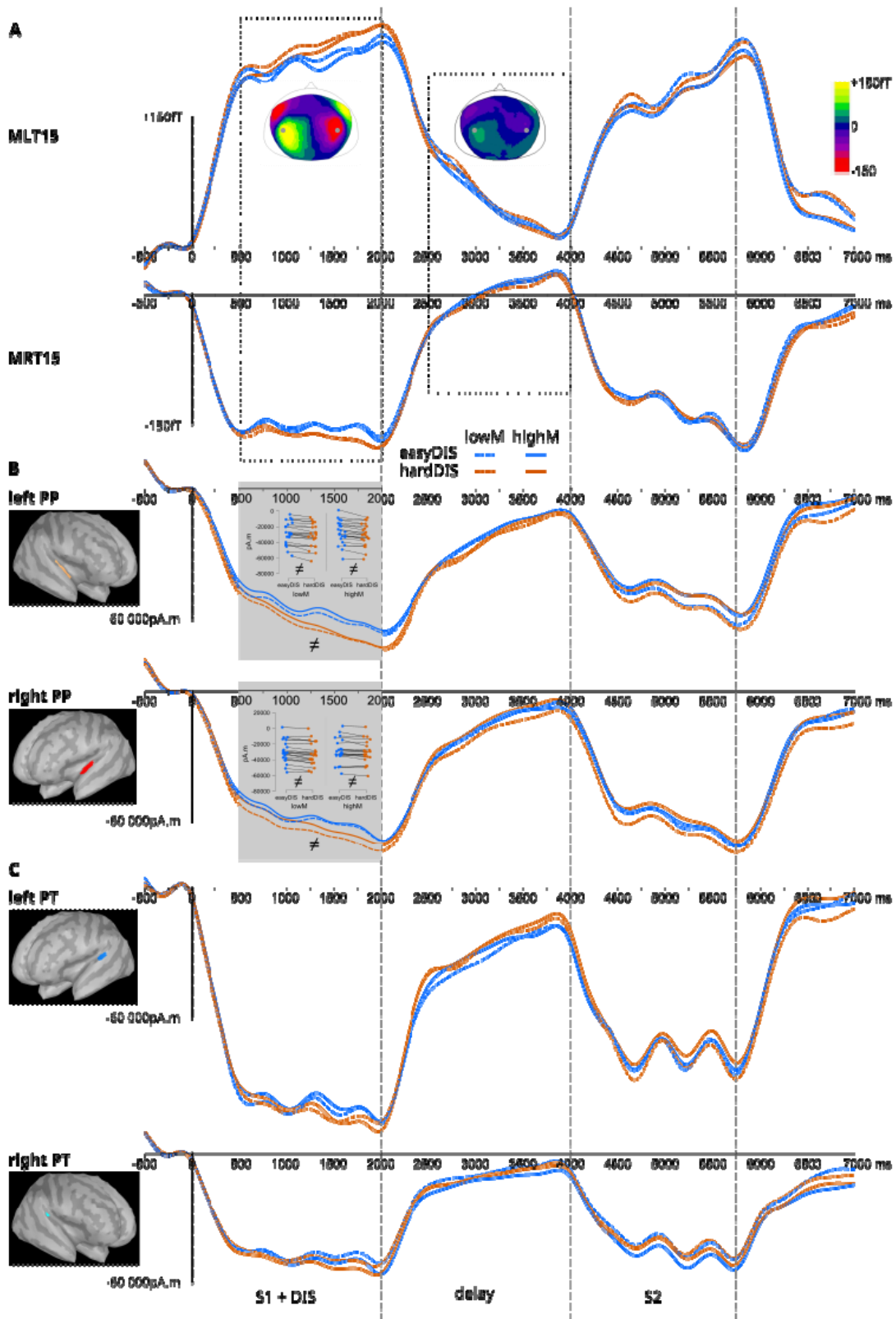
In the right Planum Temporale, the best model explaining sustained evoked response amplitude during S1 and DIS is the null model (for all other models,  $BF_{10} < 0.65$ ).

During the retention delay (time window 2500–4000 ms), sustained evoked responses are observed only in the left hemisphere, irrespective of S1 side, in the same areas as during S1 and DIS presentation. Activity in these left temporal ROIs is examined with Bayesian repeated-measure ANOVAs with S1side, DISdiff, and MEMdiff as factors.

In the left Planum Polare, the best model explaining sustained response amplitude is the null model (for all other models,  $BF_{10} < 0.57$ ).

In the left Planum Temporale, the best model explaining sustained response amplitude is the model with only the S1side effect ( $BF_{10} = 1.13$ ). Other models, including the null model, explain almost as well the data, and the analysis of effects reveals only weak evidence for the effect of S1side ( $BF_{\text{inclusion}} = 1.13$ ), with larger amplitudes ipsilaterally.





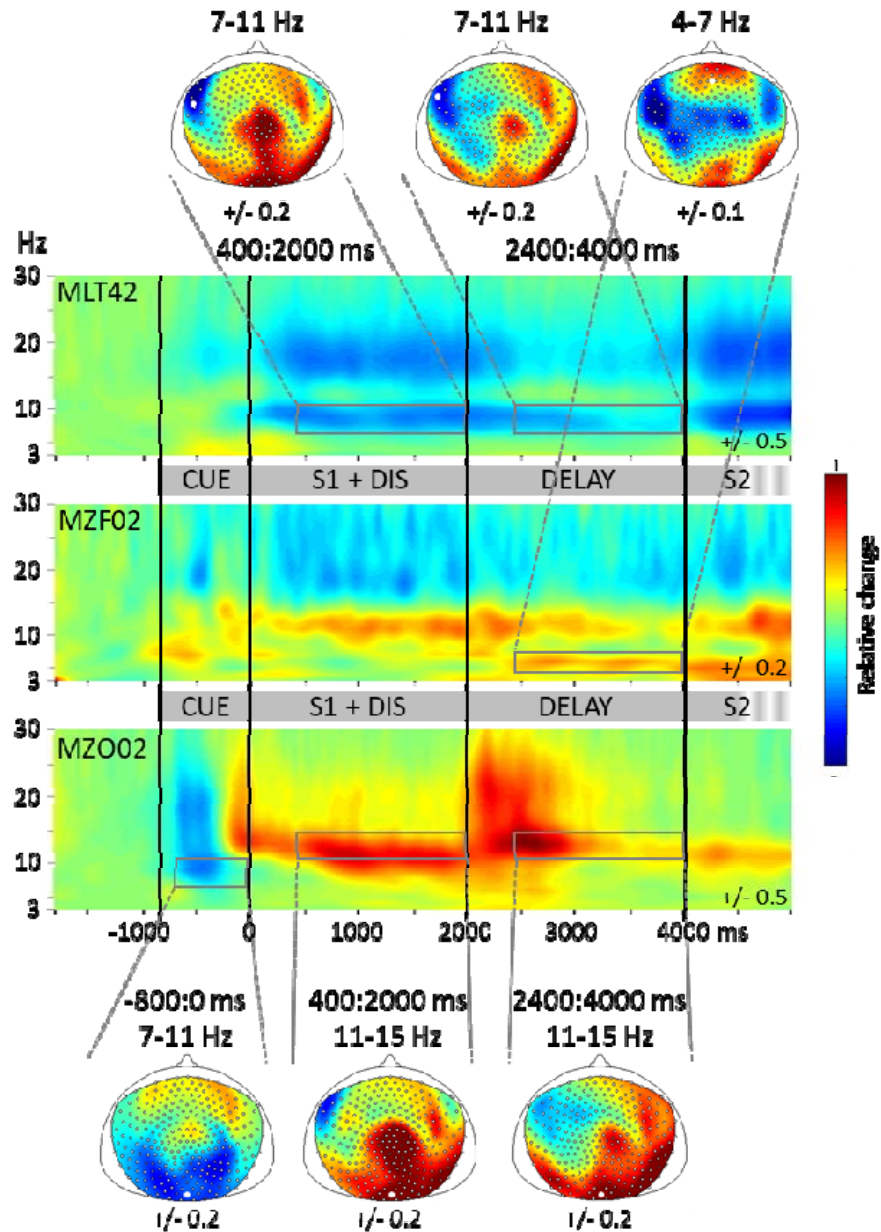
*Figure 9 – Sustained evoked responses. (A) In the sensor space, time course of the ERF to S1 & DIS melodies, the delay and to S2 (S1 onset at 0ms), for each DISdiff and MEMdiff condition, at MLT15 and MRT15 (above the left and right temporal lobes, respectively). Topoplots show sensor data over the time periods of interest, indicated by the dotted rectangles (500 to 2000 during S1 & DIS melodies,*

2500 to 4000 during the delay). Gray dots on topographies indicate corresponding sensor position. (B & C) In the source space, time course of the ERF for each DISdiff and each MEMdiff condition, in the corresponding ROIs represented on the MNI template. The strip plot shows individual data averaged by condition in the gray periods showing positive or greater evidence (see Table 1 for time-windows and results). Lines connect data from the same participant.

### *Time-Frequency results*

#### Sensor-level activation

The time-frequency power (relative change) plots computed on sensor-level data (see **Error! Reference source not found.**) with a baseline from -1.8 to -1s relative to S1 onset reveal a decrease in alpha power after cue onset at occipital sensors. A decrease in alpha power (7-11 Hz) is observed during the presentation of the S1 and DIS melodies and during the delay at left temporal sensors; while an increase in alpha power (11-15 Hz) is observed at occipital sensors. These two alpha sub-bands will be named low and high alpha in the following. Finally, an increase in theta power (4-7 Hz) is observed during the retention delay at frontal sensors.



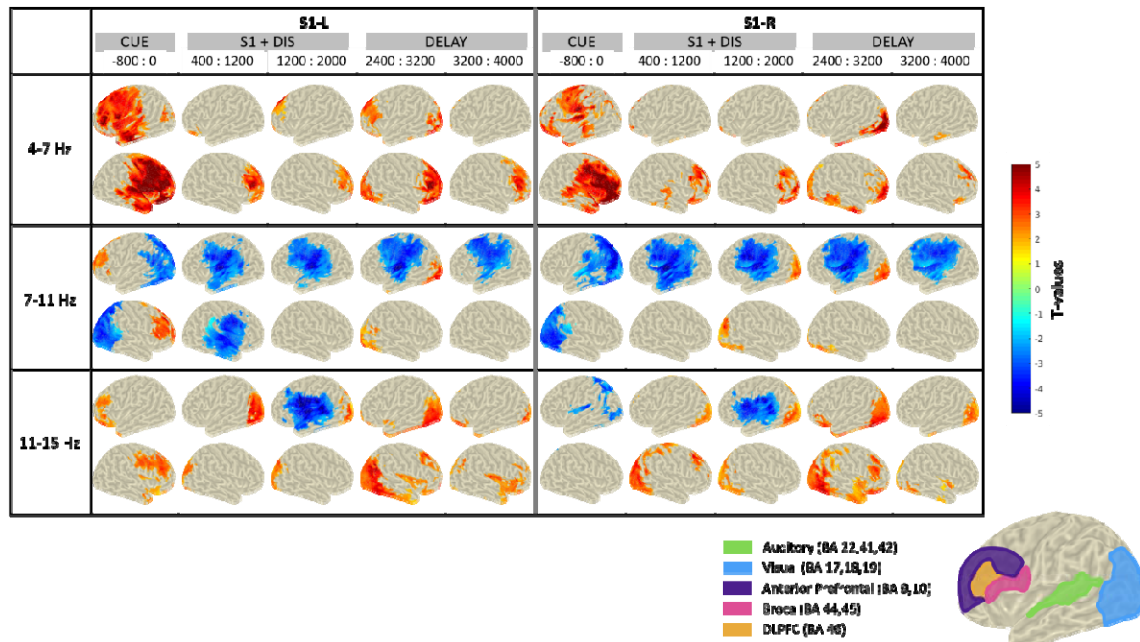
**Figure 10 – Time-frequency plots in the sensor space.** Time-frequency power (relative change) plots during Cue presentation, S1 & DIS melodies, and the delay (S1 onset at 0ms), for all conditions averaged, at a temporal (MLT42), a frontal (MZF02) and an occipital sensor (MZO02) and corresponding topographies. Response to S2 is not fully represented here. In comparison to baseline (-1800 to -1000 ms relative to S1 onset), a decrease in power appears in blue and an increase in power appears in red. White dots on topographies indicate corresponding sensor position.

### Source-level whole brain activation

Sources of theta and alpha activities are estimated using DICS beamformer in different time-frequency windows of interest, and contrasted to a pre-cue baseline period using non-parametric cluster-based permutation testing, for S1 presented to the left or right ear separately (Figure 11).

The main power modulations are:

1. An increase in theta power in anterior prefrontal regions (BA 9, 10) during cue, melody presentation, and delay, more pronounced in the right hemisphere (Figure 11, top row);
2. A decrease in low alpha power in auditory regions in superior temporal cortices (BA 22, 41, 42), Broca area (BA 44, 45), and dorsolateral prefrontal cortex (DLPFC, BA 46) during melody presentation in both hemispheres, and during the delay in the left hemisphere (Figure 11, middle row);
3. A decrease in low alpha power in visual regions in occipital cortices (BA 17, 18, 19) during cue presentation (Figure 11, middle row) followed by an increase in high alpha power during melody presentation and delay (Figure 11, bottom row).



**Figure 11 – Source activity in theta and alpha bands.** Distributions of T values for each time-frequency window in comparison to a pre-cue baseline (-1800ms to -1000ms locked to S1 onset) for trials with S1 presented to the left or the right, separately (S1-L & S1-R). The results are masked with the p-value coming from the cluster-based permutation tests: only significant clusters are shown ( $p < 0.05$ ). In comparison to baseline, a decrease in power appears in blue and an increase in power appears in red. In the right bottom corner, the chosen regions of interest for further analyses are presented. The corresponding Brodmann areas are indicated in brackets for each region of interest.

### Source-level ROI activation

According to the analysis of the individual peak frequency in each ROI, we investigated the following frequency bands: 4-7 Hz in anterior prefrontal regions; 8-11 Hz for decrease in

alpha power in the auditory, visual, Broca and DLPFC ROIs; and 9-12 Hz for increase in alpha power in the visual ROI. To investigate the impact of the memory task and distractor difficulties, power values in time-frequency windows of interest are examined using Bayesian repeated-measure ANOVAs with S1side, DISdiff, and MEMdiff as factors (see Table 2 and Figure 12).

*Anterior prefrontal theta.* In the anterior prefrontal regions, the best model explaining results in the 4-7 Hz band after cue onset and before S1 onset is the one with the factors DISdiff and S1side in the left hemisphere ( $BF_{10} = 5.0$ ) and with the factor MEMdiff in the right hemisphere ( $BF_{10} = 1.2$ ). The analysis of effects, in the left hemisphere, revealed positive evidence for the effect of S1side ( $BF_{inclusion} = 3.7$ ) and weak evidence for the effect of DISdiff ( $BF_{inclusion} = 1.4$ ). The increase in theta power is larger after the left cue presentation. The best model explaining results in the 4-7 Hz band after S1 onset is the one with the factor DISdiff in the left hemisphere ( $BF_{10} = 1.9$  between 400 and 1200 ms;  $BF_{10} = 3.3$  between 1200 and 2000 ms;  $BF_{10} = 4.5$  between 3200 and 4000 ms) and in the right hemisphere ( $BF_{10} = 10.6$  between 3200 and 4000 ms); otherwise the null model is the best model (for all other models,  $BF_{10} < 0.89$ ). The increase in theta power is larger in the hardDIS condition.

*Auditory and prefrontal low alpha.* In the left auditory regions, the best model explaining results in the 8-11 Hz band during the presentation of S1 and DIS melodies is the one with the factor MEMdiff only ( $BF_{10} = 3.4$  between 400 and 1200 ms,  $BF_{10} = 1.7$  between 1200 and 2000 ms), and during the delay, it is the null model. The decrease in alpha power is larger in the lowM condition.

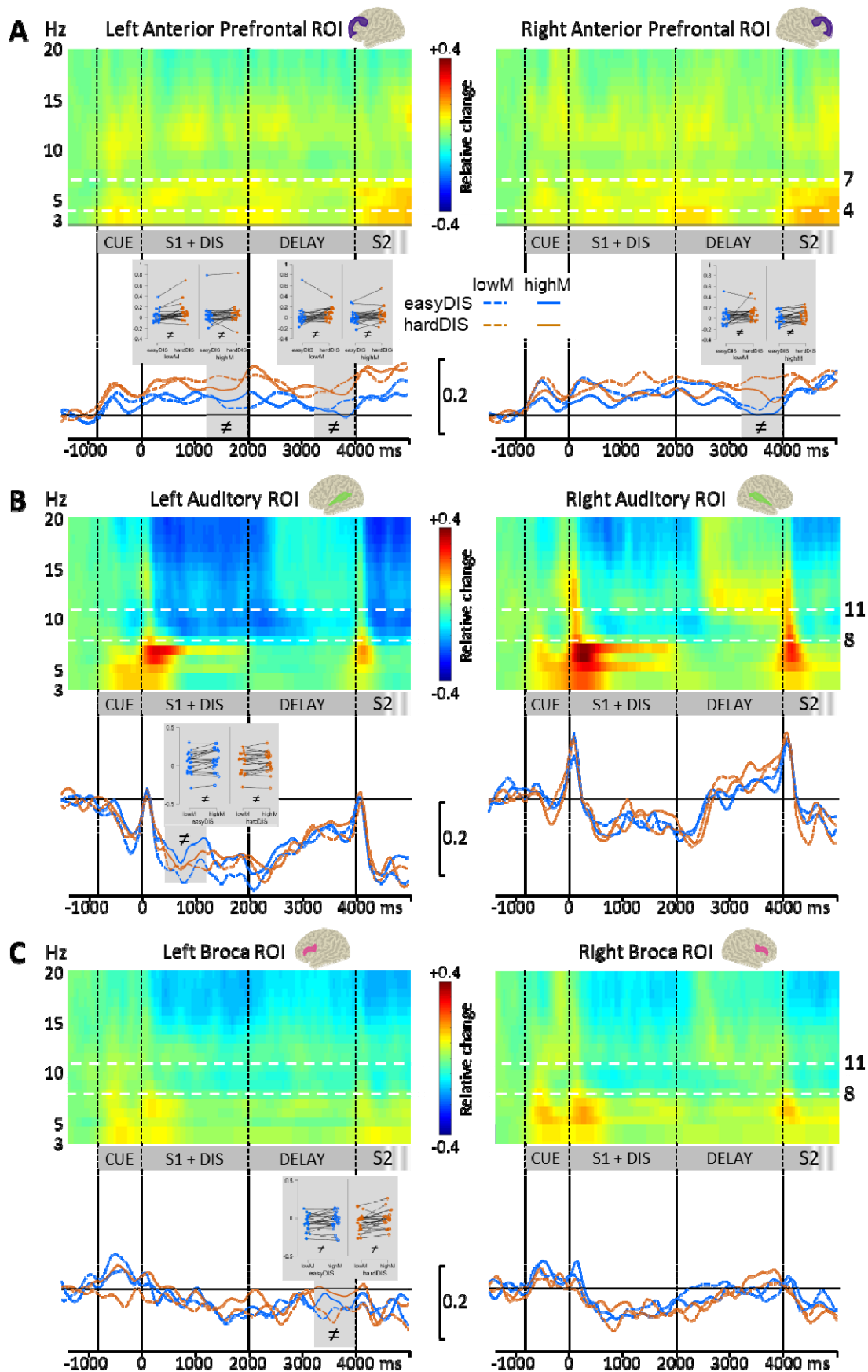
In the right auditory regions, the best model explaining results in the 8-11 Hz band during presentation of S1 and DIS melodies is the one with the factor S1side ( $BF_{10} = 1.5$  between 400 and 1200 ms). Between 1200 and 2000ms, the best model is the null model (for all other models,  $BF_{10} < 0.94$ ).

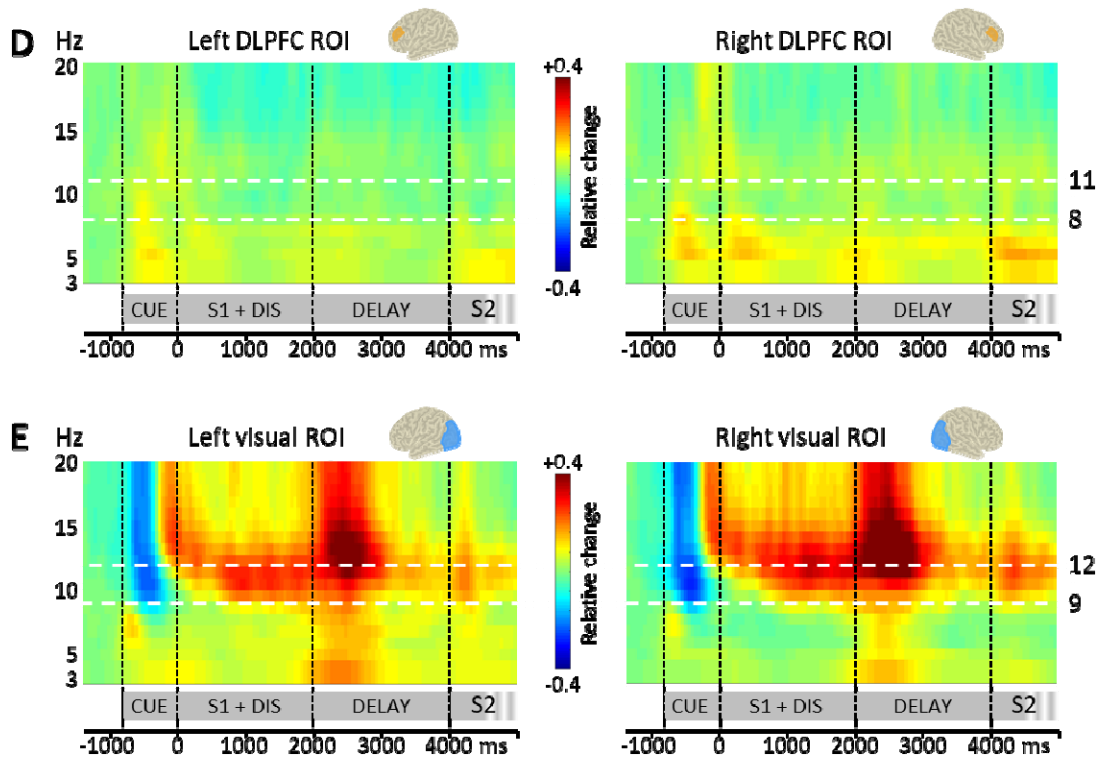
In the Broca areas, the best model explaining results in the 8-11 Hz band after S1 onset is the null model (for all other models,  $BF_{10} < 0.41$ ), except between 400 and 1200 ms (best model with factor S1side:  $BF_{10} = 1.1$ ) and between 3200 and 4000 ms (best model with factor MEMdiff:  $BF_{10} = 3.2$ ) in the left hemisphere. The decrease in alpha power is larger in the lowM condition.

In the left DLPFC, the best model explaining results in the 8-11 Hz band after S1 onset is the null model (for all other models,  $BF_{10} < 0.54$ ).

*Visual low and high alpha.* In the bilateral visual regions, the best model explaining results in the 8-11 Hz band during cue presentation is the null model. In the bilateral visual

regions, the best model explaining results in the 9-12 Hz band during S1 and DIS melodies and during the delay is the null model, except in the right visual regions between 400 and 1200 ms (best model with factor S1side:  $BF_{10} = 1.0$ ) and between 3200 and 4000 ms (best model with factors DISdiff and S1side:  $BF_{10} = 2.6$ ) (for all other models,  $BF_{10} < 0.77$ ). The decrease after the cue and the increase after S1 onset in alpha power do not seem to be modulated by any of the investigated factors.





**Figure 12 – Time-frequency plots and time profiles in the source space.** Time-frequency power (relative change) plots during Cue presentation, S1 & DIS melodies, and the delay (S1 onset at 0ms), for all conditions averaged, in the left and right Anterior Prefrontal regions (A), in the left and right Auditory cortices (B), in the left and right Broca areas (C), in the left and right Dorso-Lateral Prefrontal Cortex (DLPFC, D), and in the left and right Visual cortices (E). Response to S2 is not fully represented here. In comparison to baseline (-1800 to -1000 ms relative to S1 onset), a decrease in power appears in blue and an increase in power appears in red. Regions of interest were defined based on the results from the cluster-based permutation tests performed on the DICS-reconstructed sources for the whole brain. Time course of the power (relative change) for each DISdiff and each MEMdiff condition, in the corresponding ROIs represented on the MNI template: alpha band (8 to 11 Hz) in the Auditory (A) and BROCA (B) ROIs, theta band (4 to 7 Hz) in the Anterior Prefrontal (C) ROIs. The strip plot shows individual data averaged by condition in the gray periods showing positive or greater evidence (see Table 2 for time-windows and results). Lines connect data from the same participant.



## Discussion

In the present study, we investigate auditory working memory and selective attention, in a delayed-matching-to-sample task (DMST) requiring to filter out distractors during encoding of melodic sequences in memory. Behavioral and MEG results allow to further understand working memory, auditory selective attention, and their interactions, as discussed below.

### *Electrophysiological markers of non-verbal auditory working memory*

During the DMST at the core of the MEMAT paradigm, we observe a series of electrophysiological markers that were expected based on prior studies: (1) following the presentation of the visual cue (which itself generated visual ERFs and an alpha decrease in visual areas), in anticipation of the sequence to encode, a slow magnetic field develops bilaterally (magnetic counterpart of the CNV, see below), notably in the Planum Polare, and theta power increases in anterior prefrontal regions; (2) transient and sustained evoked responses are observed during sequence encoding in superior temporal and inferior frontal areas, along with an increase in theta power in anterior prefrontal areas, a decrease in alpha power in a fronto-temporal network, and an increase in alpha power in visual areas; (3) a sustained evoked response persists in superior temporal areas during the retention delay, also along with an increase in theta power in anterior prefrontal areas, a decrease in alpha power in a left fronto-temporal network, and an increase in alpha power in visual areas.

This pattern of transient and sustained ERFs is consistent with previous descriptions in auditory non-verbal DMST (Albouy et al., 2013; Grimault et al., 2014). Here the addition of a visual cue at a fixed delay prior to S1 onset allows to characterize the slow response developing in anticipation of the sound sequences, that could reflect the sensory contribution to the CNV (see Brunia & Van Boxtel, 2001) and strongly resembles the auditory preparatory potential observed with intracranial recordings in epileptic patients slightly more posteriorly in Heschl gyri (Hu et al., 2020).

Power in the alpha band is modulated along the course of a trial: a transient decrease in visual areas following the visual cue, and then a sustained increase in visual areas associated with a sustained decrease in fronto-temporal areas during encoding and maintenance (we did not study the retrieval phase). Following the interpretation of the alpha rhythm as an inhibitory process (e.g., Klimesch et al., 2007; Foxe & Snyder, 2011; Jensen & Mazaheri, 2010; Thut et al., 2006; Palva & Palva, 2011), this pattern suggests a transient activation of the visual system to process the visual cue, followed by an inhibition of task-irrelevant occipital visual areas and an activation of the task-relevant fronto-temporal auditory

network during sound encoding and maintenance in memory. In keeping with ElShafei et al. (2018, 2020), alpha oscillations are centered around a higher frequency in visual areas compared to auditory areas during auditory processing.

Power in the theta band increases in anterior frontal areas during cue processing and the subsequent encoding and maintenance phases. Studies of short-term and working verbal memory with EEG/MEG have almost always uncovered increased frontal theta oscillations, in particular during the maintenance phase (review in Pavlov & Kotchoubey, 2022). As discussed in Hsieh and Ranganath (2014), the specific role of theta oscillations (and theta-gamma coupling) in short-term/working memory processes is debated, and might further depend on the regions involved (frontal vs. hippocampal areas for example). Midline frontal theta oscillations have been in particular associated with maintaining temporal relationships between items (Hsieh et al., 2011). The present study reveals that frontal theta oscillations are also involved in non-verbal auditory memory, both during encoding and maintenance of pitch sequences.

Here, we manipulate memory task difficulty at the block level, and participants were warned about the difficulty of the upcoming block of trials. At the behavioral level, as expected (Blain, Talamini, et al., 2022; Blain, de la Chapelle, et al., 2022), accuracy decreases and response time increases when the difficulty of the memory task increases. At the neurophysiological level, an increase in the amplitude of the slow ERF (CNV) in anticipation of the target melody is observed in the high difficulty memory task relative to the low difficulty one when the left ear is cued, in the contralateral right auditory cortex (Figure 4). This result confirms the efficiency of the manipulation of task difficulty, with more pronounced anticipation of the relevant sound when the memory task is more difficult.

Beyond this anticipation effect, a smaller decrease in alpha oscillations was observed in the high difficulty memory condition relative to the low difficulty one, in the left auditory cortex during encoding of the S1 melody in memory (Figure 12B), and in the left inferior frontal cortex (Broca's area) during the retention delay (Figure 12C). These results in the alpha band suggest that in the difficult memory condition, the left auditory fronto-temporal network is less recruited than during the easier memory condition. We will return to this point when discussing the interaction between memory and attention.

#### *Deployment of auditory selective attention during a working memory task*

During sequence encoding in MEMAT, a distracting melody is presented in the other ear, which is either easy or hard to ignore (on different trials within the same blocks). Participants

succeed in selecting to-be-attended (S1) over to-be-ignored (DIS) melodies as evidenced by larger ERFs for target tones over distracting tones in temporal and frontal regions (N1, P2, late response for notes 2-3-4, see Figures 5, 6, 7, 8 and Table 1; review in Giard et al., 2000). The difficulty of the attentional filtering impedes as expected on performance and reaction times (Blain, Talamini, et al., 2022; Blain, de la Chapelle, et al., 2022), with poorer performance and longer RTs for difficult-to-ignore distractors. This filtering difficulty modulates several of the electrophysiological markers listed above (see Tables 1 and 2), during the encoding phase of the DMST (transient and sustained ERFs, theta oscillations), as well as during the maintenance phase (theta oscillations). These modulations of electrophysiological responses shed light on how selective attention operates during a working memory task.

In response to the first distracting tone, a larger N1 amplitude is observed in response to the hard-to-ignore distractor than to the easy-to-ignore distractor in the left temporal areas (Figure 5). As in MEMAT we manipulate the frequency similarity between to-be-attended and to-be-ignored sounds to create two levels of filtering difficulty, the hard-to-ignore sounds being closer in frequency to the to-be-attended melody could catch more attention and be more difficult to suppress than the easy-to-ignore sounds, in line with contingent stimulus-driven orienting (Folk et al., 1992; Corbetta & Shulman, 2002). This suggests a more efficient inhibition of the easy-to-ignore distracting tones as observed in previous EEG studies of auditory selective attention (Alain & Woods, 1994; Melara et al., 2005).

Critically, in bilateral superior temporal regions, in response to subsequent tones, N1 amplitude for the to-be-attended tones is larger when accompanied with easy-to-ignore distracting melodies, whereas the N1 to the to-be-ignored tones is not modulated by filtering difficulty (Figure 7). It suggests a facilitation of the processing of the target, more efficiently so when the distracting sounds are dissimilar to the target, in line with previous findings (Alain & Woods, 1994; Alain et al., 1993).

Later on, more anteriorly, in bilateral planum polare, the amplitude of the P2 to the tones of the melody to ignore is smaller when these tones were easy rather than difficult to ignore, in keeping with previous results (Alain & Woods, 1994). This suggests a more efficient inhibition of the distracting tone processing when they are easy to ignore (Figure 8).

Around 250 ms, a larger ERF amplitude for to-be-attended tones than for to-be-ignored tones in right temporal areas seems to be related to an additional component superimposed to the obligatory P2, such as the PN (« Processing Negativity »; Näätänen, 1982, 1992). This effect is more pronounced when the to-be-ignored tones are easy to ignore,

i.e. more dissimilar to the to-be-attended tones (Alho et al., 1987) or when the task is easier (Melara et al., 2005). This increased component suggests a larger differential processing of relevant and irrelevant tones when distractors are easy to ignore, and has been interpreted as reflecting active suppression of irrelevant signal (Alho et al., 1987; Melara et al., 2005).

Taken together, these findings highlight that distinct attentional mechanisms are at play, with facilitation of target processing preceding inhibition of irrelevant tones, in keeping with previous findings (Michie et al., 1993; Alho et al., 1987, 1994; Bidet-Caulet et al., 2007, 2010; Alain & Woods, 1994; Alain et al., 1993; Melara et al., 2005). These two effects have distinct localizations: auditory areas in the vicinity of the primary auditory cortex for target facilitation, and more anterior superior temporal areas in the planum polare for distractor inhibition, in line with previous observations (Rif et al., 1991). Except for the later differential effect (~250 ms) which was observed only in the right hemisphere, all these effects on transient ERFs were bilateral in agreement with most previous studies. All these mechanisms are less efficient when targets and distractors are more similar (Alain & Woods, 1994; Alain et al., 1993).

During sound sequence encoding, in addition to transient ERFs following each tone of the target or distracting melodies, a sustained evoked response was observed in bilateral superior temporal areas. In bilateral planum polare, the sustained evoked response is larger when the distractors are hard-to-ignore compared to easy-to-ignore, suggesting that this component reflects the deployment of cognitive resources (listening effort) to solve the difficult filtering task. A similar modulation of the sustained evoked response during S1 encoding by task difficulty in an auditory DMST was also observed in Albouy et al. (2013). It is noteworthy here that sustained evoked responses and target-related transient ERFs are modulated in opposite directions by the difficulty to filter out the distracting melodies, suggesting that the deployment of additional resources when the distractors are hard-to-ignore (reflected in the sustained response) is not sufficient to restore the same level of differential processing between targets and distractors in auditory areas (reflected in target and distractor-related transient ERFs). This failure translates in behavioral data as costs of filtering difficulty, both for  $d'$  and RT.

These effects on the ERFs highlight that during sound sequence encoding in memory, the processing of targets (and distractors) is modulated by attentional processes, possibly resulting in more or less precise memory traces of target sounds, which could impact on performance in the retrieval phase. Furthermore, we observe that theta power during sound sequence encoding and retention is larger when the distracting melodies is hard to ignore

(compared to when they were easy to ignore). As described above, frontal theta oscillations have been associated with working memory processes including the processing of serial order in sequences (Hsieh et al., 2011). The current result would thus imply that a stronger involvement of these time-based memory processes is necessary when parsing interleaved target and distracting sounds is more demanding. This increase in theta power with increasing filtering difficulty is also in line with a link between theta activity and increased effort (Wisniewski et al., 2017).

#### *Interactions between auditory selective attention and working memory*

At the behavioral level, we observe, as in Blain, de la Chapelle et al. (2022) and Blain, Talamini et al. (2022), an interaction between filtering difficulty and the memory task difficulty on performance ( $d'$ ), with greater differences between easy and hard-to-ignore distractors in the low difficulty memory task than in the high difficulty memory task. In Blain, Talamini, et al. (2022), based on several lines of evidence derived from behavioral measures in non-musician and musician participants, we have argued that this interaction observed in  $d'$  reflects shared cognitive resources between auditory selective attention and working memory, compatible with the *cognitive load theory* (Lavie, 2005; Lavie et al., 2004; Yi et al., 2004).

In the neurophysiological data, we observe an interaction between filtering difficulty and the memory task difficulty on the amplitude of the N1 to to-be-attended sounds in the left auditory cortex during sequence encoding, with a difference of target N1 amplitude according to filtering difficulty only in the low difficulty memory task. This neurophysiological result exactly mirrors the behavioral data (Figures 3 and 7). It suggests that under low memory load, attentional filtering is more efficient, resulting in larger response amplitudes for the to-be-attended sounds when the distractors are easy to ignore. Conversely, under high memory load, less resources would be available for attentional filtering, resulting in a reduced facilitation of relevant sound processing when the distractors are easy to ignore. Interestingly this interaction between filtering difficulty and memory task difficulty on the amplitude of the N1 to target sounds is only observed in the left auditory cortex, where a smaller decrease in alpha power is observed under high memory task difficulty. Hence, in the left auditory areas, under high memory load, the level of excitability is lower (larger alpha power) and the attentional facilitation of transient evoked responses to relevant sounds is reduced when distracting sounds are hard-to-ignore. A possible interpretation is that the left auditory cortex plays a critical role in attentional filtering (Bidet-Caulet et al., 2007), and that increasing the cognitive load with enhanced memory task difficulty impedes on these processes. In the framework of

the cognitive load theory, we could interpret this finding as attributing less cognitive resources to a process subserving selective attention.

Further evidence for an interplay between attentional filtering and memory processes was obtained by analyzing frontal theta oscillations. During both sound sequence encoding and the maintenance delay, the power of theta oscillations which are thought to reflect time-based serial order processes in memory tasks (Hsieh et al., 2011) was increased when target selection was difficult. This suggest that time-based processes, which are relevant both for information selection and retention could be shared between attention and memory.

### *Conclusion*

Here by manipulating the difficulties of an auditory memory task (DMST) and of attentional filtering of distracting sounds, we could shed light on the neurophysiological processes subserving working memory, selective attention, and their interactions in the auditory modality. Attentional selection during sound sequence encoding operates through a combination of target processing facilitation and distractor inhibition that are reduced with increasing filtering difficulty. Increasing memory demands results in better anticipation of the sound sequences to encode (higher CNV amplitude) but also in a smaller desynchronization of alpha oscillations in the left auditory and frontal areas which could hinder attentional filtering, as reflected in target-related ERFs. Conversely, increasing attentional demands increases sustained evoked activity in superior temporal areas, which could favor filtering, but also enhances theta oscillations in anterior frontal areas which could reflect the involvement of a general time-based processing system. Future work is needed to understand how the interplay between these different processes is orchestrated.

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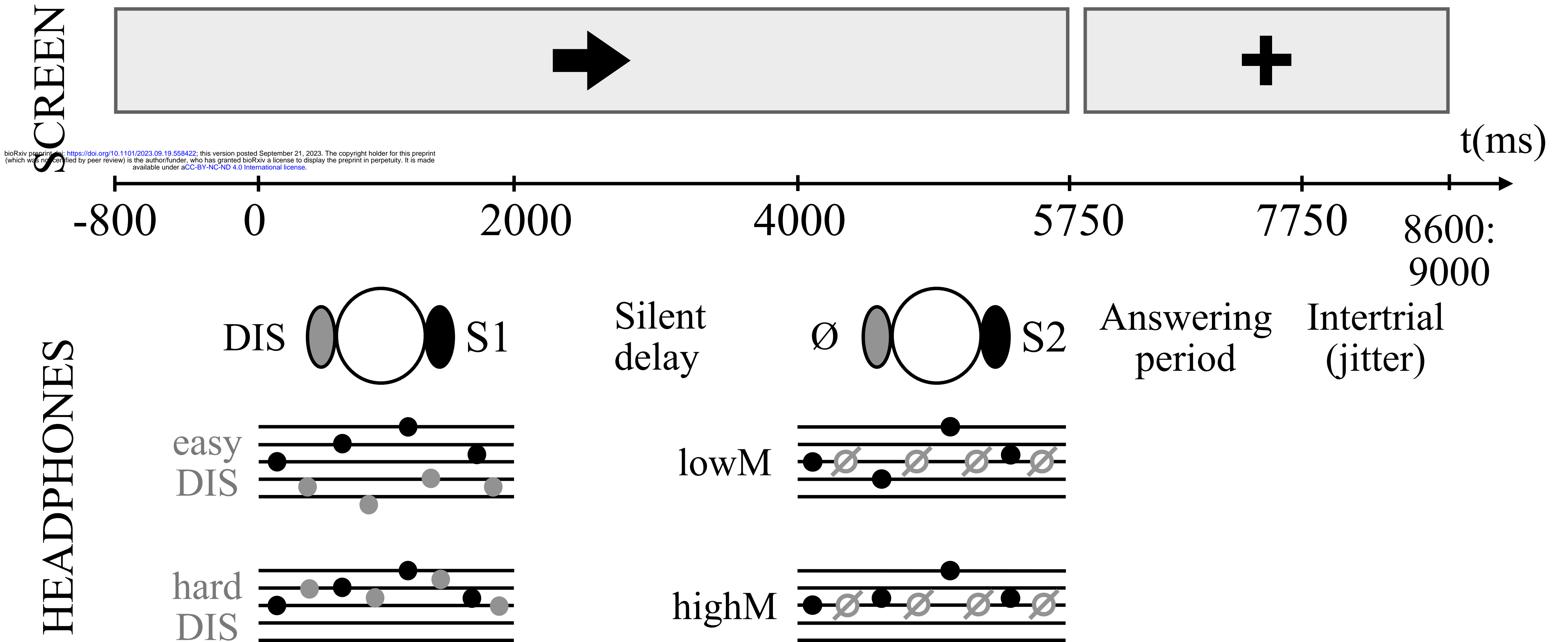


Figure 1 – Trial design. The same paradigm is described in Blain, de la Chapelle et al. (2022). The ear of interest is indicated by an arrow on the screen during the trial. The to-be-attended melody S1 played in this ear must be encoded in memory while a to-be-ignored melody DIS is played in the other ear, interleaved with S1 tones. After a 2s retention delay, a melody S2 is played in the ear of interest and participants indicate whether S1 and S2 are identical or different. The melody DIS can be either easy (easyDIS) or hard (hardDIS) to ignore based on their frequency similarity with S1. When S2 is different from S1, one note is changed of either 5-6 semi-tones, entailing a contour change in the melody (low difficulty memory task; lowM blocks) or 1-2 semi-tones without contour change (high difficulty memory task; highM blocks).

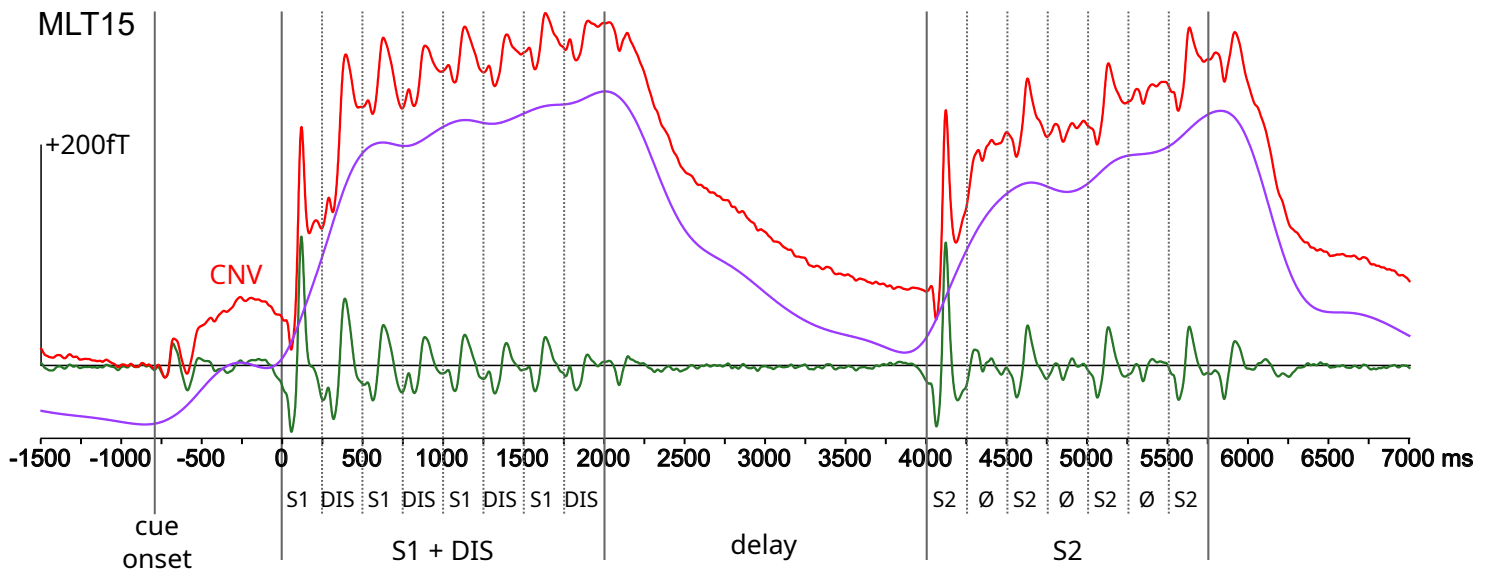


Figure 2 – Filters used for ERF analyses (grand-average ERF). In red, a 30Hz low-pass filter was applied to preserve the CNV, between the onset of the visual cue (-800ms) and the onset of S1 (0ms), with a 1050 to -800 ms pre-cue baseline. In green, a 2-30Hz band-pass filter was applied to study the ERF to each S1 and DIS tone (between 0 and 2000ms), with a -250 to 0 ms pre-S1 baseline. In purple, a 2Hz low-pass filter was applied to highlight the sustained response during the S1/DIS melodies (0 to 2000ms) and the retention delay (2000 to 4000ms), with a -250 to 0 ms pre-S1 baseline.

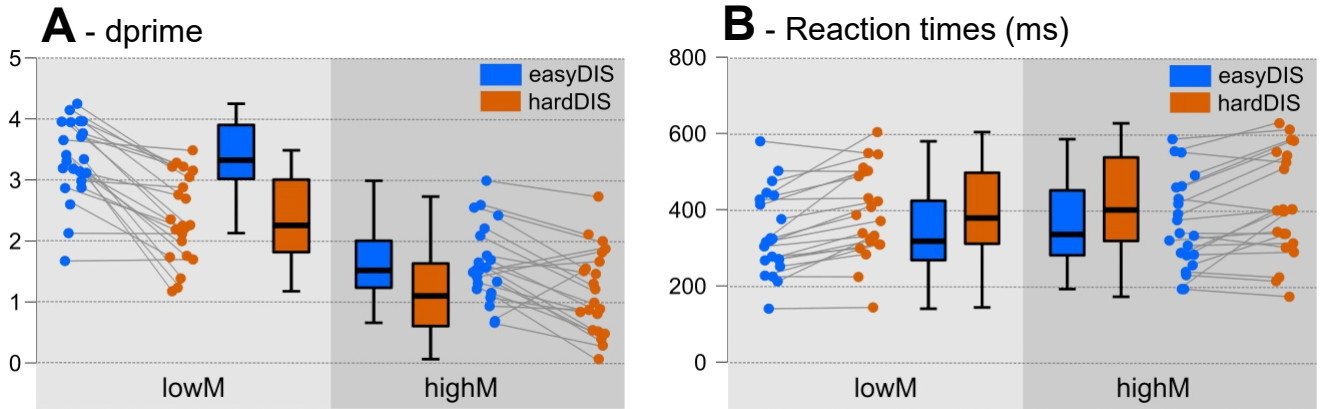


Figure 3 – Behavioral results. Effect of the difficulty of the task (lowM: low difficulty, highM: high difficulty) and of the difficulty of the distractor (easyDIS: easy to ignore, hardDIS: hard to ignore) on performance  $d'$  (A) and on reaction times (B). Whisker plots show the median  $\pm$  quartile and the minimum/maximum values. Lines in the strip plots connect data from the same participant.

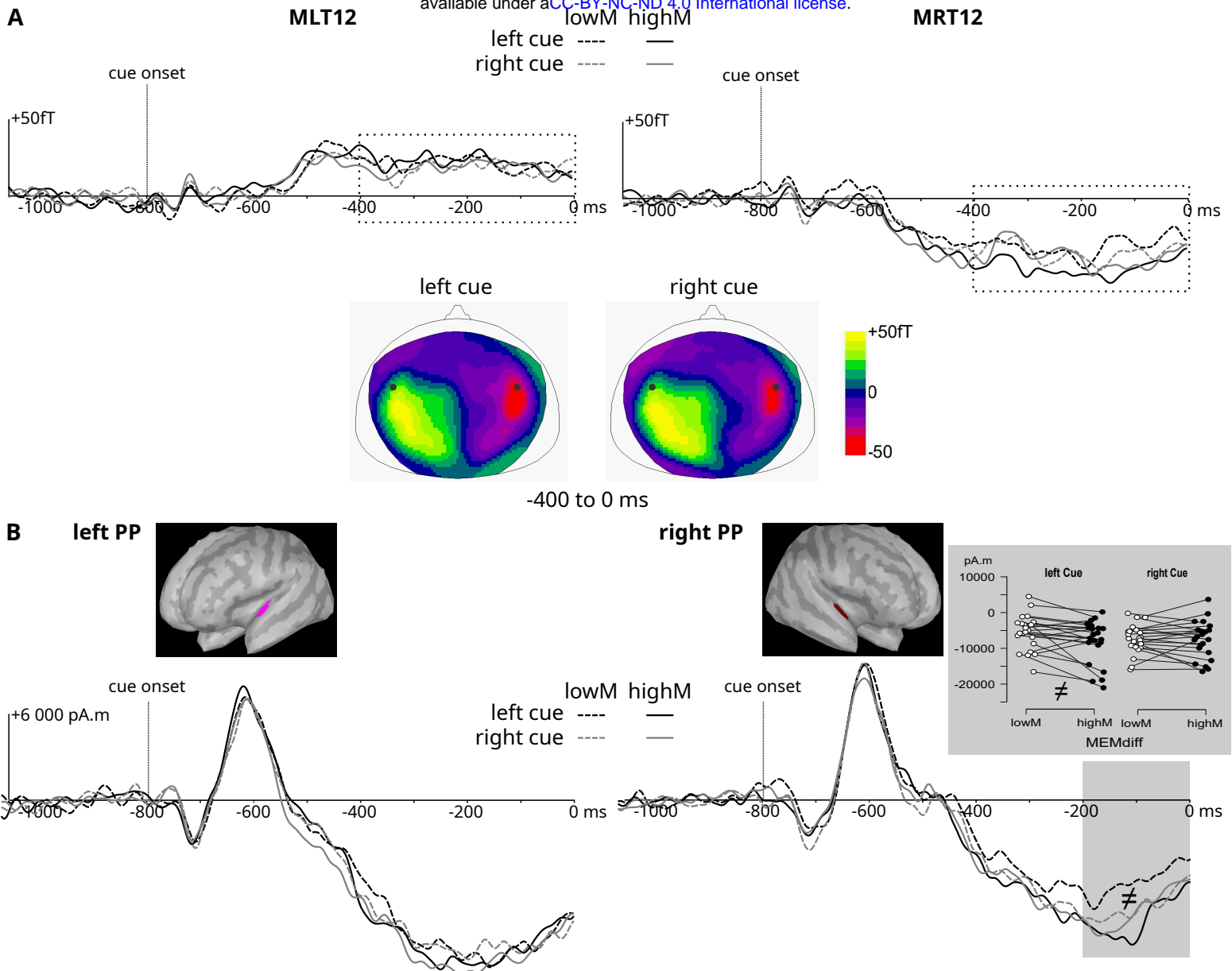


Figure 4 – Contingent Negative Variation (CNV). (A) In the sensor space, time course of the ERF to the visual cue onset (arrow, -800ms relative to S1 onset), for each MEMdiff and Cued Side condition, at MLT12 and MRT12 (above the left and right temporal lobes, respectively). Topoplots show sensor data to left and right cues, over the time period of interest, indicated by the dotted rectangles (-400 to 0 ms). Black dots on topographies indicate corresponding sensor position. (B) In the source space, time course of the ERF to the visual cue onset, for each MEMdiff and Cued Side condition, in the corresponding ROI represented on the MNI template. The strip plot shows individual data averaged by condition in the gray period (-200 to 0 ms) showing positive or greater evidence (see Table 1 for time-windows and results). Lines connect data from the same participant. leftPP: left Planum Polare, right PP: right Planum Polare.

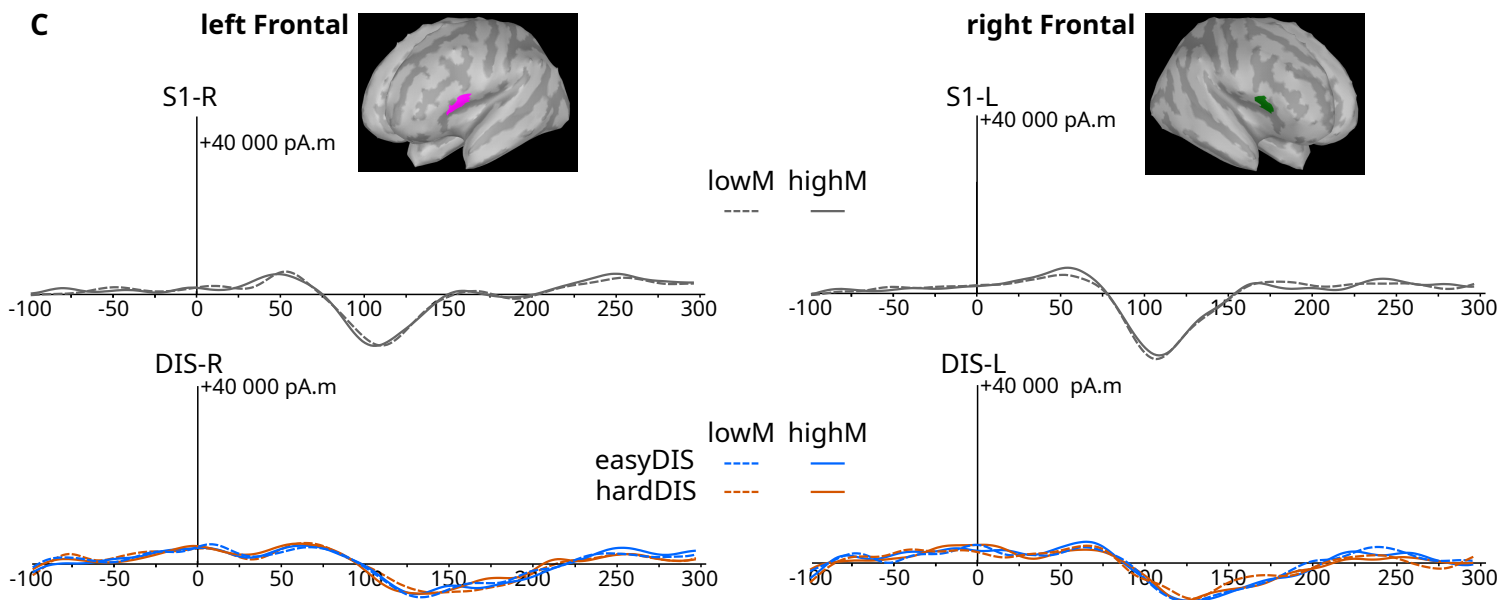
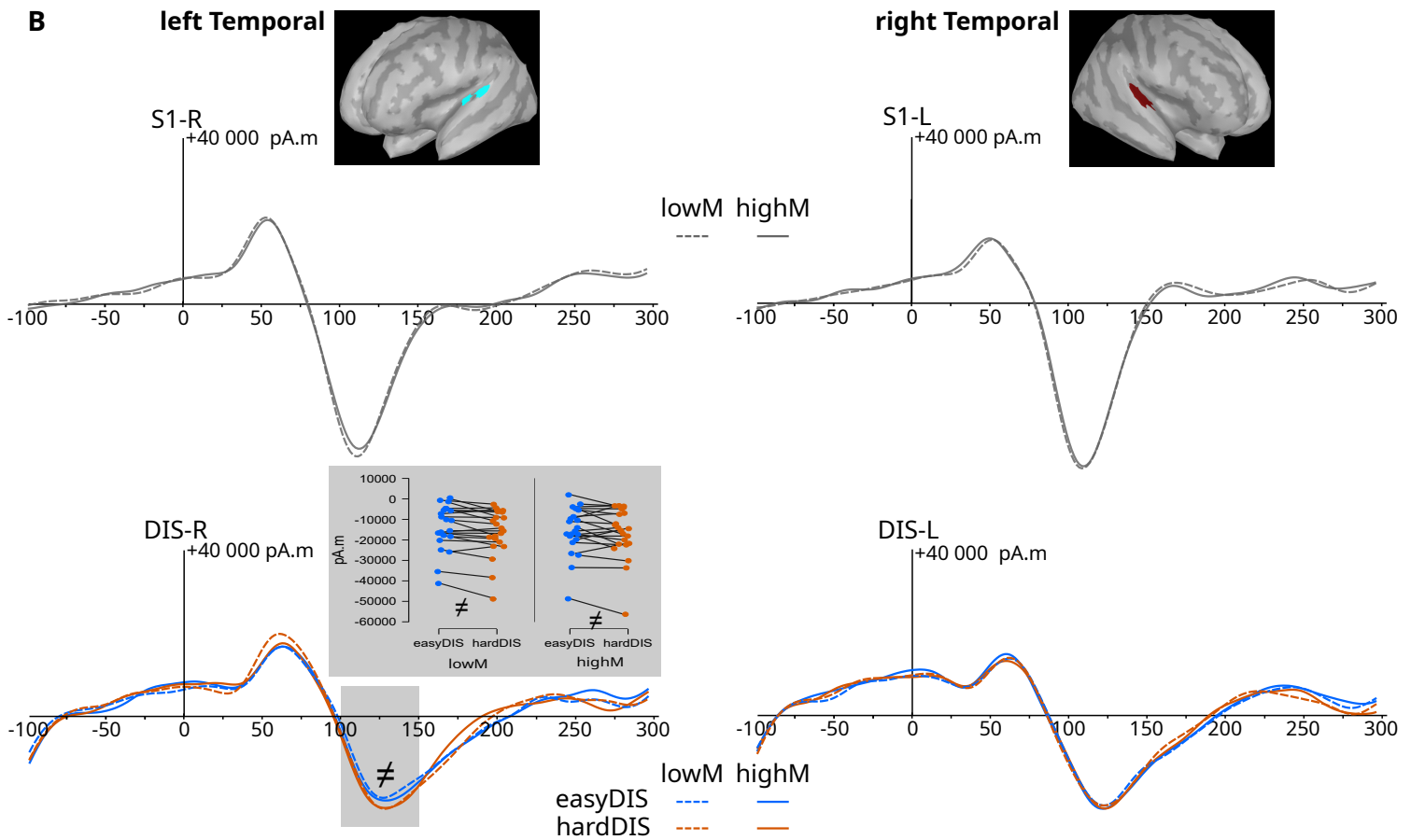
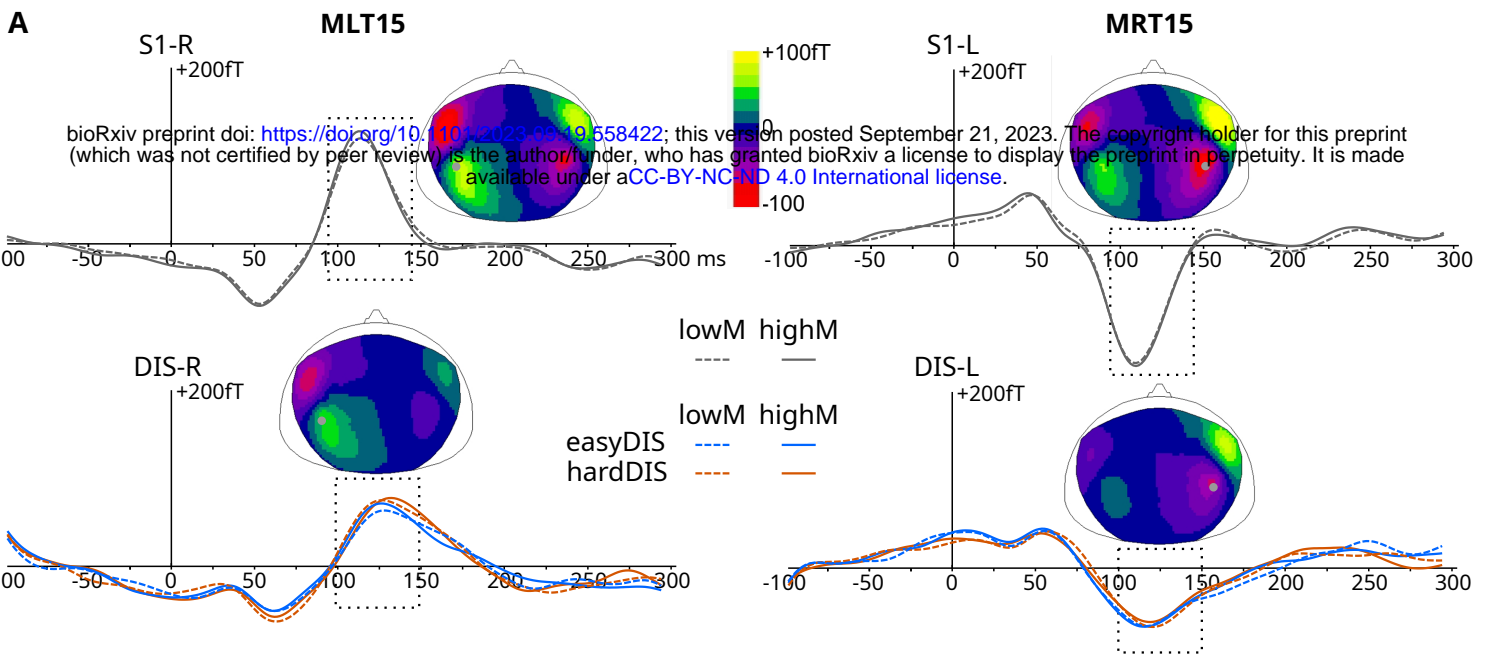




Figure 5 – Transient evoked responses to the first tone. (A) In the sensor space, time course of the ERF to the first tone of the to-be-attended melody S1 and of the to-be-ignored melody DIS (tone onset at 0ms) for each DISdiff (DIS only) and MEMdiff condition (S1 and DIS), at MLT15 and MRT15 (above the left and right temporal lobes, respectively). Topoplots show sensor data over the time period of interest, indicated by the dotted rectangles (90 to 140 or 100 to 150 ms for S1 or DIS, respectively). Gray dots on topographies indicate corresponding sensor position. (B & C) In the source space, time course of the ERF to the first tone of S1 and DIS melodies, for each DISdiff (DIS only) and each MEMdiff condition, in the corresponding ROIs represented on the MNI template. The strip plot shows individual data averaged by condition in the gray period showing positive or greater evidence (see Table 1 for time-windows and results). Lines connect data from the same participant. Only contralateral tones are analyzed here: S1-R and DIS-R for left sensors and sources, and S1-L and DIS-L for right sensors and sources. S1-L or S1-R: S1 melodies presented to the left or right ear, respectively. DIS-L or DIS-R: DIS melodies presented to the left or right ear, respectively.

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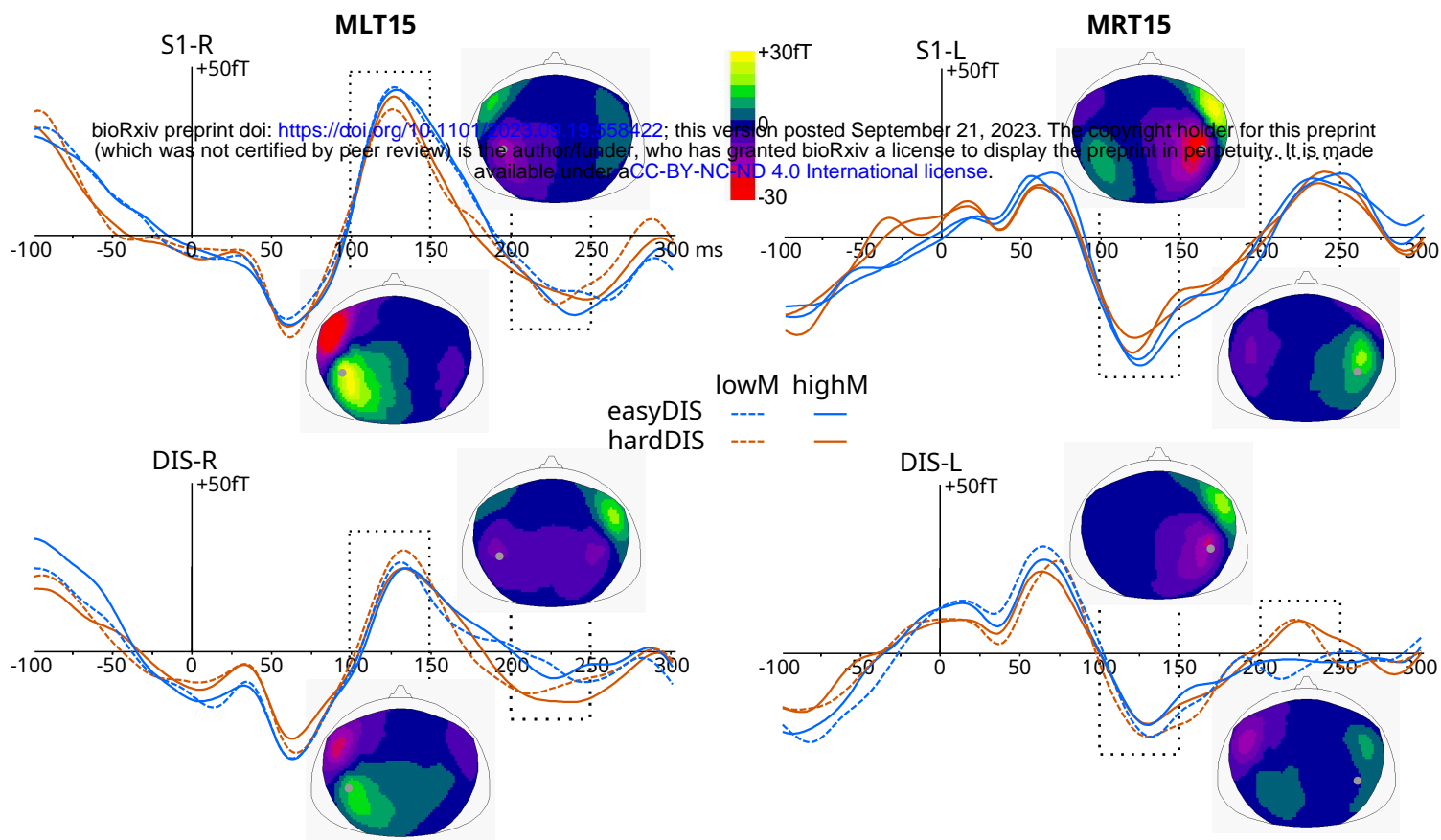
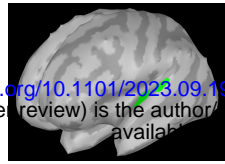
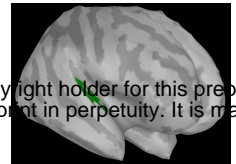


Figure 6 – Transient evoked responses to the tones 2, 3 and 4 in the sensor space. Time course of the averaged ERF to the tones 2, 3 and 4 of the to-be-attended melody S1 and of the to-be-ignored melody DIS (tone onset at 0ms), for each DISdiff and MEMdiff condition, at MLT15 and MRT15 (above the left and right temporal lobes, respectively). Topoplots show sensor data over the time periods of interest, indicated by the dotted rectangles (100 to 150 ms and 200 to 250 ms for N1 or P2 responses, respectively). Gray dots on topographies indicate corresponding sensor position. Only contralateral tones are studied here: S1-R and DIS-R for left sensors, and S1-L and DIS-L for right sensors. S1-L or S1-R: S1 melodies presented to the left or right ear, respectively. DIS-L or DIS-R: DIS melodies presented to the left or right ear, respectively.

**A****left Temporal****right Temporal**

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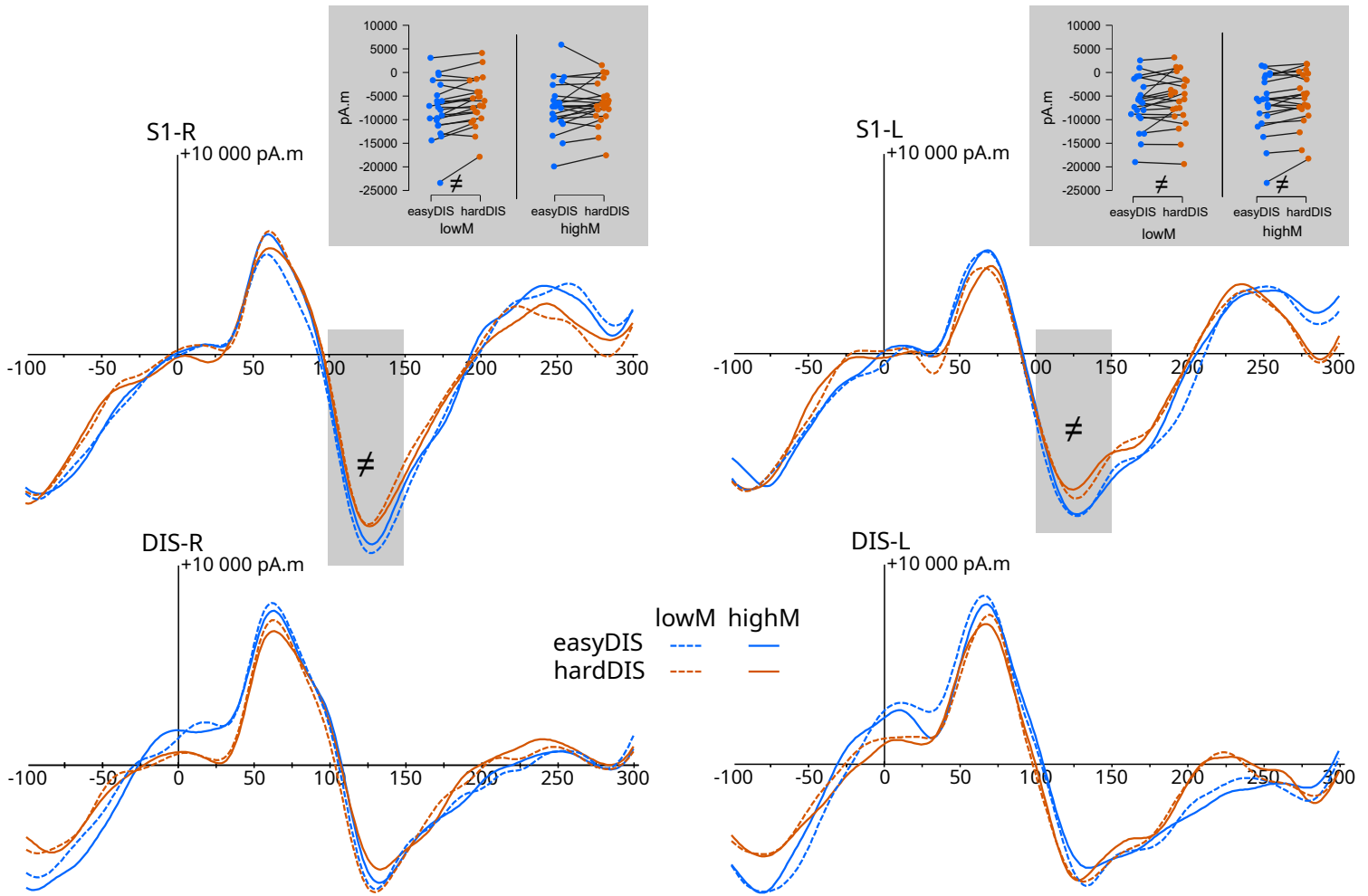
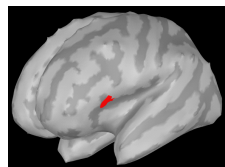
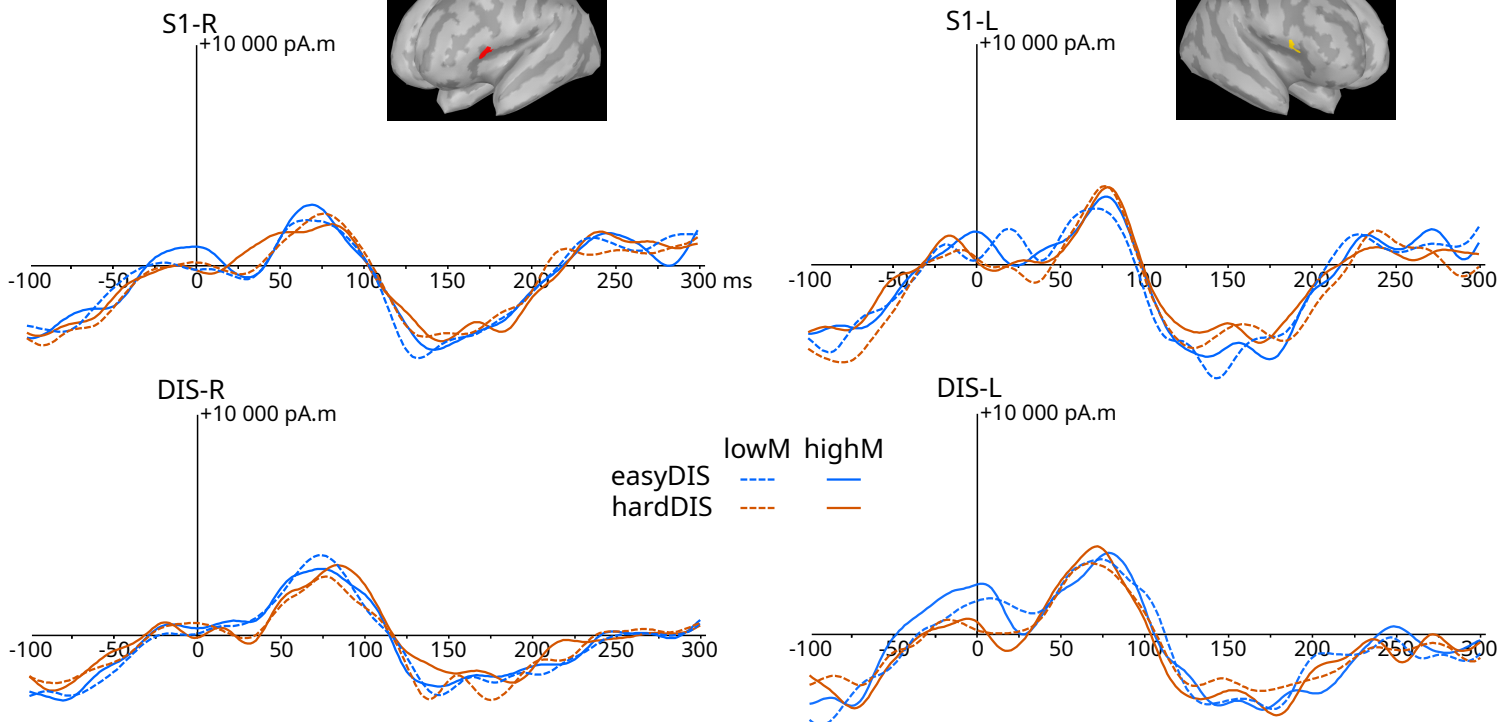
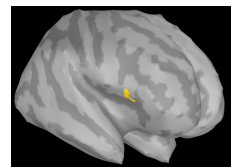
**B****left Frontal****right Frontal**

Figure 7 – Transient evoked responses to the tones 2, 3 and 4 in the source space (N1 ROIs). Time course of the averaged ERF to the tones 2, 3 and 4 of the to-be-attended melody S1 and of the to-be-ignored melody DIS (tone onset at 0ms), for each DISdiff and MEMdiff condition (S1 and DIS), in the corresponding ROI represented on the MNI template. The strip plots show individual data averaged by condition in the gray periods showing positive or greater evidence (see Table 1 for time-windows and results). Lines connect data from the same participant. Only contralateral tones are analysed here: S1-R and DIS-R for left sources, and S1-L and DIS-L for right sources. S1-L or S1-R: S1 melodies presented to the left or right ear, respectively. DIS-L or DIS-R: DIS melodies presented to the left or right ear, respectively.

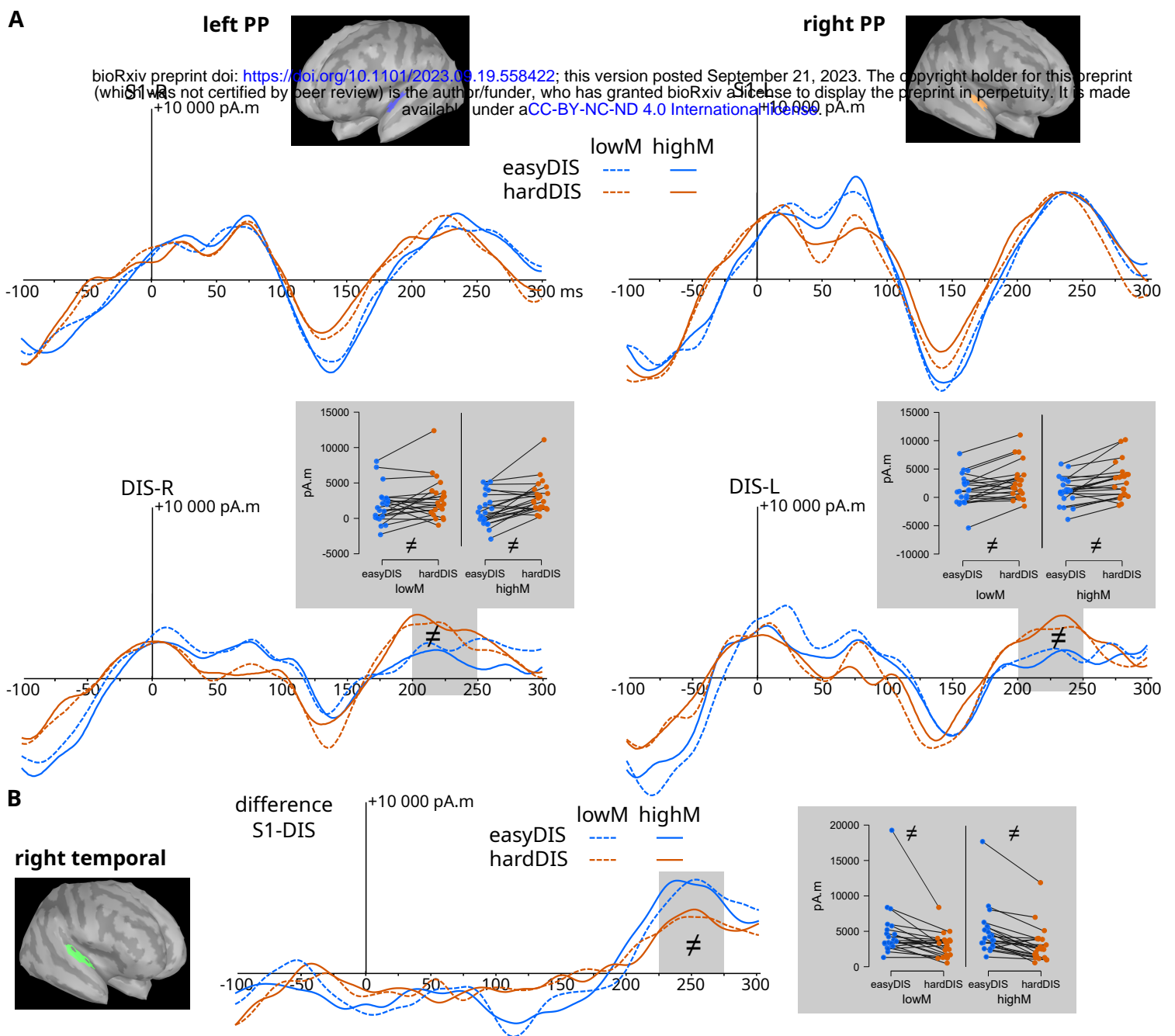
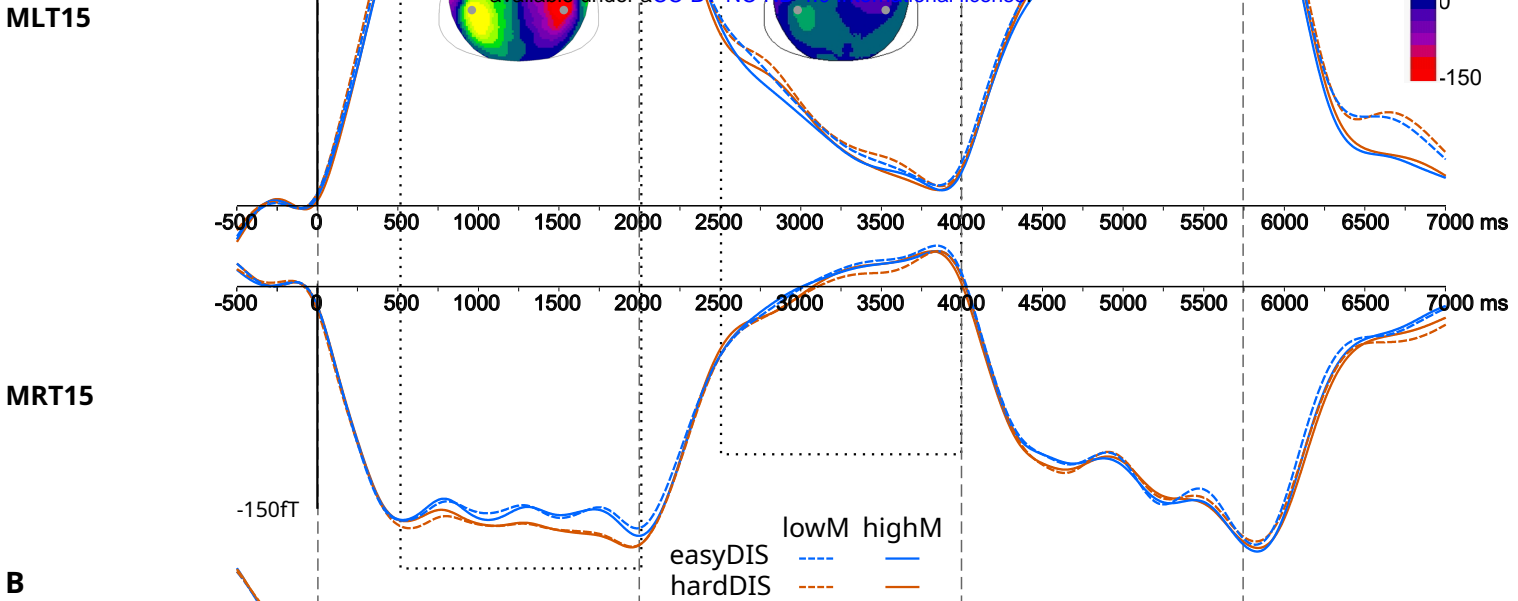
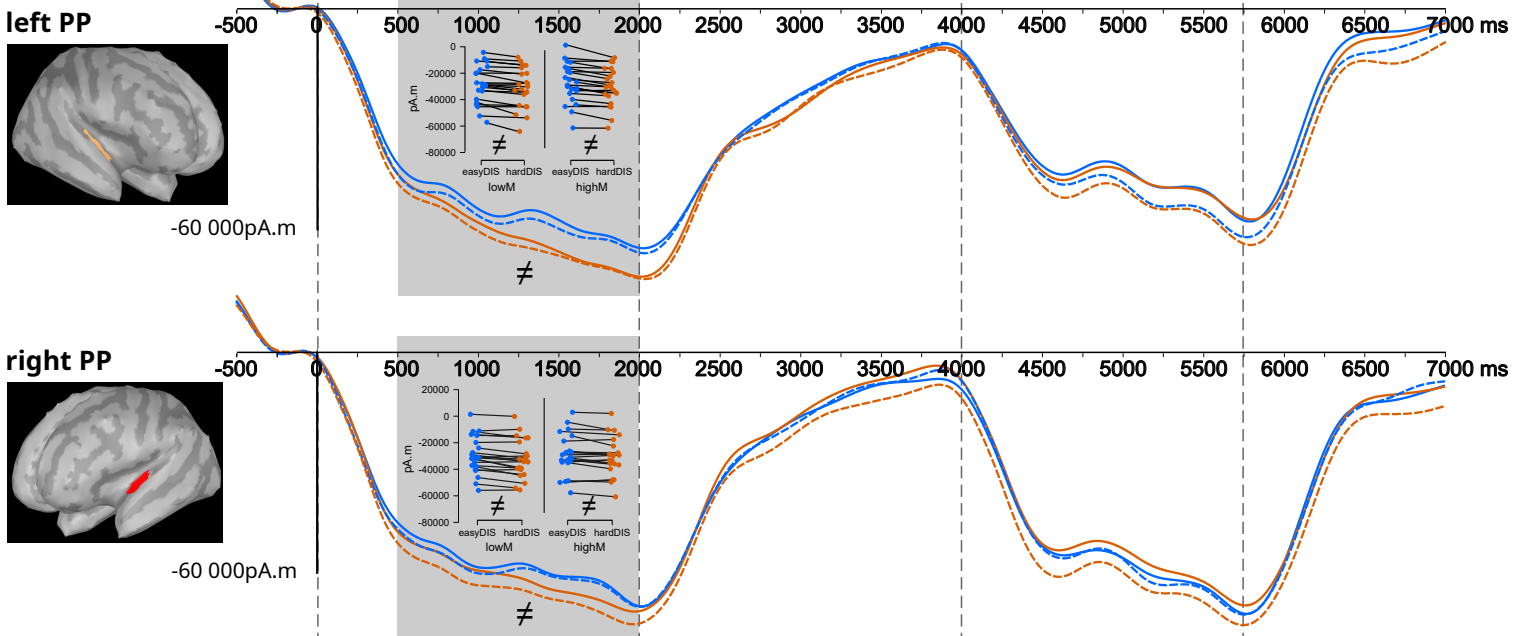
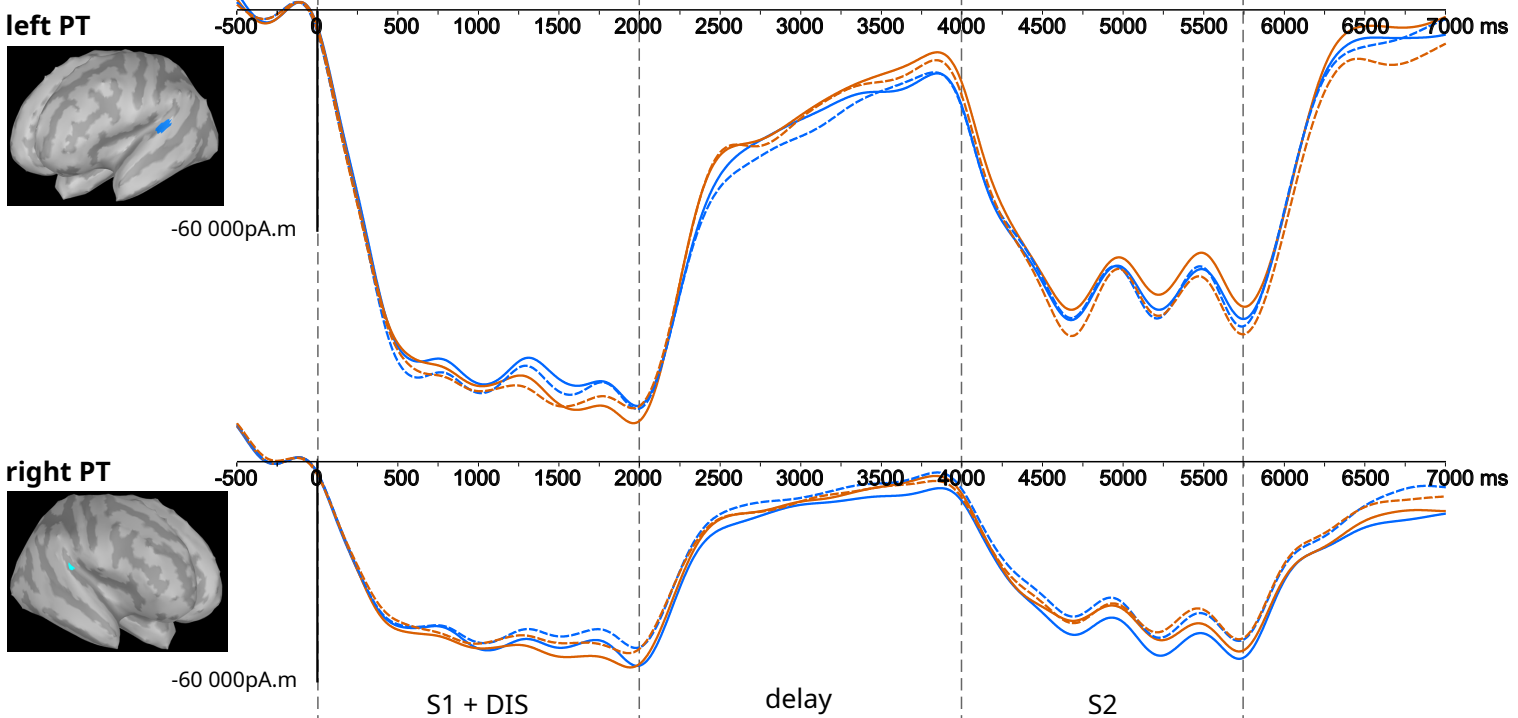


Figure 8 – Transient evoked responses to the tones 2, 3 and 4 in the source space (P2 and late differential response ROIs). (A) Time course of the averaged ERF to the tones 2, 3 and 4 of the to-be-attended melody S1 and of the to-be-ignored melody DIS (tone onset at 0ms), for each DISdiff and MEMdiff condition (S1 and DIS), in the corresponding ROI represented on the MNI template. (B) Time course of the difference (S1-DIS) between averaged ERF to the tones 2, 3 and 4 of the to-be-attended melody S1 and of the to-be-ignored melody DIS (tone onset at 0ms), for each DISdiff and MEMdiff condition, in the corresponding ROI represented on the MNI template. The strip plots show individual data averaged by condition in the gray periods showing positive or greater evidence (see Table 1 for time-windows and results). Lines connect data from the same participant. Only contralateral tones are analyzed here: S1-R and DIS-R for left sources, and S1-L and DIS-L for right sources. S1-L or S1-R: S1 melodies presented to the left or right ear, respectively. DIS-L or DIS-R: DIS melodies presented to the left or right ear, respectively. leftPP: left Planum Polare, right PP: right Planum Polare.

**A**

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**B****C**

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**Figure 9 – Sustained evoked responses.** (A) In the sensor space, time course of the ERF to S1 & DIS melodies, the delay and to S2 (S1 onset at 0ms), for each DISdiff and MEMdiff condition, at MLT15 and MRT15 (above the left and right temporal lobes, respectively). Topoplots show sensor data over the time periods of interest, indicated by the dotted rectangles (500 to 2000 during S1 & DIS melodies, 2500 to 4000 during the delay). Gray dots on topographies indicate corresponding sensor position. (B & C) In the source space, time course of the ERF for each DISdiff and each MEMdiff condition, in the corresponding ROIs represented on the MNI template. The strip plot shows individual data averaged by condition in the gray periods showing positive or greater evidence (see Table 1 for time-windows and results). Lines connect data from the same participant.

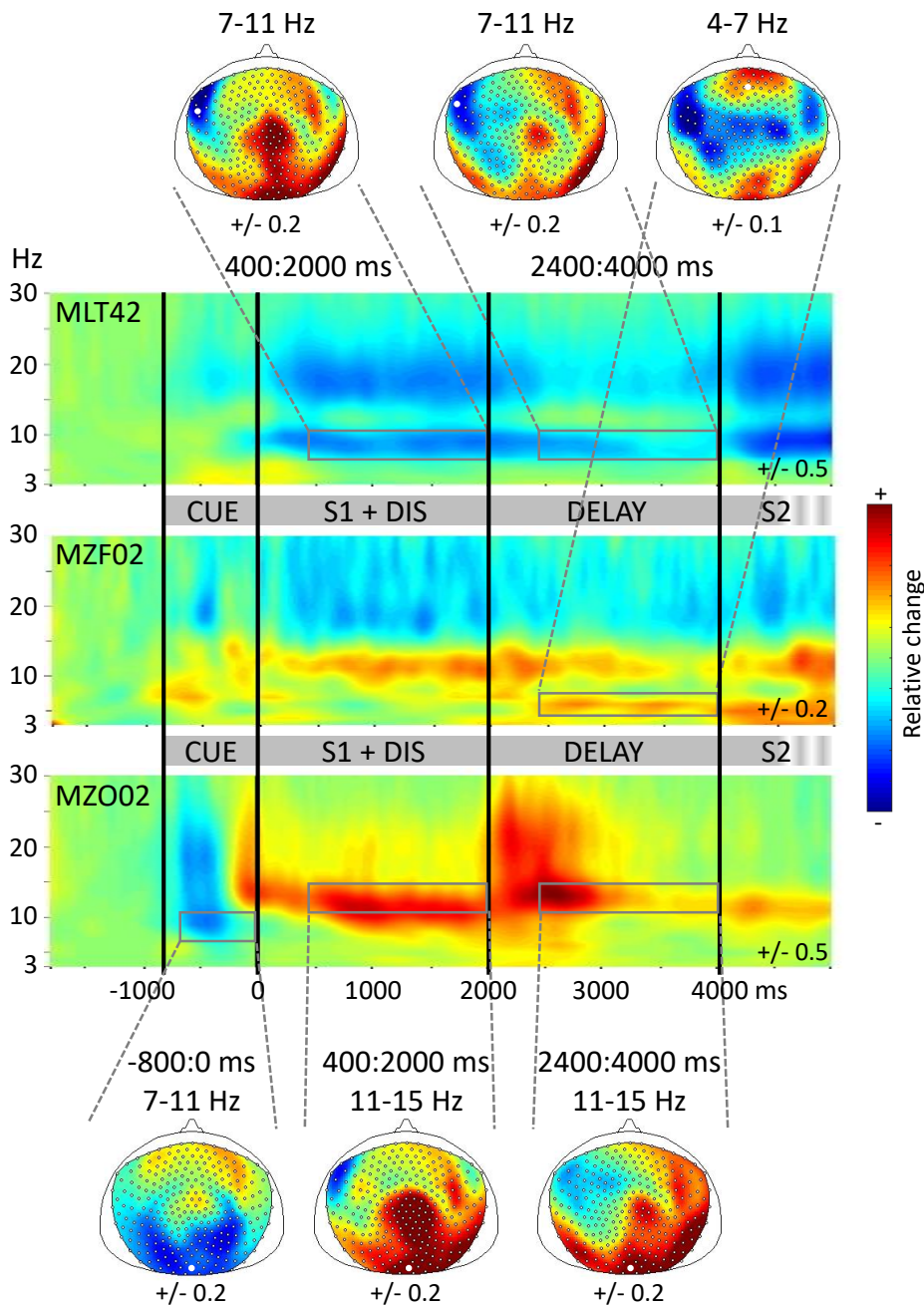


Figure 10 – Time-frequency plots in the sensor space. Time-frequency power (relative change) plots during Cue presentation, S1 & DIS melodies, and the delay (S1 onset at 0ms), for all conditions averaged, at a temporal (MLT42), a frontal (MZF02) and an occipital sensor (MZO02) and corresponding topographies. Response to S2 is not fully represented here. In comparison to baseline (1800 to -1000 ms relative to S1 onset), a decrease in power appears in blue and an increase in power appears in red. White dots on topographies indicate corresponding sensor position.



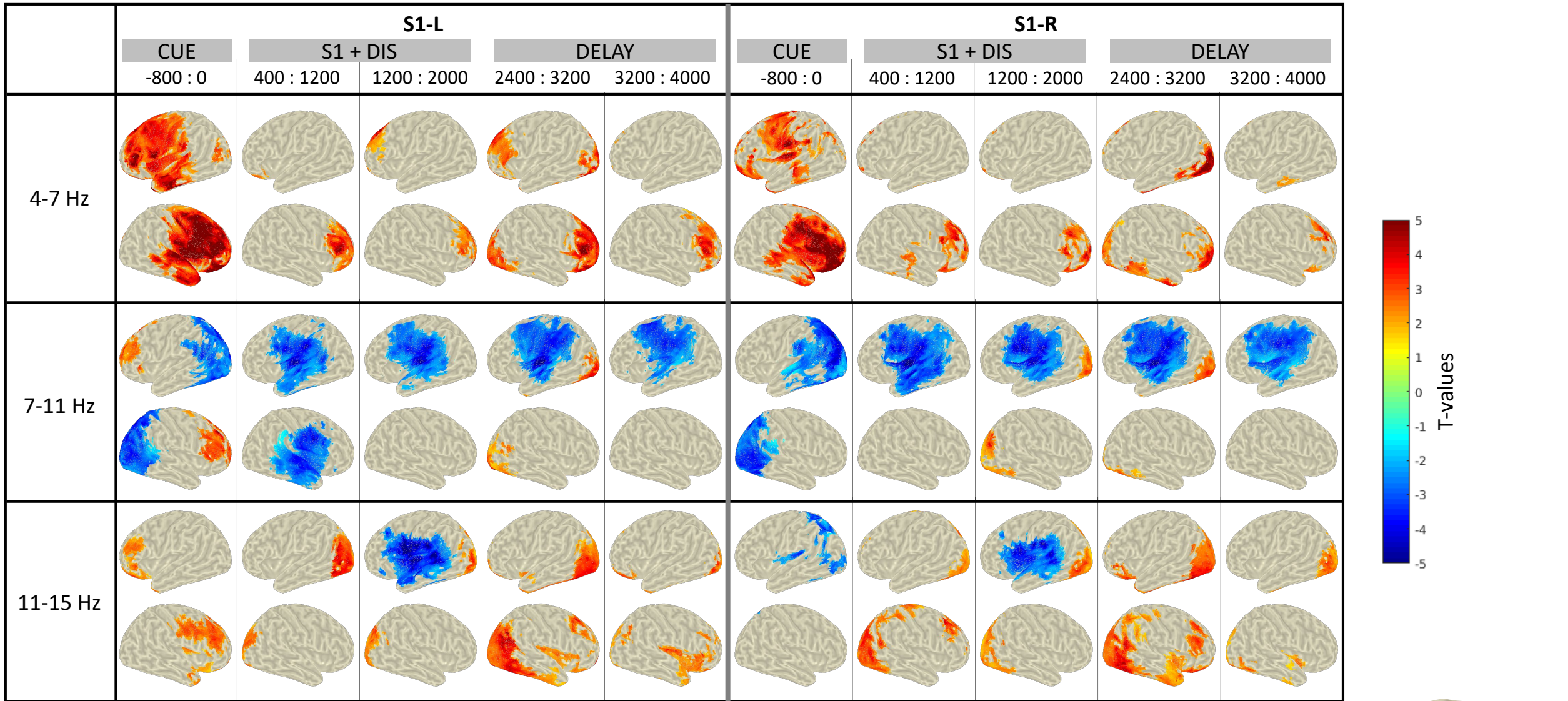
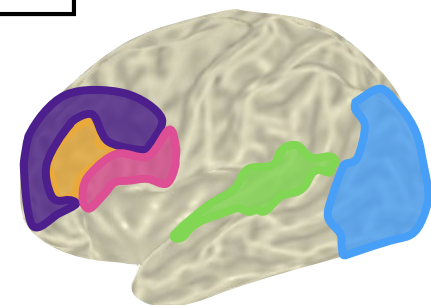
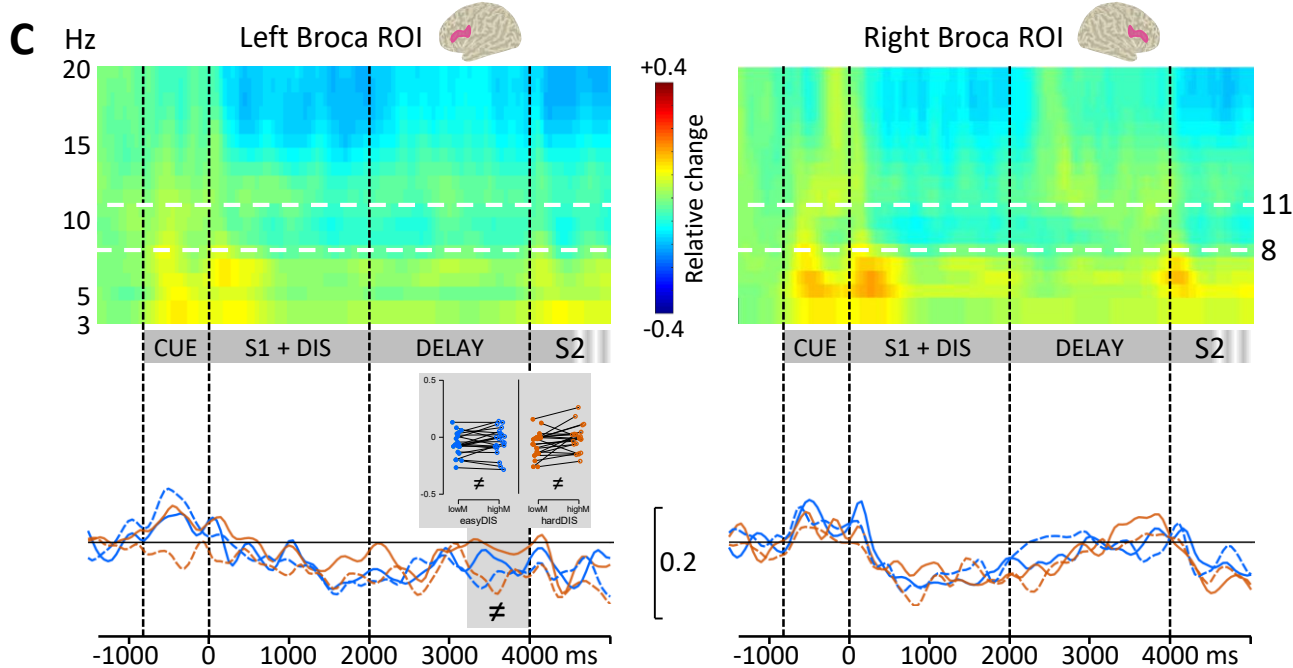
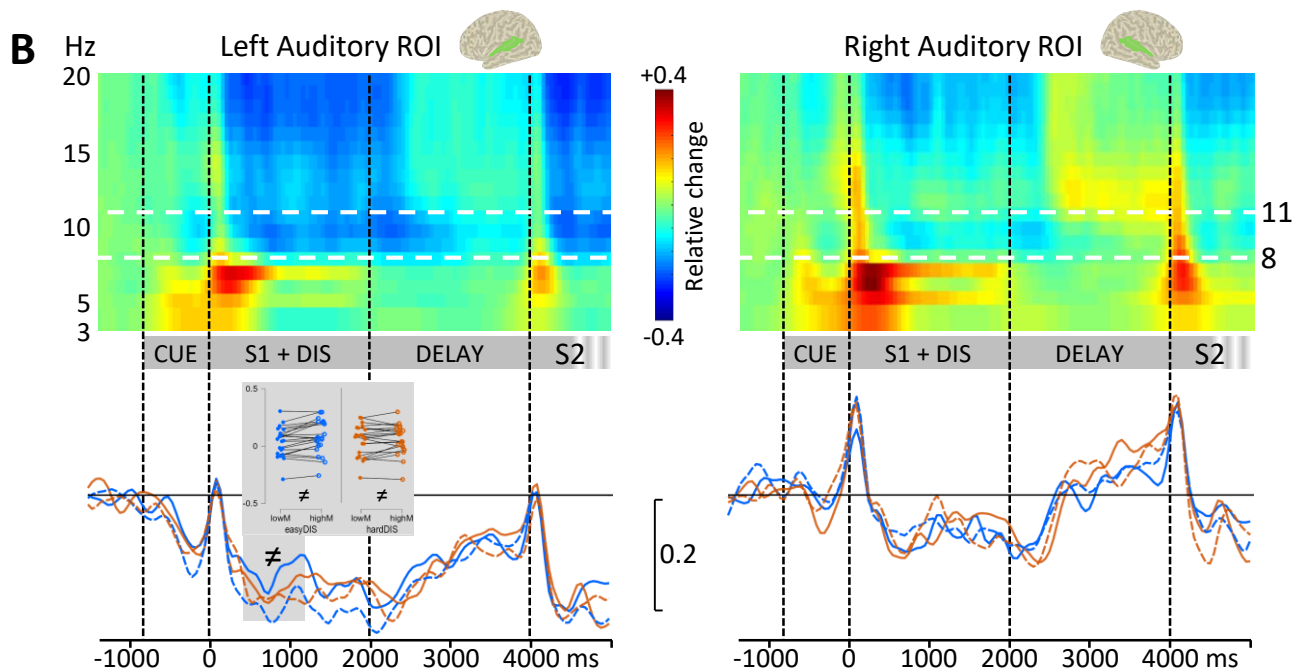
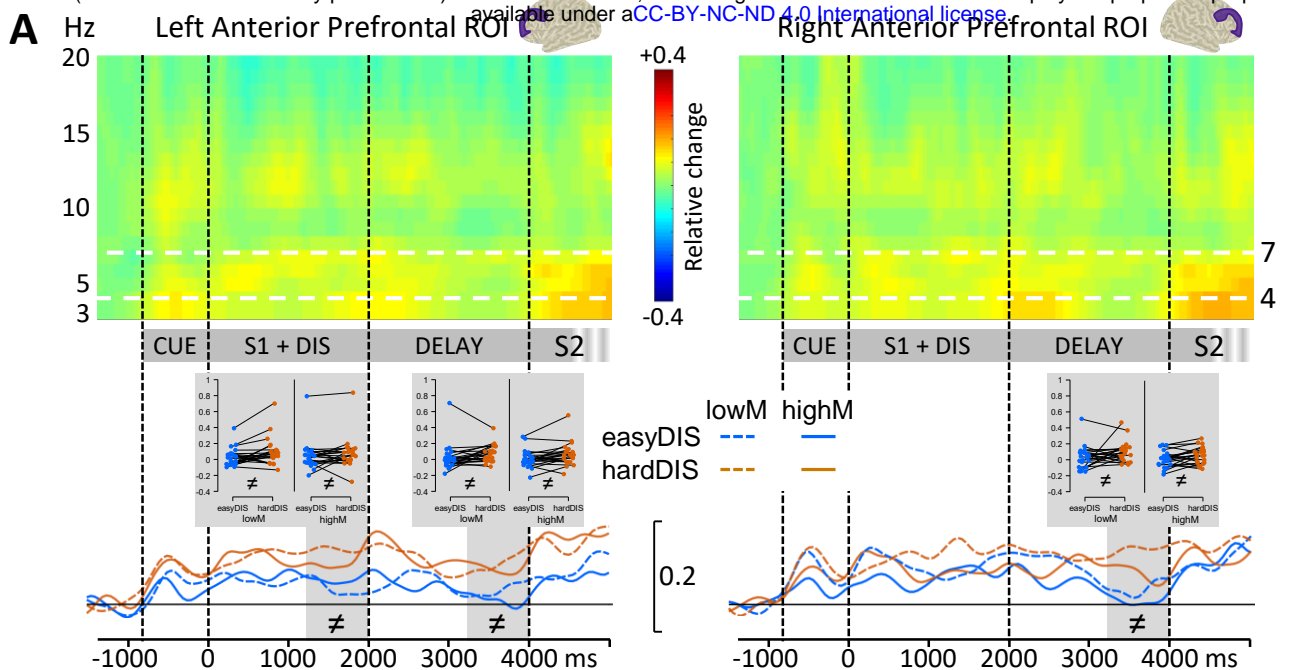


Figure 11 – Source activity in theta and alpha bands. Distributions of T values for each time-frequency window in comparison to a pre-cue baseline (-1800ms to -1000ms locked to S1 onset) for trials with S1 presented to the left or the right, separately (S1-L & S1-R). The results are masked with the p-value coming from the cluster-based permutation tests: only significant clusters are shown ( $p < 0.05$ ). In comparison to baseline, a decrease in power appears in blue and an increase in power appears in red. In the right bottom corner, the chosen regions of interest for further analyses are presented. The corresponding Brodmann areas are indicated in brackets for each region of interest.

- Auditory (BA 22,41,42)
- Visual (BA 17,18,19)
- Anterior Prefrontal (BA 9,10)
- Broca (BA 44,45)
- DLPFC (BA 46)





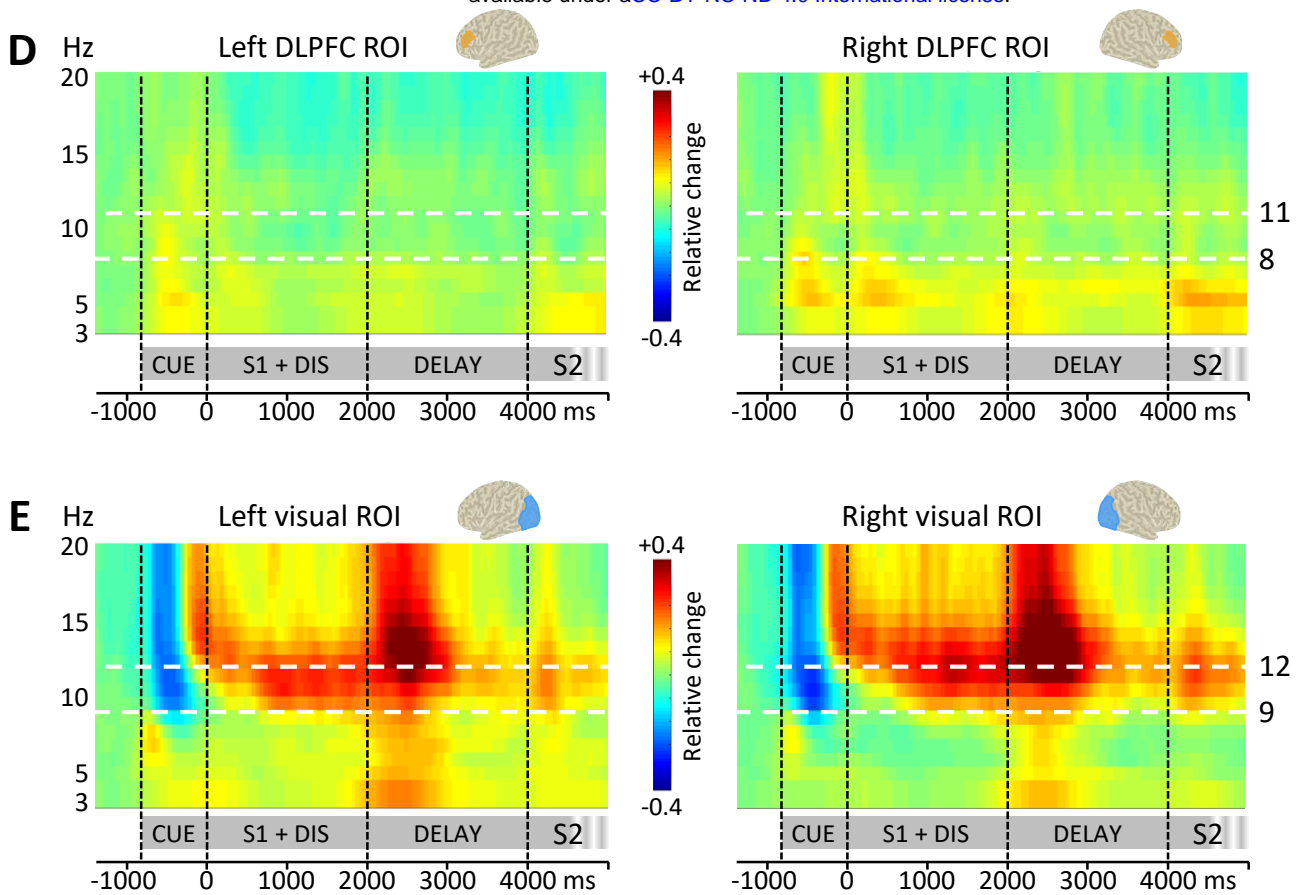


Figure 12 – Time-frequency plots and time profiles in the source space. Time-frequency power (relative change) plots during Cue presentation, S1 & DIS melodies, and the delay (S1 onset at 0ms), for all conditions averaged, in the left and right Anterior Prefrontal regions (A), in the left and right Auditory cortices (B), in the left and right Broca areas (C), in the left and right Dorso-Lateral Prefrontal Cortex (DLPFC, D), and in the left and right Visual cortices (E). Response to S2 is not fully represented here. In comparison to baseline (-1800 to -1000 ms relative to S1 onset), a decrease in power appears in blue and an increase in power appears in red. Regions of interest were defined based on the results from the cluster-based permutation tests performed on the DICS-reconstructed sources for the whole brain. Time course of the power (relative change) for each DISdiff and each MEMdiff condition, in the corresponding ROIs represented on the MNI template: alpha band (8 to 11 Hz) in the Auditory (A) and BROCA (B) ROIs, theta band (4 to 7 Hz) in the Anterior Prefrontal (C) ROIs. The strip plot shows individual data averaged by condition in the gray periods showing positive or greater evidence (see Table 2 for time-windows and results). Lines connect data from the same participant.

# Study 1 – Dreaming, Attention, and Memory

Study 1c -

*Differences in auditory selective attention under memory load  
between low and high frequency dream recallers: a MEG study*

In preparation

# Differences in auditory selective attention under memory load between low and high frequency dream recallers: a MEG study

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## Abstract

In a challenging working memory task (melody to be remembered, S1) under auditory distraction (distracting melody - DIS, MEMAT paradigm), subjects with a high dream recall frequency (HR) showed decreased performance compared to subjects with a low dream recall frequency (LR), especially in highly distracting conditions (Blain, de la Chapelle, et al., 2022). The current study intended to investigate the neural activity underlying these behavioral effects using MEG recordings. Compared to HR, LR presented a larger late difference (225-275 ms) between the ERF to S1 and DIS in the right auditory cortex. These results showing a better differential processing between S1 notes and DIS notes in LR than in HR suggest that LR are better able to differentiate between to-be-attended and to-be-ignored stimuli, i.e. display more efficient top-down selective attention. This result supports the hypothesis that when HR face challenging conditions, top-down processes cannot increase enough to compensate for their previously identified increased bottom-up processes (Ruby et al., 2022). The results of this study confirm attentional differences between HR and LR both at the behavioral and electrophysiological level. Further studies manipulating attention during sleep are warranted to further understand the link between attentional and dream recall abilities.

# Introduction

Dreaming can be defined as a subjective experience occurring during sleep that may be recalled and reported during wakefulness (Schredl, 2018). As a consequence, the dreaming experience cannot be accessed directly and dream researchers are limited to the investigation of dream reports (Ruby, 2020). The average dream recall frequency (DRF) in a representative sample of the German population is about 1 dream recalled per week (Schredl, 2008). Interestingly, DRF variability is high, and ranges from no dream memory for several months to a dream memory every morning. Multiple trait and state factors have been proposed to explain the variability in DRF, such as sleep stages (Nielsen, 2000), circadian rhythms (Chellappa & Cajochen, 2013), intra-sleep awakenings (Schredl et al., 2003; Eichenlaub, Bertrand, et al., 2014; Vallat et al., 2017; van Wyk et al., 2019), interest in dreams (Schredl & Göritz, 2017; Beaulieu-Prévost & Zadra, 2005), personality traits (i.e. creativity, openness to experience, thin boundaries; Schredl et al., 2003), neurophysiological traits (Ruby et al., 2013, 2022; Eichenlaub, Bertrand, et al., 2014; Eichenlaub, Nicolas, et al., 2014; Vallat et al., 2020, 2022), and more recently cognitive traits (Blain, de la Chapelle, et al., 2022).

During an attentional task, we observed an increase of the cerebral correlates of both bottom-up and top-down attention processes in people with a high DRF (HR,  $\geq 5$  dreams recalled per week) compared to people with a low DRF (LR,  $\leq 2$  dreams recalled per month), but no performance difference (Ruby et al., 2022). We proposed that increased bottom-up and top-down processes in HR compensated each other leading to unchanged performance and further hypothesized that in challenging conditions, this attentional balance would more easily fail in HR than LR. To test this hypothesis, we asked LR and HR to do an auditory delayed-matching-to-sample task (DMST) with auditory distractors (Blain, de la Chapelle, et al., 2022), using a challenging paradigm called MEMAT (Blain, Talamini, et al., 2022). More precisely, a melody to encode was presented in one ear while an intertwined to-be-ignored melody was presented in the other ear; a few seconds later only one melody was presented and participants had to tell whether it was identical or different from the melody to encode (Figure 1). Two levels of difficulty were used for attention filtering and working memory. Results suggested no between-group auditory working memory difference, in agreement with the mixed and inconclusive results in the literature regarding the association between working memory abilities during wakefulness and DRF (Blain, de la Chapelle, et al., 2022). Regarding attention, HR performed worse in the presence of a hard- rather than easy-to-ignore distractor compared to LR, showing that HR were more sensitive to irrelevant stimuli than LR. This effect is coherent with previous results showing an increased cerebral reactivity to unexpected

stimuli in HR compared to LR (Eichenlaub, Bertrand, et al., 2014; Vallat et al., 2017; Ruby et al., 2022) and increased resting-brain activity in HR compared to LR during both wakefulness and sleep in the TPJ (Eichenlaub, Nicolas, et al., 2014), which is involved in involuntary attention orientation (e.g. Wilterson et al. 2021, Uncapher et al. 2011). In other words, this result confirmed our hypothesis, showing that HR were less able than LR to maintain an efficient balance between bottom-up and top-down processes in challenging conditions and that DRF is more related to attentional abilities than to working-memory abilities.

The MEMAT paradigm allowed us to show attentional differences between HR and LR at the behavioral level for the first time. The present study intends to further understand this group difference in attention abilities by investigating the brain mechanisms at play using MEG recordings. We expected between-group differences in the attention-related rather than memory-related evoked or oscillatory activities.

# Methods

The experimental protocol was described in Blain et al. (2022) and in de la Chapelle et al. (2023). The group analysis of the behavioral data collected in the present study is presented in Blain et al. (2022). The effects of memory and attention difficulties on electrophysiology were investigated irrespective of the DRF in de la Chapelle et al. (2023).

## Participants

A total of 22 participants were recruited for this experiment (11 men and 11 women, 20 right-handed, aged 20-33). Only non-musicians, i.e. people with less than 1 year of instrument practice or singing outside compulsory education programs participated in the study. They were selected based on their DRF, with criteria similar to previous studies (Eichenlaub, Bertrand, et al., 2014; Eichenlaub, Nicolas, et al., 2014; Ruby et al., 2013, 2022; Vallat et al., 2017, 2020, 2022; etc): 11 were LR (i.e. remembered a dream  $\leq 2$  mornings/month) and 11 were HR (i.e. remembered a dream  $\geq 5$  mornings/week). School education, age, gender, and laterality were matched between groups; group comparison of additional neuropsychological testing and questionnaire data revealed no group difference except DRF and can be found in Blain et al. (2022) (Pittsburgh Sleep Quality Index, PSQI, Buysse et al., 1989; State-Trait Anxiety Inventory, STAI, Spielberger et al., 1970; Big Five Inventory, BFI, John et al., 1991; Guilford Alternative Uses Task, GAUT, Bonk, 1967).

All participants were free from neurological or psychiatric disorders and had normal hearing and normal vision. All subjects gave written informed consent to participate. Experimental procedures were approved by the appropriate regional ethics committee.

## Paradigm

The paradigm is presented in Figure 1 and is the same as in Blain et al. (2022) and de la Chapelle et al. (2023). In each trial, the ear of interest is indicated by an arrow on a screen. After 800ms, a to-be-attended melody S1 and to-be-ignored melody DIS, both consisting of four notes, are played in an alternating manner, creating a 2000-ms sequence where each note from one melody is followed by a note from the other. S1 is played in the ear indicated by the arrow on the screen, and DIS is played in the other ear. The first sound to be played is always the first note of S1. After a 2000-ms delay, a melody S2 is played in the ear of interest; when it stops, a central fixation cross replaces the arrow and participants have 2000 ms to answer the question "Is S2 identical or different from S1?" with two response buttons. S2 differs from S1 in half the trials, in which case only one of the four sounds is altered, but not

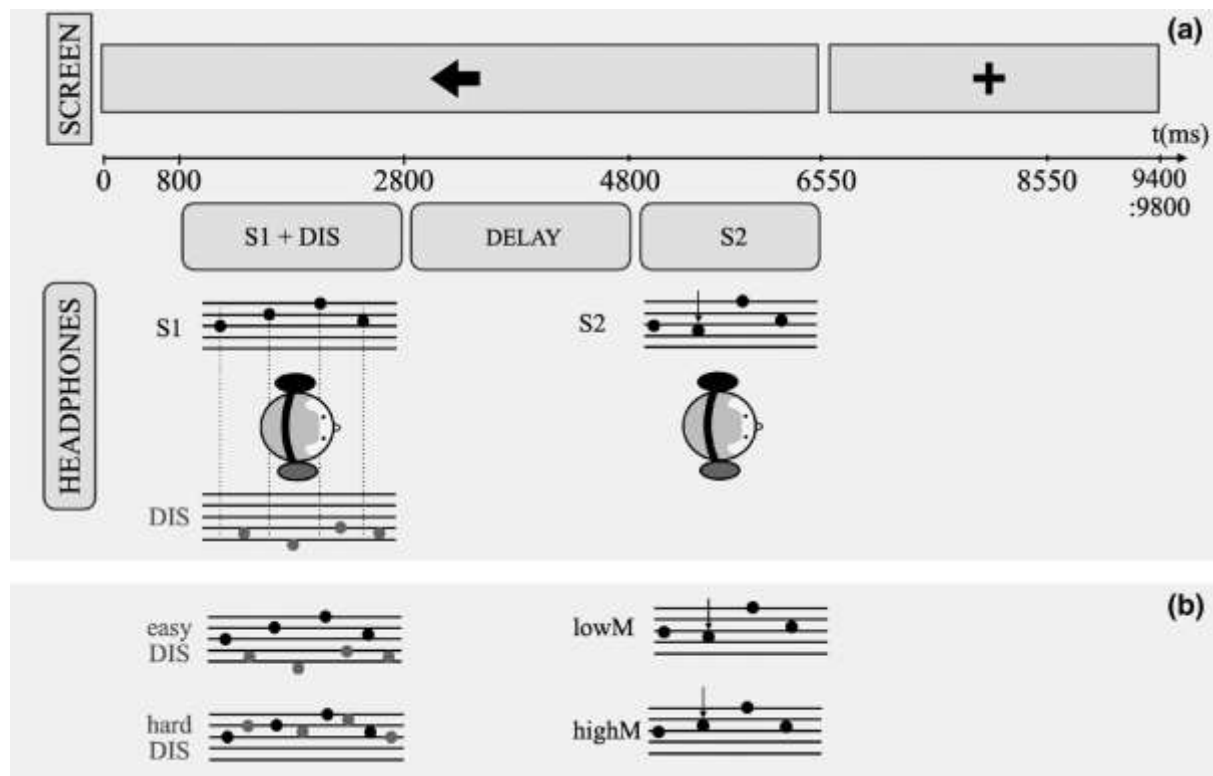


the first to prevent excessive salience. Subsequently, a random pause ranging from 850 ms to 1250 ms follows before the subsequent trial commences.

In a trial, the DIS melodies can be easy (easyDIS) or hard (hardDIS) to filter. An easyDIS melody consists of sounds that are shifted approximately 6 or 7 semi-tones higher or lower in frequency compared to the corresponding frequency range of the S1 melody, while hardDIS melodies have the same frequency range as the corresponding S1 melodies.

In the low memory version (lowM), if S2 differs from S1, one sound is substituted with another that is 5 or 6 semi-tones apart, either higher or lower, resulting in a modified melodic contour. In the high memory version (highM), when S2 differs from S1, the altered sound deviates by only 1 or 2 semi-tones and without affecting the melody contour.

There are 10 blocks of 48 trials each. The memory task difficulty (MEMdiff) is fixed within a block, and participants are informed of the memory difficulty level at the beginning of each block. Presentation of easy- or hard-to-ignore melodies is randomized within a given block (participants are thus unaware of their difficulty in advance). Block order is randomized between participants. Ear of interest (left or right), distractor difficulty (easyDIS or hardDIS), and associated answer (*identical* or *different*) are balanced within each block.



**Figure 1 - Trial design (from Blain, de la Chapelle et al., 2022).** (a) Trial timeline. The ear of interest is indicated at the beginning of each trial by an arrow on the screen. Participants have to encode the target melody presented in the ear of interest in memory (S1, black headphone), while filtering out an interleaved distracting melody presented in the other ear (DIS, gray headphone). After a silent retention delay, a second melody (S2) is presented in the ear of interest, and participants have to compare S1 and S2. (b) Examples of the different experimental

*conditions. Distracting melodies can be either easy (easyDIS) or hard (hardDIS) to ignore, depending on their frequency proximity with the S1 melody. In trials where S2 differs from S1, the changed sound is 6 or 7 semi-tones different from the original one in the low difficulty memory task (lowM) versus 1 or 2 semi-tones in the high difficulty memory task (highM)*

## Statistical analyses

We employed Bayesian statistics for all analyses, utilizing the JASP software (v0.16.3, JASP Team, 2022; Marsman & Wagenmakers, 2017; Wagenmakers et al., 2018; van den Bergh et al., 2022). This approach allowed us to assess the similarity between measures and estimate the level of logical support or belief in specific results. Bayes Factor ( $BF_{10}$ ) was reported as a relative measure of evidence, typically compared to the null model, unless stated otherwise. To interpret the strength of evidence against or in favor of another model, we considered specific ranges of BF values. A BF between 1 and 3 indicated weak evidence, between 3 and 10 indicated positive evidence, between 10 and 100 indicated strong evidence, and a BF higher than 100 indicated decisive evidence (Lee & Wagenmakers, 2014). Similarly, to interpret evidence in favor of the null model, we considered BF ranges of 0.33 to 1 as weak evidence, 0.01 to 0.33 as positive evidence, 0.001 to 0.01 as strong evidence, and a BF lower than 0.001 as decisive evidence. For clarity, we report information about the best model only, unless several models account almost as well for the data (as assessed when comparing models to the best model).

Furthermore, we provide results of an analysis of effects, which compares models with a specific effect to equivalent models without that effect, providing relative evidence supporting the inclusion of a factor ( $BF_{inclusion}$ ).

## Electrophysiological analyses

The MEG procedure, the data pre-processing and the ERF analyses are described in de la Chapelle et al. (2023). The ERF analyses are also described in Table 1. To present the procedure briefly, we studied separately and with different frequency filters the Contingent Negative Variation (CNV), the ERF to the note 1 and to the notes 2, 3, and 4 of S1 and DIS, and the sustained response during S1/DIS presentation and the delay. Using the Freesurfer

software package (Fischl, 2012; <http://surfer.nmr.mgh.harvard.edu>), each individual T1-weighted MRI was segmented and coregistered with the MEG sensors, serving as the base for computation of the forward model in OpenMEEG (Gramfort et al., 2010; <https://openmeeg.github.io/>). The sources of the sensor data were estimated using a linear inverse weighted minimum-norm current estimate algorithm. After filtering of the data (lowpass 2Hz, bandpass 2-30Hz, or lowpass 30Hz depending on the targeted ERF), we extracted from the sensor data each ERF of interest and an associated time-window. We further computed the difference between the ERF to S1 and to DIS to evidence any ROI related to their differential processing. For each obtained ERF, we then conducted emergence tests on the whole group at the source level to extract corresponding ROIs (see Table 1). In addition to this procedure, which was described in de la Chapelle et al. (2023), we conducted the emergence test for LR and HR separately, but because of the lower sample size no additional LR-specific or HR-specific ROI could be identified. The ROIs considered in this article are therefore the same as in de la Chapelle et al. (2023). ROI time-courses of source activity are extracted for each participant, each condition and each presentation side.

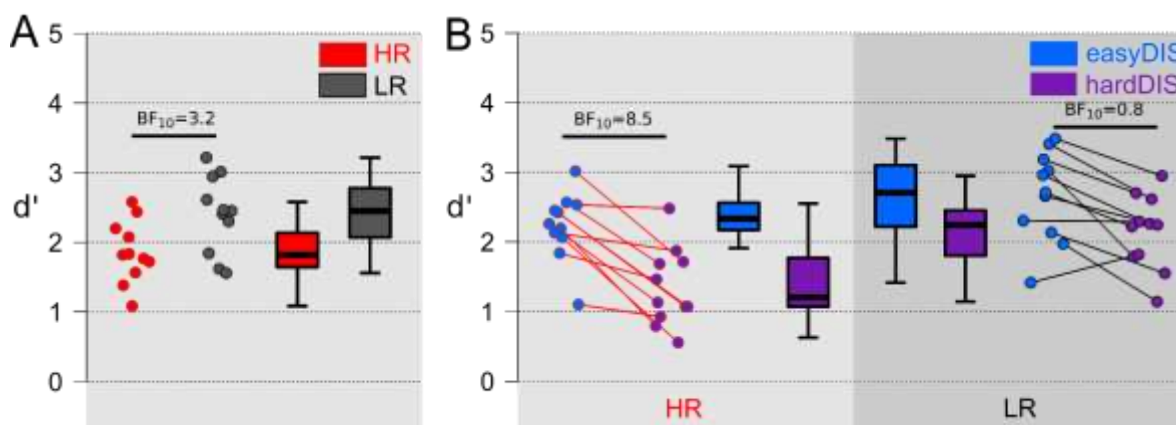
Finally, Bayesian ANOVA are carried on the data from each studied ROI, averaged on each time window, with at least a between-subject factor *Group* (LR or HR). Similarly to de la Chapelle et al. (2023), additional factors were considered in some analyses: *MEMdiff* (easyM or hardM), *DISdiff* (easyDIS or hardDIS), *CuedSide* (as shown by the arrow cue: Left or Right) and *StimType* (S1 or DIS); the only difference is the removal of the factor *MEMdiff* from the analysis of the notes 2, 3 and 4 of the S1 and DIS melodies as well as the factor *S1side* from the analysis of the sustained response to reduce the number of factors for the sake of parsimony, as they were shown to have no explanatory power in de la Chapelle et al. (2023). All conducted analyses are described in Table 1; for the sake of clarity, only analyzes presenting at least positive evidence for a *Group* effect or its interaction with another parameter are reported in detail in the Results section (i.e.  $BF_{10} \geq 3$ ). Effects of other factors are reported irrespective of the *Group* factor in de la Chapelle et al. (2023).

Time-frequency analyses similar to those presented in de la Chapelle et al. (2023) were conducted while including the *Group* factor, in ROIs defined by whole-group and group-specific cluster-based permutation tests; group-specific emergence tests did not highlight any additional ROI. These analyses are not presented here as only weak to strong evidence for an absence of any *Group* effect or interaction could be found in all tested ROIs and time-windows.

# Results

## Behavior

Behavioral results are reported in Blain, de la Chapelle et al. (2022) and represented in Fig. 2 to compare the electrophysiological results with the behavioral data more easily. Briefly, there was positive evidence for a *Group* difference in accuracy (measured with the  $d'$ ;  $BF_{inc}=3.9$ ) as well as weak evidence for an interaction between the *Group* and *DISdiff* ( $BF_{inc}=1.6$ ) on the  $d'$ . Post-hoc t-tests supported both the *Group* effect (LR vs HR:  $BF_{10}=3.2$ ) and the interaction between *Group* and *DISdiff* (easyDIS vs hardDIS: for HR,  $BF_{10}=8.5$ ; for LR,  $BF_{10}=0.8$ ). LR showed better performance than HR, and the performance of HR was more decreased by hardDIS (compared to lowDIS) than for LR, suggesting a stronger effect of the attentional filtering on performance in HR. No effect of memory difficulty was observed.



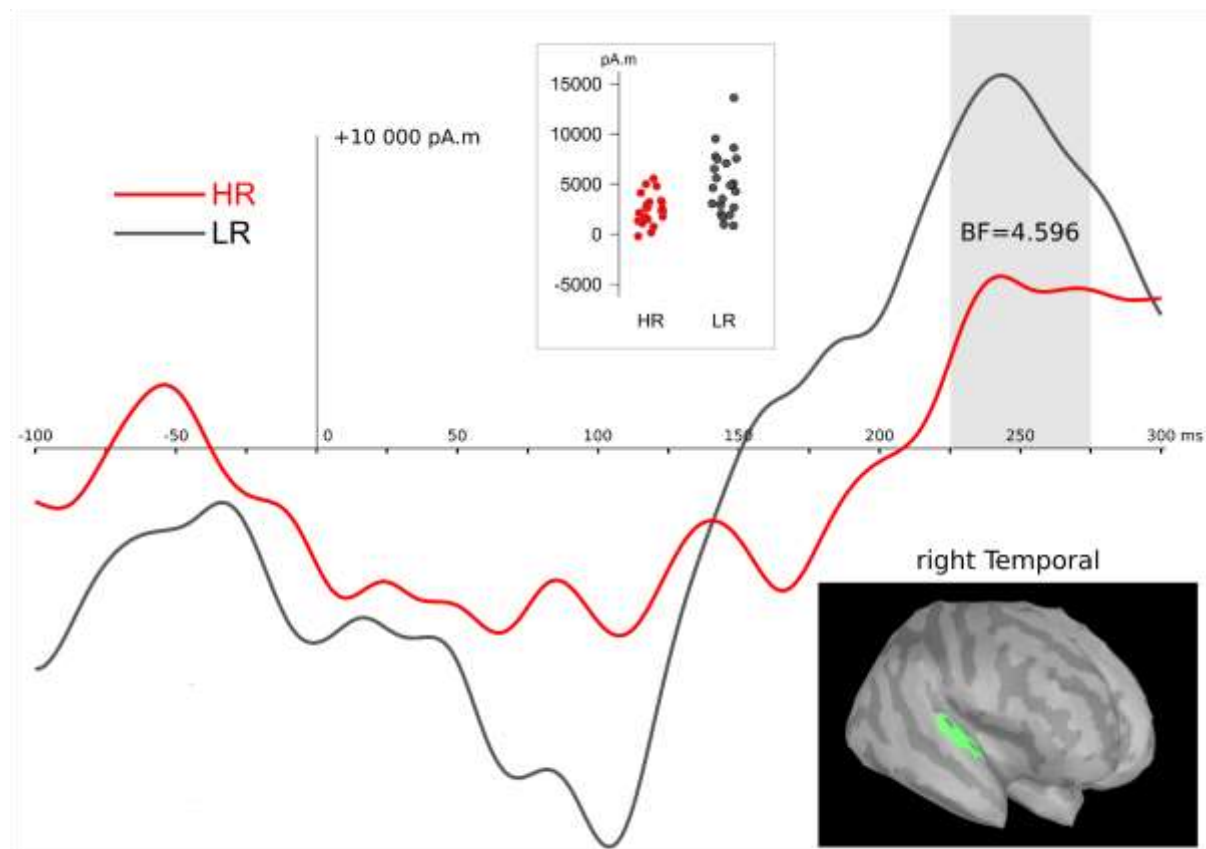
**Figure 2 - Summary of the behavioral results** reported in Blain, de la Chapelle et al. (2022) on performance ( $d'$ ). Results are shown A) for each *Group* (LR: low DRF, HR: high DRF) on average across the four conditions and B) for each *Group* and each difficulty of the distractor (easyDIS: easy to ignore, hardDIS: hard to ignore), averaged across memory difficulty levels. Whisker plots show the median $\pm$ quartile and the minimum/maximum values. Lines in the strip plots connect data from the same participant.

## Electrophysiology

For each analysis conducted, we report in Table 1 the event of interest, the filter used for preprocessing, the ERF studied, the ROI in which the analysis is conducted, the time-window where the data was averaged before analysis, the factors included in the ANOVA in addition to the between-subject *Group* factor, the model best explaining the data without the *Group* factor and the best one including it, and finally the  $BF_{10}$  comparing these two models as well as the  $BF_{inclusion}$  of the relevant factors and interactions. In all analyses, the  $BF_{10}$  of the null model is 1. In all analyses but one (N1 to Notes 2, 3, 4 of S1 & DIS in the right Frontal

ROI), the best model without the *Group* factor is the same as the best model in the same analysis conducted without the *Group* factor, as presented in de la Chapelle et al. (2023).

Among all analyses conducted and presented in Table 1, only the analysis of the late differential response between the ERFs to S1 and DIS (225-275ms post stimulus onset) showed positive evidence ( $BF_{10}>3$ ) for an effect of *Group*. In the Right Temporal ROI, the ANOVA with factors *DISdiff* and *Group* showed positive evidence for the best model without the *Group*, which only presented an effect of *DISdiff* ( $BF_{10}=6.414$ ). When including the *Group* factor, the best model included both the effects *DISdiff* and *Group* and was supported with strong evidence ( $BF_{10}=29.335$ ). The comparison of these models showed positive evidence for the model *DISdiff+Group* ( $BF_{10} = 29.335/6.414 = 4.573$ ). The analysis of effects revealed positive evidence for an effect of both *DISdiff* ( $BF_{inc}=6.228$ ) and *Group* ( $BF_{inc}=4.596$ ), with HR having a lower difference than LR between the ERF to S1 and DIS. We further tested whether this ERF related to the behavioral results by testing for inter-individual correlations between behavioral performance ( $d'$ , RT) and the ERF amplitude (see Supplementary Results). The analysis resulted in limited evidence for any group-related effects. In the Left Temporal ROI, we did not find a similar *Group* effect.



**Figure 3 - Time course of the difference between the transient evoked response to the tones 2, 3 and 4 of the to-be-attended melody S1 and of the to-be-ignored melody DIS (difference S1-DIS) in the Right Temporal ROI, represented here on the MNI template, for HR (red) and LR (black). Only responses to contralateral stimuli were analyzed (S1-L and DIS-L). Strip plots show the averaged signal in the gray area for HR and LR.**

Results table

Event of interest	Filtering	Studied ERF	STATISTICS					
			ROI [number of vertices]	Time-window for analysis (ms)	Factors	Best model without <i>Group</i> [BF <sub>10</sub> ]	Best model including <i>Group</i> [BF <sub>10</sub> ]	Evidence for best model including <i>Group</i> vs. best model without <i>Group</i>
S1	lp 30Hz	CNV	left PP [32]	-400 to -200	CuedSide, MEMdiff	<i>null</i>	Group [0.715]	BF <sub>10</sub> = 0.715
				-200 to 0		<i>null</i>	Group [0.655]	BF <sub>10</sub> = 0.655
			right PP [40]	-400 to -200		<i>null</i>	Group [0.965]	BF <sub>10</sub> = 0.965
				-200 to 0		MEMdiff [1.156]	MEMdiff + Group [0.729]	BF <sub>10</sub> = 0.631
S1: note1	bp 2-30Hz	N1	left temporal [55]	90 to 140	MEMdiff	<i>null</i>	Group [0.909]	BF <sub>10</sub> = 0.909
			right temporal [66]			<i>null</i>	MEMdiff + Group + MEMdiff*Group [2.007]	BF <sub>10</sub> = 2.007 BF <sub>inc</sub> (Group) = 0.849 BF <sub>inc</sub> (Group*MEMdiff) = 6.267 <sup>#</sup>
			left frontal [54]			<i>null</i>	Group [0.646]	BF <sub>10</sub> = 0.646
			right frontal [60]			<i>null</i>	Group [1.034]	BF <sub>10</sub> = 1.034 BF <sub>inc</sub> (Group) = 0.851
DIS: note1	bp 2-30Hz	N1	left temporal [55]	100 to 150	MEMdiff, DISdiff	DISdiff [3.565] <sup>#</sup>	DISdiff + Group [2.789]	BF <sub>10</sub> = 0.782
			right temporal [66]			<i>null</i>	Group [1.195]	BF <sub>10</sub> = 1.195 BF <sub>inc</sub> (Group) = 1.040
			left frontal [54]			MEMdiff + DISdiff + MEMdiff*DISdiff [1.858]	MEMdiff + DISdiff + MEMdiff*DISdiff + Group [0.971]	BF <sub>10</sub> = 0.523
			right frontal [60]			<i>null</i>	Group [2.791]	BF <sub>10</sub> = 2.791 BF <sub>inc</sub> (Group) = 2.510
S1 & DIS: notes 2,3,4	bp 2-30Hz	N1	left temporal [68]	100 to 150	StimType, DISdiff	StimType + DISdiff + StimType*DISdiff [61305] <sup>###</sup>	StimType + DISdiff + Group + StimType*DISdiff [46892] <sup>###</sup>	BF <sub>10</sub> = 0.765
			right temporal [65]			StimType + DISdiff + StimType*DISdiff [7985] <sup>###</sup>	StimType + DISdiff + Group + StimType*DISdiff + StimType*Group [6614] <sup>###</sup>	BF <sub>10</sub> = 0.828
			left frontal [27]			StimType + DISdiff [2641] <sup>###</sup>	StimType + DISdiff + Group [1971] <sup>###</sup>	BF <sub>10</sub> = 0.746

			right frontal [24]			StimType [23] ##	StimType + DISdiff + Group + StimType*DISdiff + DISdiff*Group [57] ###	$BF_{10} = 2.459$ $BF_{inc}(DISdiff*Grp) = 2.044$ $BF_{inc}(Group)=0.941$
		P2	left PP [46]	200 to 250	<b>StimType, DISdiff</b>	StimType + DISdiff + StimType*DISdiff [36] ###	StimType + DISdiff + Group + StimType*DISdiff [82] ###	$BF_{10} = 2.262$ $BF_{inc}(Group) = 2.569$
			right PP [44]			StimType + DISdiff + StimType*DISdiff [503] ###	StimType + DISdiff + Group + StimType*DISdiff [508] ###	$BF_{10} = 1.008$
S1-DIS: notes 2,3,4		Late differential response	right temporal [78]	225 to 275	DISdiff (only contralateral stimuli)	DISdiff [6.414] #	DISdiff + Group [29.335] ###	$BF_{10} = 4.573^{\#}$
					DISdiff (only ipsilateral stimuli)	DISdiff [42] ###	DISdiff + Group [37] ###	$BF_{10} = 0.894$
S1	lp 2Hz	Sustained response	left PP [51]	500 to 2000	<b>MEMdiff, DISdiff</b>	DISdiff [26957] ###	All effects and interactions [8479] ###	$BF_{10} = 0.315$
			right PP [44]			DISdiff [136] ###	DISdiff + Group [126] ###	$BF_{10} = 0.931$
			left PT [37]			null	Group [0.776]	$BF_{10} = 0.776$
			right PT [11]			null	Group [0.691]	$BF_{10} = 0.691$
			left PP [51]	2500 to 4000		null	Group [1.101]	$BF_{10} = 1.101$
			left PT [37]			null	Group [0.638]	$BF_{10} = 0.638$

**Table 1 - Summary of the ERF analysis** for the group comparison: event of interest, filtering used, studied ERF, ROI information, time-window for the statistical analysis, factors tested, and results for the Bayesian repeated-measure ANOVAs. Each ANOVA uses the within-subject factors shown in the column “Factors”, and always included the between-subject factor Group. “Best model without Group”: model showing the highest evidence among all that do not include the Group factor or its interaction with another factor. “Best model including Group”: model showing the highest evidence among all models including the Group factor or its interaction with another factor. “Evidence for best model including Group vs. best model without Group”: comparison of the two previously mentioned models by computing the ratio between their  $BF_{10}$ ; this newly computed  $BF_{10}$  ( $=BF_{10}(Group)/BF_{10}(noGroup)$ ) represents evidence for the model that includes the Group factor compared to its absence, and if above 1, we further report the  $BF_{inclusion}$  of the factors and interactions present in the best model including the Group factor. In all analyses,  $BF_{10}(null\ model) = 1$ . #:  $BF_{10}>3$  (positive evidence), #:  $BF_{10}>10$  (strong evidence), ###:  $BF_{10}>100$  (decisive evidence)

# Discussion

We identified electrophysiological brain activity corresponding to the Group difference observed at the behavioral level showing better performance in LR than in HR during the MEMAT task. In the right auditory cortex, the ERF to relevant stimuli (S1 notes) is higher than the ERF to to-be-ignored stimuli (DIS notes) between 225 and 275ms (post note onset), which translates to a more efficient processing of relevant stimuli. This late differential processing between S1 and DIS was interestingly larger in LR than in HR.

This result suggests that LR are better able to process differentially relevant from to-be-ignored stimuli. Electrophysiological components at this latency have been associated with selective attention processes (Giard et al., 2000; Bidet-Caulet et al., 2007) notably the Processing Negativity (PN) or Negative Difference (Nd), typically observed when comparing ERFs to attended and unattended stimuli in EEG (Giard et al., 2000; Näätänen, 1982) and in MEG (Hari et al., 1989; Arthur et al., 1991). The early PN component (early PN, 110-275ms, generated in the auditory cortex), which presents temporal and spatial similarity with our observed difference between S1 and DIS notes, has been associated with a consciously controlled process of identification of relevant incoming stimuli. According to this literature, the smaller early PN in HR compared to LR could imply less differential top-down processing of the relevant incoming stimuli, in other words a worse signal-to-noise ratio in processing relevant vs irrelevant sounds. This smaller PN possibly hampers optimal processing of the to-be-remembered stimuli in HR. Interestingly, with a less challenging attentional task (Bidet-Caulet et al., 2015) we previously identified an increase of both top-down and bottom-up attentional processes in HR vs LR (Ruby et al., 2022). We interpreted this result as a costly coping mechanism (increase of top-down processes to compensate for the increase in bottom-up processes) to maintain good performance. We thus expected HR to show more decreased performance than LR in challenging conditions, which we indeed observed with the MEMAT task at the behavioral level (Blain, de la Chapelle, et al., 2022), and we also show here that it is associated with a decrease in top-down related components in the auditory cortex. This result is coherent with the hypothesis that in HR faced with challenging conditions such as the intensive memory task in MEMAT, there are not enough cognitive resources available for top-down attention processes to compensate for the increase in bottom-up attention processes.

The results of this study confirm attentional differences between HR and LR both at the behavioral and electrophysiological level. Attentional differences between the two groups could explain DRF differences through different mechanisms (Blain, de la Chapelle, et al., 2022). Increased bottom-up processes would participate in increased brain reactivity, increasing the probability of long awakenings during sleep, favoring dream recall (e.g., Vallat



et al., 2017). Increased top-down processes (not directly investigated here) would favor consciousness and memory recall of dream content at awakening (Dresler et al., 2012; Voss et al., 2014). Further studies manipulating attention during sleep (such as in Takahara et al., 2006) are warranted to further understand the link between attentional and dream recall abilities.

### **Limitations**

The results did not show any interaction effect in electrophysiological responses similar to the one observed at the behavioral level with a greater impact of the hard-to-ignore distractors in HR. It may be explained by the small size of the behavioral effect and an insufficient number of subjects to objectivate the corresponding electrophysiological correlates. Note nonetheless that one electrophysiological result (supported by weak evidence) could explain the interaction effect observed at the behavioral level. The early part of the N1 to the notes 2, 3 and 4 of both S1 and DIS melodies tended to be lower in hardDIS compared to easyDIS in the right prefrontal cortex in HR but not in LR (Table 1). The observed effect applied both to to-be-attended (S1) and to-be-ignored (DIS) stimuli, meaning that this effect cannot be considered as a selective attention effect. One may speculate that if the early part of the N1 does not reach a minimum level the subserved cognitive processing (sound discrimination) could not be optimized. In that case this result could explain the lower behavioral performance of HR in hardDIS compared to LR: in hardDIS conditions, the N1 component would be degraded for all sounds in HR which would consequently diminish their performance at memorizing the melody to-be-remembered. Further studies will be needed to confirm or refute this interpretation of the results.

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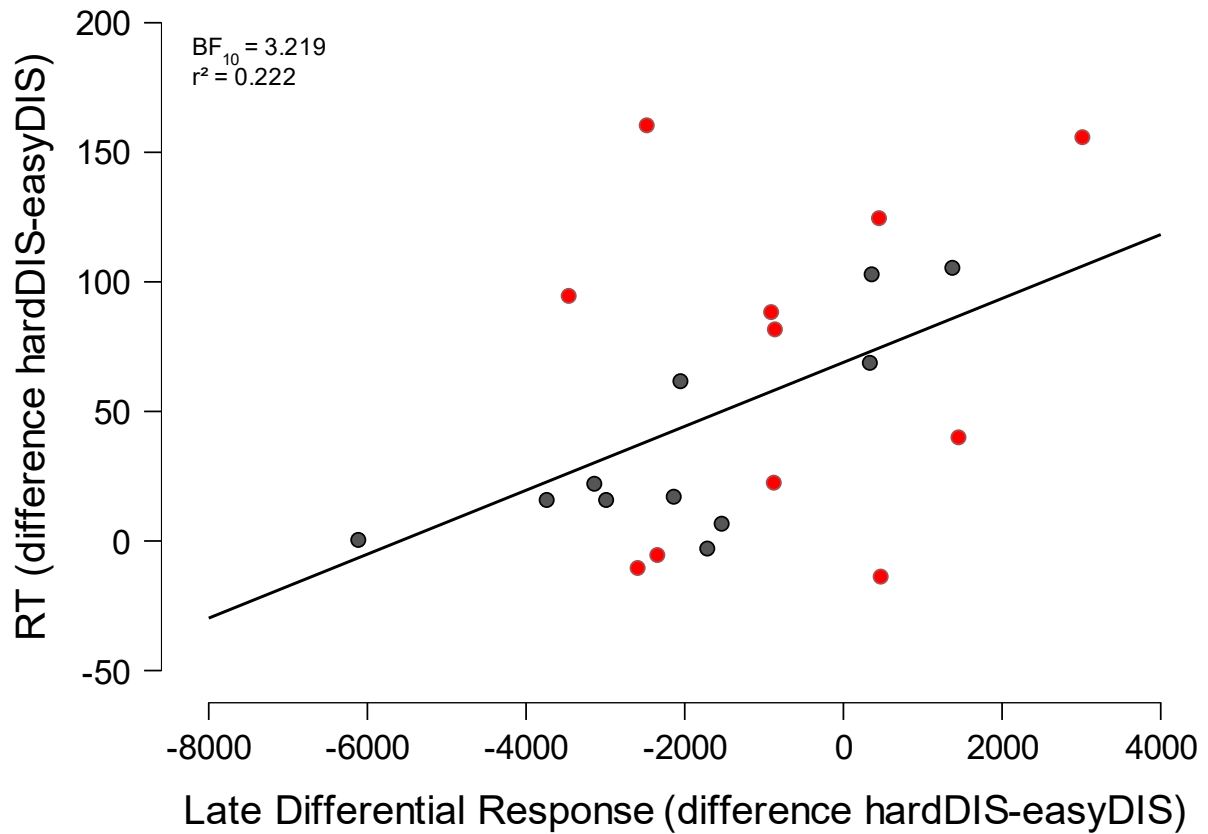
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# Supplementary Results

To assess the relationship between behavioral performance ( $d'$ , RT) and the main effect of Group on the difference between the ERF to the notes 2, 3 and 4 of S1 and of DIS in the Right Temporal ROI (225-275ms), we conducted Bayesian Pearson correlations between the behavioral measures ( $d'$ , RT) and the electrophysiological signal averaged over all trials and in each DISdiff condition (easyDIS or hardDIS), independently of the Group. We also compared the difference between the behavioral measures in hardDIS and easyDIS to the difference between the electrophysiological signal in hardDIS and easyDIS to test the influence of variation of the electrophysiology on the behavior.

In this ROI and this time-window (right Temporal, 225-275ms), there was positive evidence for one correlation: on one hand we computed the difference between the RT in hardDIS and in easyDIS, and on the other hand the late differential response between S1 and DIS (Notes 2, 3, 4) in easyDIS was subtracted to the same difference in hardDIS. These two values correlated positively ( $r=0.471$ ,  $BF_{10}=3.2$ ), as represented on Fig. S1. In other words, the difference in processing between S1 and DIS (i.e., how well the to-be-attended stimuli are processed compared to the to-be-ignored stimuli) is higher in easyDIS than in hardDIS when there is no difference in response time between the easyDIS and the hardDIS condition. On the contrary, longer response times in the hardDIS condition are associated with lower or no difference between the differential processing of S1 and DIS stimuli in the hardDIS and the easyDIS condition. Additional post-hoc t-tests support a difference between LR and HR of RT difference between easyDIS and hardDIS with weak evidence ( $BF_{10}=1.6$ ) and an absence of between-group difference between the differential response (to S1 and DIS) in easyDIS and in hardDIS with weak evidence ( $BF_{10}=0.73$ ). For all other tested correlations there was weak evidence for or against any correlation ( $0.478 < BF_{10} < 1.3$ ).

The positive evidence for this correlation would suggest that better differentiation between to-be-attended and to-be-ignored stimuli in a more difficult context prevents any cost in response time associated with the hardDIS compared to the easyDIS, while an absence of differential processing between the two conditions implies a longer processing and therefore a later response. It is however difficult to generalize this result to LR and HR specifically as the post-hoc tests only provided limited evidence for a difference between them on either of the parameters tested, especially since the behavioral result did not support a Group effect on the RT and since the ERF analysis did not show any DISdiff effect on the differential response between S1 and DIS.



**Figure S1** - Correlation between the difference in response time between hardDIS and easyDIS (in ms) and the difference in late differential response of S1 and DIS between hardDIS and easyDIS between 225 and 275 ms in the Right Temporal ROI (in pA.m). A higher RT in hardDIS than in easyDIS is indicated at the top of the plot; a short RT corresponds to enhanced performance in the task. The differential late response between S1 and DIS, which is always positive, is higher in hardDIS than in easyDIS, on the right of the plot; a large differential processing of S1 compared to DIS is synonymous with an efficient processing of relevant stimuli. Red dots represent HR; black dots represent LR.

# Study 2 – Dreaming in Epilepsy

Study 2a –  
*Determinants of dream recall in epilepsy: a systematic study*

In preparation

## Methods

### Participants

Patients of the Epilepsy Centre of the Pierre Wertheimer Neurological Hospital (Lyon, France) were systematically proposed to participate in the study at the end of their medical appointments. Exclusion criteria were age below 18 and above 65 years old, a non-confirmed epilepsy diagnostic and major cognitive deficits. A total of 126 patients were screened, among which 108 fit the inclusion criteria and 84 agreed to participate (42 women, mean age=41±12 years old). One patient was excluded as they answered the questionnaires randomly. Patients gave their consent to participate and the study was approved by the Comité de Protection des Personnes Sud-Méditerranée II (CCP N°222 C18).

### Study procedure

At the end of their medical appointment, participants were informed about the study by the epileptologist and provided their consent to participate in the study. They completed a 20min online survey on the platform LimeSurvey with the assistance of a lab member (Maxime Linard).

Questions addressed the patients weekly DRF, their nightmares, their recurrent dreams, the impact of epilepsy of dream content, their subjective sleep quality (i.e. nocturnal awakenings), their potential sleep disorders and their night and day seizure frequency. The dream frequency was estimated with the average of a 5-point scale (question “Generally, I remember dreams”: “less than once per month”=0.125, “once per month”=0.25, “several times per month but less than once per week”=1, “several times per week”=3.5, as in Schredl, 2004) and of the self-reported number of mornings with a dream recall in the last week (“How many mornings did you have a dream in head when waking up in the last week?”).

Additional information was extracted from their medical records by an epileptologist (LPD): birthdate, age at epilepsy onset, gender, seizure type (generalised or focal), epilepsy syndrome, location of the epileptic focus (lobe and hemisphere) in case of focal epilepsy, seizure frequency, reported sleep-related seizures, abnormal EEG activity, presence of a lesion on MRI, antiseizure medication, comorbid depression/anxiety and cognitive disorders.

### Data analysis

Because of the high number of investigated factors and the heterogeneity of the population, and as the recruitment is still ongoing, all factors could not be tested in a single



model yet. The factors age, sex, duration since epilepsy onset, seizure frequency, seizure type, reported sleep quality, reported number of nocturnal awakenings, and reported sleep-related seizures were included in a GLM (Generalized Linear Model) that was fitted using the lme4 R package (R Core Team, 2020; Bates et al., 2015) to investigate their role on DRF. Since positive continuous values such as the DRF can be fitted with either an inverse gaussian, a gamma or a gaussian distribution, we compared nine models, fitted with either a gamma, an inverse gaussian or a gaussian distribution and with either an identity-link function, a log-link function or an inverse-link function. After rejecting the non-converging models, we chose the model with the lowest AIC (Akaike Information Criterion, a measure of the fit between the model and the data it was generated from). Then, we used an AIC-based stepwise regression algorithm from the stats R package (R Core Team, 2020) to remove non-parsimonious factors from the linear model. This algorithm tests dropping (or adding if possible) one parameter to the model and keeps the model with the lowest AIC at each iteration. The returned model is a simplified model with only relevant and parsimonious factors. Finally, statistical tests were performed using type II Wald chi-square analysis of variance using the car package (Fox & Weisberg, 2019) on the final model.

## Results

### Characteristics of epilepsy

The final sample of 83 participants ( $41.0 \pm 12.5$  years old; 41 men, 42 women) consisted of 27 patients with generalized idiopathic epilepsy, 37 with focal structural epilepsy (26 acquired, 11 genetic), and 19 with undetermined type. Among the participants, 29 had generalized seizures, 24 focal seizures, 29 combined focal and generalized seizures, and 1 undetermined seizures. Epilepsy had lasted for  $20.9 \pm 15.0$  years. Seizure frequency was weekly (N=8), at least monthly (N=14), at most monthly (N=14), at most yearly (N=10) or nul (N=33) (undetermined for 4 patients). A total of 37 patients were drug-resistant, and 8 patients had benefitted from epilepsy-related surgery. Sixteen patients reported having or having had sleep-related seizures, contrary to 7 patients; this information was however not reported for 60 patients. The last EEG performed in the participants (in average  $2.9 \pm 2.7$  years before the visit) was normal in 37 patients, and abnormal in 41 including interictal paroxysmal activity in 28 patients, and abnormal slow activity for 13 of them (no available EEG report for 5 patients). Lesions were detectable on the last MRI in 42 patients (including 4 epilepsy-unrelated lesions), and absent in 36 (no MRI for 5 patients). No recruited patient had any severe cognitive impairment, but 14 presented minor or mild impairments (memory, attention, and/or language). An history of depression was assessed in 12 patients, of anxiety in 12 patients, and of psychosis in 2 patients. Prescribed ASM were Lamotrigine (39.8% of patients), Levetiracetam (32.5%), Sodium Valproate (20.5%), Carbamazepine (12.0%), Lacosamide (12.0%), Zonizamide (7.2%), Briveracetam (7.2%), Phenobarbital (4.8%), Eslicarbazepine (4.8%), Cannabidiol (3.6%), Cenobamate (3.6%), Perampanel (3.6%), Topiramate (3.6%), Lorazepam (2.4%), Oxcarbazepine (2.4%), Clonazepam (1.2%), and Phenytoine (1.2%); Clobazam was also prescribed on demand in 37.3% of patients.

### Characteristics of dreams

In this sample, the average reported DRF was  $1.65 \pm 1.40$ /week. Nightmares were recalled less than once a week ( $0.37 \pm 0.66$ /week). The frequency of recurrent dreams was, as follows: never (N=41), rarely (N=14), sometimes (N=20), or often (N=8). The patients reported having generally very vague (N=6), vague (N=32), clear (N=36) or very clear (N=9) dreams. When asked about the presence of seizures in dreams, 66 patients never had had a seizure in their dreams, it had rarely happened to 12, sometimes to 3, and none said it happened often (no answer for 2 patients). However, 9 patients could sometimes identify stereotyped symptoms of their epileptic seizures occurring in their dreams (shaking, falling, shouting, feeling unwell, out of breath, headaches, out-of-body experience, confusion, deja-

vu), and 6 believed that seizures in their dreams corresponded to an actual sleep seizure. Most of them did not dream of their epilepsy or its consequences on their life: never (N=60), rarely (N=11), sometimes (N=8), or often (N=4). They mostly couldn't tell whether their DRF had changed since they were epileptic (N=39, notably including people who had been epileptic since early childhood), and the others generally did not see any change (N=31; increase for 5 patients, decrease for 8 patients). The patients reported their sleep quality as very good (N=7), good (N=36), average (N=18), bad (N=18), or very bad (N=4), including 2 patients with CPAP treatment for sleep apnoea and 1 using benzodiazepine as an hypnotic. They also reported waking up  $1.7 \pm 1.5$  times every night on average.

### Determinants of Dream Recall Frequency

After stepwise regression, only the three most parsimonious factors were preserved for the GLM analysis of the DRF: sex of the patient (*Sex*), number of nocturnal awakenings (*NbNocturnalAwakenings*) and duration since epilepsy onset (*EpilepsyDuration*). DRF significantly decreased with increased *EpilepsyDuration* ( $p=0.002$ ), barely not significantly increased with *NbNocturnalAwakenings* ( $p=0.054$ ) and was not significantly influenced by *Sex* ( $p=0.12$ ). Results are shown below in Figure 1.

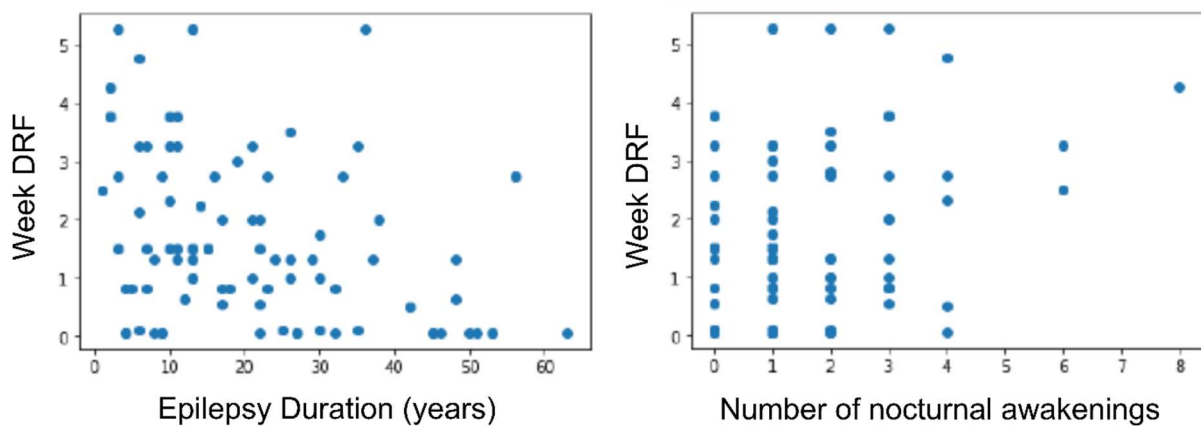


Figure 1 – Associations between Dream Recall Frequency (per week) and epilepsy duration (A) and subjective number of awakenings (B) in Study 2a. These representations don't factor the variability explained by other factors in the GLM and are therefore only partially representative of their own effect.

## Discussion

In this preliminary analysis, increased DRF was associated with an increase in subjective nocturnal awakenings, a lower epilepsy duration (rather than age), but not with seizures frequency. Moreover, the DRF was surprisingly elevated compared to the global population (e.g., 0.8/week in a representative sample of the German population: Schredl, 2008), especially since Bentes et al. (2011) suggested a decrease in DRF in temporal lobe epilepsies (2.4/week) compared to healthy controls (5.8/week); it should however be noted that the DRF in the healthy controls was unusually elevated in this work (as compared to 0.8/week in Schredl, 2008). As we systematically recruited patients after their medical appointments, and as they mostly agreed to participate (77%), it is unlikely that there was a strong enough recruitment bias that would explain this high DRF. Interestingly, previous studies of dreaming in epilepsy similarly reported a high DRF: in Bonanni et al. (2002), patients with complex partial seizures had a DRF of 3.9/week and those with generalized seizures had a DRF of 1.8/week, and Bentes et al. (2011) reported a DRF of 2.4/week for temporal lobe epilepsies. As nocturnal awakenings increase DRF (Schredl et al., 2003; Eichenlaub et al., 2014; Vallat et al., 2017; van Wyk et al., 2019), this increased recall may at least partly originate from the increased sleep fragmentation in epilepsy. We will discuss this effect further in the paragraph regarding the effect of awakenings on DRF. It is also important to note that we did not include a control group, as it would not have been possible to conduct the interview with the same methodology (inclusion following regular visit) and as such methodology is a major parameter involved in DRF.

Our hypothesis that seizures would decrease dream recall by erasing memory content was not supported. According to the arousal-retrieval model (Koulack & Goodenough, 1976), dream recall could occur during any awakening, including before the seizure or after falling asleep again. In that case, even if the dream memory stored during the seizure is disrupted, a following or previous dream memory could be remembered. While single events (i.e. seizures) did not influence DRF, their accumulation seems to influence DRF as epilepsy duration was negatively correlated with DRF independently of age, a factor which has been reported to have a small but significant influence on DRF (Stepansky et al., 1998; Schredl, 2008; Vallat et al., 2018; Mangiaruga et al., 2018). It is possible that ictal and interictal activity might lead to progressive remodelling and damage of brain tissue, associated with impairment in specific cognitive abilities, some of which are involved in dream production, memorization, and/or retrieval (Breuer et al., 2016). Alternatively, epilepsy comorbidities such as cognitive disorders or anxiety/depression, might be involved; unfortunately, these data were missing for a high number of patients, preventing us from testing if such comorbidities were more frequent in patients with long lasting epilepsy. It is important to note that, in this study, seizures were reported subjectively by patients or their relatives, which may have led to underestimation, particularly in the case of sleep-related seizures.

On the contrary, as epilepsy, including seizures and interictal activity, is associated with increased sleep fragmentation (Peter-Derex et al., 2020), we supposed that the increased sleep fragmentation would lead to increased dream recall. This was confirmed both by the elevated DRF in our population compared to healthy subjects, but also by the almost significant correlation between the subjective number of awakenings and DRF (Figure 1b). Such an association between subjective awakenings and DRF is consistent with existing literature in healthy subjects (Campbell & Webb, 1981; Winser et al., 2013; Schredl et al., 2003; Vallat et al., 2017; van Wyk et al., 2019) and confirms that the arousal-retrieval model remains compatible with the pathological framework of epilepsy.

As a conclusion, our results suggest that patients with epilepsy may share at least some of the dream recall mechanisms at play in healthy patients, with the added effect of the duration of the epilepsy. While preliminary, these findings are encouraging regarding the study of dreaming in the context of epilepsy, and will need to be confirmed with the full-sized target population (N=300).

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# Study 2 – Dreaming in Epilepsy

Study 2b –  
*Influence of epilepsy on dreaming: a SEEG study*

In preparation



## Data collection

### Participants

In this prospective multi-centre study, patients with drug-resistant epilepsy who underwent intracranial exploration with SEEG electrodes in the course of their presurgical evaluation were included between September 2019 and June 2023. Patients were recruited at two international centres: the Montreal Neurological Institute (Montreal, Canada) and Pierre Wertheimer Neurological Hospital (Lyon, France). Exclusion criteria were age <18yo and major cognitive deficit. A total of 45 patients were screened among which 24 were included (14 at the MNI and 10 in Lyon); a detailed flowchart of the recruitment process is shown in Figure 1. The clinical characteristics of the patients are described in Table 1. For this thesis, analyses were conducted on 23 patients only, as the last patient has been included recently.

Patients gave their written consent to participate and the study was approved by the Research Ethics Board of the Montreal Neurological Institute (2020-5595) and the Comité de protection des personnes de Grenoble (09-CHUG-12).

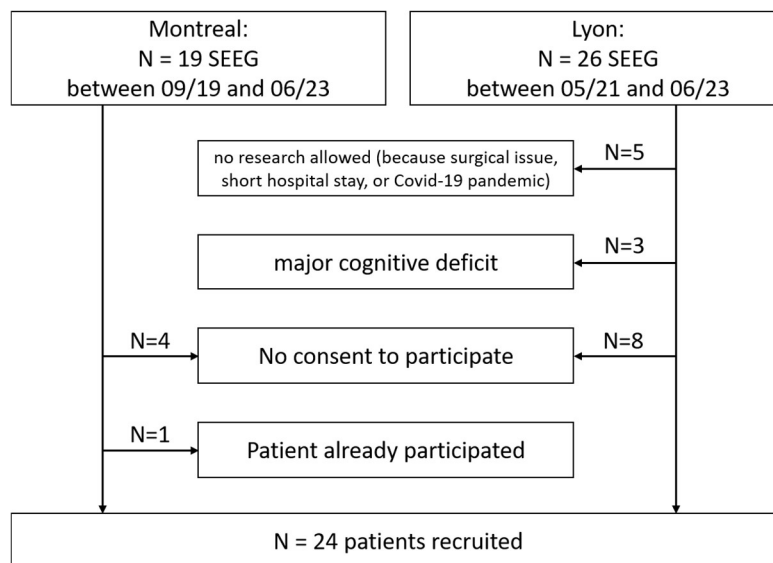


Figure 1 – Flowchart of the recruitment process in Study 2b. Among all SEEG presurgical evaluations in Lyon and Montreal, some patients were not available for research studies, did not meet our inclusion criteria, or did not consent to participate in the study. One patient who was implanted twice was recruited for our study the first time and excluded the second time.

## Study procedure

After study inclusion, multiple questionnaires to assess dream habits, sleep disturbances, sleepiness, anxiety and depression, quality of life and sleep apnea were completed. Study participants were asked to fill out a dream diary every morning during their hospital stay, lasting from 4 to 18 nights (mean=10). To assess the dream contents, participants were provided paper and a voice recorder to write or record their dreams every morning (or to report the absence of a dream). For each dream, patients were asked to rate the positive and negative emotions, the intensity of the action, the bizarreness, their control over the dream, its relation to wake life, and its relation to their epilepsy (symptoms, seizures...) on a 5-point Likert scale (1=not at all to 5=very important). The procedure is described in Figure 2.

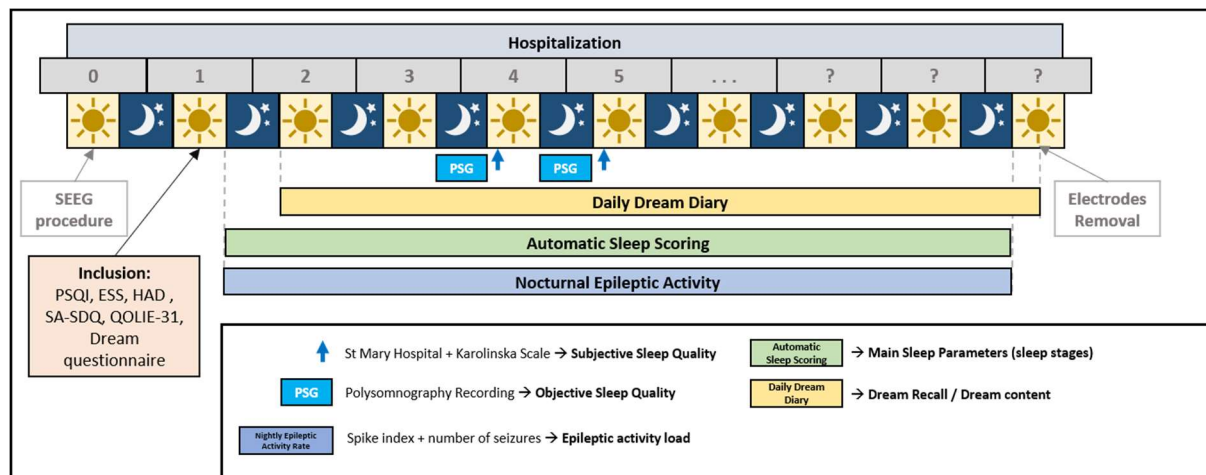


Figure 2 – Protocol of the Study 2b.

## Questionnaires

At the beginning of the study, patients filled out a dream Questionnaire, the Pittsburgh Sleep Quality Index (PSQI), the Epworth Sleepiness Scale (ESS), the Hospital Anxiety and Depression (HAD), the Sleep Apnea (SA-SDQ) and the questionnaire for quality of life in epilepsy (QOLIE-31).

The dream questionnaire (adapted from Vallat et al., 2018) assesses habitual dream recall frequency, lucid dreaming frequency and recurring dreaming frequency. The PSQI (Buysse et al., 1989) records sleep quality and sleep disturbances during the previous 4 weeks. The following seven subscales can be extracted: subjective sleep quality, sleep latency, sleep duration, sleep habits, sleep disorders, use of medication related to sleep, and daytime functioning, as well as a global score which is indicative of poor sleep quality when above 5. The ESS (Johns, 1991) measures excessive daytime sleepiness. Patients rate the likelihood of

falling asleep or dozing in eight different situations on a Likert-scale of 0-3. The maximum score is 24 and a value  $>10$  indicates significant sleepiness. The HAD (Zigmond & Snaith, 1983) was developed to detect states of anxiety (HAD-A) or depression (HAD-D) in a non-psychiatric hospital setting; each subscale score ranges from 0 to 21, and a score of 8-10 indicates doubtful cases, while 11 or higher confirms the diagnosis. The SA-SDQ (Douglass et al., 1994; Weatherwax et al., 2003) is a screening instrument for sleep apnoea with existing cut-off scores for epilepsy patients (29 for men, 26 for women; score range: 12 to 60). The QOLIE-31 (Cramer et al., 1998) is a survey of health-related quality of life for adults (18 years and older) with epilepsy and consists of 31 items for seven subscales (emotional well-being, social functioning, overall quality of life, energy/fatigue, cognitive functioning, seizure worry, medication effect) and an overall score consisting of the weighted scores. The authors also proposed a normative scale of the QOLIE-31 (“T-scores”) so that a cohort of 304 epileptic patients had a mean score of 50 with a standard deviation of 10.

In addition, following two nights with additional polysomnography (PSG) recording, patients filled out the Karolinska Sleepiness Scale (KSS; Akerstedt & Gillberg, 1990) which assesses instantaneous sleepiness (in the past 10 minutes) on a Likert scale. Afterwards, the St. Mary Hospital (Ellis et al., 1981) questionnaire was administered, which measures the subjective perception of the previous night sleep quality, sleep duration, awakenings at night and sleep satisfaction.

At the end of their hospitalisation, participants filled out a last questionnaire about their subjective feeling of the relation between their dreams and their epilepsy.

## Recordings

Electrophysiological data was collected with the Neuroworkbench EEG system (Nihon Koden; Tokyo, Japan) in Montreal and with a Micromed (Treviso, Italy) system in Lyon.

### SEEG recordings

In average, 12.2 (range 6-15) SEEG DIXI (10-15 contacts of 2 mm separated by 1.5 mm) electrodes were implanted stereotactically using an image-guided system. Recording frequency was 256Hz or 2048Hz in Montreal and 128Hz or 2048Hz in Lyon, with a common reference (epidural electrode fixed in the bone). For intracranial analyses, we used bipolar montages using neighbouring contacts on each SEEG electrode. The location of the electrodes is specified for each patient in Table 1.

### Polysomnography

For two nights during the hospital stay for SEEG investigation, additional PSG recording with electrooculography (EOG) and chin electromyography (EMG) and, for patients explored at the Montreal Neurological Institute and Hospital, scalp subdermal thin wire EEG electrodes (according to the 10-20 system: F3, C3, P3, Fz, Cz, Pz, F4, C4, P4; as the SEEG electrodes prevented the placement of some scalp electrodes, only Fz, Cz, F3 and/or F4, C3 and/or C4, P3 and/or P4 were present in all subjects) were added in the 21 participants who agreed (including one who was recorded a single night) for this additional recording. For sleep scoring, we used a bipolar montage for the scalp EEG (F3-C3, C3-P3, Fz-Cz, Cz-Pz, F4-C4, C4-P4 when available) and not a more typical mastoid reference montage because of the proximity of some depth electrodes to the mastoid region and the risk of infection and because the reference could be contaminated by epileptic activity (for temporal epilepsies).

Patient ID	Age	Gender	Seizure onset zone location	MRI	ASM and other psychotropic drugs before first PSG	SEEG Electrodes
1	37	M	R temporal	PNH R temporal	CLO (40) OxCBZ (900) CTP (10)	R: H, Fus, T1, T2, T3, TP  R : A, pC, CO, Fus, H, F2, F3, FO, aI, pI, PO, PP, T2, T3, SM L: A, Ec, H, PP, T1, T2, T3
2	21	F	R temporal mesial	normal	CLO (5) LAM (500) AMI (75)	R: Ag, pC, Cun, Fus, LL, T1, T2, T3, SM, sP, iO, mO, sO, PC, PO
3	18	F	R occipito-temporal	normal	None	L: aC, CO, F1, F2, F3, FO, H, aI, T1, T2, PT
4	51	M	L fronto-lateral	Vascular lesion L F3 in close vicinity to Broca	CBZ (800) LAC (200) FYC (6)	L: Fus, F2, H, pI, PP, PH, T2, T2, T3, TH
5	40	M	Widespread L temporal and hypothalamic hamartoma	hypothalamic hamartoma and L temporal surgical bed	CLO (10) LEV (1500) OxCBZ (300)	R: Ag, aC, C, pC, CO, Fus, F1, F2, F3, FO, H, aI, pI, LL, sP, PC, PT, SM, T1, T2, T3, TP
6	43	F	R insular	Bilateral frontal atrophy	OxCBZ (1200) CLO (10)	L: A, pC, Ec, Fus, F2, F3, FO, H, aI, pI, iO, sP, PP, SM, T1, T2, T3, TH, TP
7	40	M	L mesio-temporal	L fusiform gyrus lesion	LOR (4)	R: Ag, pC, Fud, H, LL, iO, mO, PC, sP, PH, SM, T1, T2, T3, TH
8	28	F	R latero-occipital	normal	AMI (10) LAC (200) LEV (250) ZOP (7.5) CBZ (200) CTP (40)	L: Ag, pC, Fus, H, iO, mO, sO, sP, PC, SM, T2, T3
9	46	M	L parieto-occipital	Lesion in the L parieto-occipital region (possible cortical focal dysplasia)	CLO (30) LAC (150) LAM (200) PER (12)	L: aC, mC, CO, F1, F2, F3, FO, FP, Fus, H, aI, pI, LL, PO, sP, PP, SMA, T1, T2, T3, TP
10	40	F	L mesio-temporal	L Temporal atrophy (mesial+lateral) extending to the Insula + perisylvian region	LAC (200) LAM (200) TOP (100) PHE (150)	R: A, Cun, Fus, aI, pI, H, LL, iO, PC, PH, PO, PP, PT, SM, sT, T1, T2, T3, TH, TP
11	33	M	Right posterior temporal / posterior Insula	Right temporal neocortex atrophy/agenesis of the right piriform cortex	BRI (50) CLOn (1) EsCBZ (400) LAC (100) PRE (75)	R: Ag, pC, CO, F2, F3, FO, aI, pI, sP,
12	29	M	R posterior	normal	CBZ (100) PB (120)	

						LEV (250)	PC, PO, PP, PT, SM, T1
13	37	F	L temporal	mild L mesial temporal sclerosis with minimal changes within the left hippocampus and left mammillary body remote postoperative changes of a R temporal		CBZ (500) LAM (200)	L: A, F1, F2, F3, FO, Fus, H, aI, LL, PH, PP, PT, T1, T2, T3, TH
14	36	F	R temporal	craniotomy with stable surgical cavity in the middle cranial fossa		TOP (50)	R: Fus, F2, F3, FO, H, aI, LL, iO, PH, PP, T1, T2, T3
15	32	F	R orbito-frontal	Normal		PER (8) OxCBZ (600) ALP (0.25) ESC (5)	R: C, F, F3a, FP, H, I, OFa, OFm, PH, TP, T2 L: TP, F3, F3a, OF
16	19	F	L periventricular heterotopia temporal	PNH		<i>no PSG</i>	L: Ag, Cun, Fus, H, Hp, LL, O, TP, T1, T1p, T2, T2a, T2p, T3p, Pi, PH R: A, C, F, F2, F3, H, I, OF, P, PM, Tp, T1, T2
17	40	F	L perisylvian	R posterior insular ganglioglioma		<i>no PSG</i>	L: OF, F3, I, F, Tp R : TP
18	21	F	L temporo-opercular	Normal (+previous SEEG related lesion)		BRI (50) CBZ (600)	L: A, Ec, aH, pH, O, PM, T, T1a, T1m, T1p, T2p, T3p, TP R: Ha, T2, T2p, PHp
19	23	F	L temporo-parieto-occipital	L temporo-occipital malformation with PNH and malformation in L hippocampus		LAC (100)	L: A, Ec, Ha, Hp, Ip, O, P, PC, PHp, T, T1p, T2, T2p, T3, T3p, TH, TP L: Ag, Cp, Ha, Hp, I, LL, O, OF, T1m, T1p, T2a, T2m, T2p, TH, TP
20	40	F	L temporal	L temporal pole mild atrophia + hippocampus hypersignal		LAM (150) LEV (500)	L: F3, Hs, I, Ia, Ii, Im, Ip, Is, SM, T1, T1m, T1p, T2, TP
21	36	M	L insulo-opercular	L hemispheric malformation (cortical malformation with polymicrogyri, heterotopia)		<i>no PSG</i>	R: Ec, Ha, Hp, I, T1, T2, T3, T3a, TP L: Ca, Cm, Cp, F1, F2, F3, FP, Ha, Ia, Ip, SMA, T2, TH, TP
22	23	F	R temporal	R DNET		CBZ (200) LAM (75)	L : Ec, F3, Ha, Hp, I, LL, O, T1, T1m, T2, T2m, T2p, TH, TP
23	28	M	L perisylvian	L hemispheric atrophia + L hippocampus dysplasia		ZON (100) LEV (500)	LAC (100) EsCBZ (400) CEN (75)
24	24	M	L TP	normal			

Table 1 – Demographic and clinical characteristics of all included patients. # = unavailable data, L=Left, R=Right; ALP=Alprazolam, AMI=Amitriptyline, BRI=Brivaracetam, CBZ=Carbamazepine, CEN=Cenobamate, CLO=Clobazam, CLOn=Clonazepam, CTP=Citalopram, ESC=Escitalopram, EsCBZ=Eslicarbazepine, LAC=Lacosamide, LAM=Lamotrigine, LEV=Levetiracetam, LOR=Lorazepam, OxCBZ=Oxcarbazepine, PB=Phenobarbital, PER=Perampanel, PHE=Phenytoin, PRE=Pregabalin, TOP=Topiramate, ZON=Zonizamide, ZOP=Zopiclone. DNET= dysembryoplastic neuroepithelial tumor; PNH= periventricular nodular heterotopia. a=anterior, g=gyrus, i=inferior, m=middle, p=posterior, s=superior; A=amygdala, Ag=angular gyrus, C=cyngulate gyrus, CO=central operculum, Cun=cuneus, Ec=entorhinal cortex, F=frontal, FO=frontal operculum, FP=frontal pole, Fus=fusiform gyrus, F1=superior frontal gyrus, F2=middle frontal gyrus, F3=inferior frontal gyrus, H=hippocampus, I=insula, LL=lingual gyrus, O=occipital, OF=orbito-frontal, P=parietal, PC=precuneus, PH=parahippocampus, PM=premotor cortex, PO=parietal operculum, PP=planum polare, PT=planum temporale, SM=supra-marginal gyrus, SMA=supplementary motor area, TH=thalamus, TP=temporal pole, T1=superior temporal gyrus, T2=middle temporal gyrus, T3=inferior temporal gyrus

Patient ID	Nights in the hospital	Recorded nights	Mornings with a recalled dream	PSG recordings	Manual / automatic sleep scoring	Spike index extraction
1	14	6	0	2	2 / 2	2
2	12	6	4	2	2 / 2	2
3	21	11	4	2	2 / 2	2
4	14	7	5	2	2 / 0	2
5	14	4	7	2	2 / 0	2
6	17	8	3	2	2 / 0	2
7	13	5	1	2	2 / 0	2
8	6	3	1	2	2 / 0	2
9	13	5	1	2	2 / 0	2
10	7	2	0	2	2 / 0	2
11	12	6	4	2	2 / 0	2
12	9	4	3	2	2 / 0	2
13	13	8	1	2	2 / 0	2
14	9	2	3	2	0 / 0	0
15	13	7	11	2	2 / 2	2
16	7	4	0	0*	0 / 0	0
17	16	14	0	0*	0 / 0	0
18	8	8	2	2	0 / 0	0
19	14	10	1	2	0 / 0	0
20	9	5	0	2	0 / 0	0
21	9	5	7	0*	0 / 0	0
22	13	11	6	2	0 / 0	0
23	8	6	4	1*	0 / 0	0
24	15	9	8	2	0 / 0	0
Total	286	156	76	41	28 / 8	28

Table 2 – Summary of the patients’ hospital stay and current state of the analyses. Patients were not recorded every night of their hospital stay. Only PSG-recorded nights are manually stage-scored. Automatic stage scoring and spike index computation have so far only been conducted on PSG nights, and will later be applied to all recorded nights. \*: patient did not consent to adding EMG/EOG electrodes for one or two nights with PSG recordings (because too cumbersome or afraid of being woken up)

## Data analysis

### Sleep analysis

Sleep stages and arousals were manually scored in 30s epochs during PSG nights based on EEG +/- SEEG, EOG, and EMG signals, according to the criteria of the American Academy of Sleep Medicine (AASM; Berry et al., 2012) by an experienced sleep scorer and board-certified neurophysiologist (LPD). Standard sleep parameters, as well as arousals number and duration, were computed from manual sleep scorings. For this thesis, the PSG data from 28 nights recorded in 14 patients is available (Table 2).

All recorded non-PSG nights will be automatically scored with SleepSEEG (von Ellenrieder et al., 2022), a sleep stage detection algorithm based on SEEG data only. We tested the automatic scoring in a sample of 8 PSG nights visually scored in 8 patients (2 from Lyon, 6 from Montreal); correspondence between manual and automatic sleep scoring amounted to 72.97% (78% in von Ellenrieder et al., 2022). The efficiency of this scoring suggests that, following this thesis, further analyses using the data from the other nights (i.e. without PSG) are possible and will allow to confirm our results.

### Spike detection

All data processing was done in Matlab 2022b. SEEG data was exported in edf format with a bipolar montage and first band-pass filtered to 0.5-100 Hz (for files recorded with a sample frequency of 256Hz) or to 0.5-600Hz (for files recorded with a sample frequency of 2048Hz) with a Butter filter. Then a notch-filter was applied to remove electric line artefacts (50Hz-filter for Lyon files; 60Hz-filter for Montreal files). Finally, an automatic interictal spike detector (Janca et al., 2015) was run on the sleep data of each night with a 10-50Hz band-pass filter ; spikes co-occurring on more than half channels within 50ms and spikes occurring within 300ms on a single channel were deleted as artefacts. Spikes were averaged over all recorded channels. Algorithm accuracy was verified by checking whether the channels with the highest spiking activity were localized in the seizure onset zone, as reported in the clinician's reports. Spike rates were computed for each sleep stage separately. For this thesis, the spike detector was applied only on the PSG nights with a manual sleep scoring, but we plan to apply it to all recorded nights.

### Statistical analyses

Comparisons of binary variables were conducted with Fischer exact tests. We used Spearman correlations to compare continuous variables. When evaluating the effect of a binary variable on a continuous variable, we used Mann-Whitney U tests.



## Results

### Participants

For this preliminary analysis, 24 patients ( $32.7 \pm 9.2$  years old; 14 women, 10 men) who had been epileptic for  $20.9 \pm 10.8$  years were recruited (Table 1). Fourteen patients had temporal lobe epilepsy (3 temporo-mesial, 7 neocortical, 4 temporal “plus” epilepsy involving the insula, occipital lobe or operculum), 3 patients had occipital or parieto-occipital epilepsy, 2 had frontal lobe epilepsy, 2 had insular epilepsy and 2 had peri-sylvian epilepsy.

### Questionnaires

Retrospective DRF (based on questionnaire at inclusion) was  $2.2 \pm 2.2$  dreams per week. Patients reported having a lucid dream: never (N=4), rarely (N=10), sometimes (N=5), or often (N=5). As for recurrent dreams, they reported having the exact same dream: never (N=9), rarely (N=7), sometimes (N=5), or often (N=3). For most of them, the dream memory is rather vague (“very vague”: N=10, “vague”: N=6) than clear (“clear”: N=6, “very clear”: N=2).

In average, HAD depression score was  $5.1 \pm 3.8$  (4 patients between 8 and 10, 2 patients above clinical cut-off of 11), HAD anxiety score was  $6.8 \pm 3.1$  (5 patients between 8 and 10, 3 patients above clinical cut-off of 11), PSQI score was  $6.3 \pm 2.6$  (15 patients above cut-off of 5), SA-SDQ score was  $24.5 \pm 7.8$  (4 men above cut-off of 29, 3 women above cut-off of 26), ESS score was  $7.0 \pm 3.6$  (5 patients above cut-off of 10), and QOLIE-31 T-score was  $43.6 \pm 9.0$  (16 patients below 50).

### Sleep analysis

As this is only a preliminary analysis, we report here data 1) from all recorded nights with a filled dream diary in the next morning (i.e. explicit presence or absence of dream recall) in 23 patients (i.e.  $n = 109$  nights, participant mean =  $4.7 \pm 2.5$  nights) for analyses of the presence of a sleep-related seizure and a dream memory in the morning, and 2) from the 28 PSG nights of 14 patients (2 per patient), for whom manual sleep scoring, spike detection, subjective sleep quality and morning dream reports are available.

- Sleep parameters

Sleep parameters retrieved from manual scoring are presented in Table 3. Overall, patients had a normal mean sleep duration of  $420.7 \pm 96.2$  min with low sleep efficiency ( $76.5 \pm 14.4\%$ ) due to high wake after sleep onset ( $99.8 \pm 95.7$  min). Arousal index was  $14.9 \pm$

5.2/h. We further computed the number of long awakenings (>120s), which is higher in HR than in LR (Vallat et al., 2017). Patients had  $6.5 \pm 6.1$  long awakening (>120sec) per night.

TST (min)	$420.7 \pm 96.2$	TIB (min)	$554.6 \pm 105.2$	SPT (min)	$519.3 \pm 106.8$
N1 (min)	$57.7 \pm 34.0$	N1 (%TST)	$14.1 \pm 8.7$	Sleep Efficiency (%)	$76.5 \pm 14.4$
N2 (min)	$196.8 \pm 60.2$	N2 (%TST)	$46.9 \pm 9.9$	Sleep Onset Latency (min)	$31.8 \pm 27.0$
N3 (min)	$93.3 \pm 44.0$	N3 (%TST)	$22.2 \pm 9.3$	REM Latency (min)	$137.7 \pm 100.5$
REM (min)	$73.0 \pm 32.8$	REM (%TST)	$16.7 \pm 6.9$	Arousal Index (per hour)	$14.9 \pm 5.2$
NREM (min)	$347.7 \pm 78.7$	NREM (%TST)	$83.3 \pm 6.9$	Arousal duration (sec)	$9.1 \pm 1.3$
WASO (min)	$99.8 \pm 95.7$	WASO (%SPT)	$18.5 \pm 15.8$	Number Awakenings (>120s)	$6.5 \pm 6.1$

*Table 3 - Sleep parameters in Study 2b obtained from the manual sleep scoring of 28 SEEG recordings of 14 epileptic patients (i.e. 2 PSG recordings per patient) during their hospital stay. TST=Total Sleep Time, TIB=Time In Bed, WASO=Wake After Sleep Onset, SPT=Sleep Period Time (first to last sleep epoch), Sleep Efficiency = TST/TIB.*

- Dream recall

Dreams were reported on a total of 76 mornings by the 24 participants. Dream recall frequency at the hospital was  $2.7 \pm 2.0$  recalled dreams per week ( $2.0 \pm 1.8$  when excluding white dreams). Their length was in average  $49.1 \pm 64.4$  words. Patients rated the positive emotions in their dreams  $2.7 \pm 1.3$ , and the negative emotions  $2.7 \pm 1.4$ . Action intensity was evaluated at  $3.3 \pm 1.0$ , bizarreness at  $3.0 \pm 1.3$ , and control at  $1.9 \pm 1.1$ . The association between dream content and awake life was estimated at  $2.7 \pm 1.5$ , and between dream content and their epilepsy at  $1.6 \pm 1.3$ .

- Epileptic activity (seizures and interictal activity) and dream recall

During the 109 recorded nights for which the morning dream diary was completed (for 23 patients only), 129 seizures in 21 nights were recorded (102 during sleep including 7 in N1 sleep, 73 in N2 sleep, 9 in N3 sleep, and 13 in REM sleep). In these 109 nights, there was no significant difference in dream recall between nights with (5 dreams in 21 nights) and without (35 dreams in 88 nights) sleep-related seizures (Fischer exact test,  $N=23$ ,  $p=0.132$ ). Neither was there any inter-individual correlation between the number of dreams and the total number of sleep-related seizures during the hospital stay (Spearman,  $N=23$ ,  $p=0.246$ ,  $r=-0.241$ ).

Considering all recorded nights with a measure of interictal activity ( $N=28$  in 14 patients), the spike detector measured an average spike index of  $3.34 \pm 2.72$  spikes per minute during the sleep epochs ( $3.21 \pm 2.97$  during N1 sleep,  $3.38 \pm 2.68$  during N2 sleep,  $4.04 \pm 2.86$  during N3 sleep and  $2.24 \pm 1.66$  during REM sleep). Interictal activity was similarly not found to influence dream recall, as nights which led to a dream memory did not have a

different sleep spike index than nights without a dream recall (Mann-WhitneyU,  $2.79 \pm 2.48$  vs  $4.07 \pm 2.96$ ,  $N=14$ ,  $p=0.195$ ).

We then tested if epileptic activity could influence epilepsy-related dream content. Participants who reported a dream did not score it as more related to their epilepsy when they had a seizure than when they did not (Mann-WhitneyU,  $1.5 \pm 1.2$  vs  $2.0 \pm 1.7$ ,  $N=23$ ,  $p=0.266$ ). For nights with a measure of interictal activity, the level of epilepsy-related content as scored by the patient was however positively correlated with the sleep spike index (Spearman,  $N=14$ ,  $p=0.029$ ,  $r=0.56$ ).

- Sleep quality and dream recall

Finally, we tested whether the objective number of long awakenings ( $>120s$ ) and the subjective reported number of awakenings were associated with dream recall. Interestingly, the objective number of long awakenings was not different between nights with and without a dream recall (Mann-WhitneyU,  $5.5 \pm 4.0$  vs  $7.8 \pm 8.1$ ,  $N=14$  patients and 28 nights,  $p=0.220$ ), contrary to the subjective number of awakenings that we collected after the PSG nights of the 24 patients (Mann-WhitneyU,  $3.0 \pm 1.7$  vs  $1.7 \pm 2.6$ ,  $N=24$  patients and 46 PSG nights,  $p=0.006$ ).

## Discussion

The retrospective DRF in our sample (2.2/week) was high compared to the average DRF in the general population, which is around 1 dream remembered per week (e.g. Schredl, 2008), and higher than in the Study 2a (1.6/week). It was even more increased when considering only dreams from the hospital stay (mean DRF = 2.7/week).

Several factors should be considered to explain this particularly high DRF. First, intra-sleep wakefulness is associated with increased DRF, and WASO was elevated in our sample (100 min, 18% of the SPT). For comparison, healthy sleep in equivalent age people (~30 years) has been reported to contain in average 20-30 min of WASO, for around 10% of the SPT (Ohayon et al., 2004; Boulos et al., 2019; Mitterling et al., 2015). The combination of epilepsy, the surgery for electrode implantation, the anti-seizure medication (and its partial withdrawal during the procedure), the presence of the cumbersome electrodes all may contribute to the high sleep fragmentation. However, increased wake after sleep onset is a common feature in patients with epilepsy, even apart from SEEG procedure (60-110 min, depending on the epilepsy and its symptoms; Sudbrack-Oliveira et al., 2019; Calvello et al., 2023; Peter-Derex et al., 2020). The combination of an increased WASO (and a high number of subjective awakenings) and a high DRF is in line with results in a healthy population (Schredl et al., 2003; Eichenlaub et al., 2014; Vallat et al., 2017; van Wyk et al., 2019) and in our previous study (2a). However, in our study, only the subjective but not objective number of awakening was correlated with the DRF, suggesting that subjectively perceived awakenings could be more specifically associated with dream recall. Overall our results are consistent with the arousal-retrieval hypothesis of dream recall (Koulack & Goodenough, 1976) already tested in healthy subjects (e.g., Vallat et al., 2017) and the previously reported sleep fragmentation induced by epilepsy (Peter-Derex et al., 2020).

We also had the participants keep a dream journal during their stay, which has previously been associated with an increased DRF (Aspy, 2016). As participants were free to participate and as the study explicitly focused on dreams, we may also have recruited people who were more interested in dreaming (12 screened patients refused to participate), a factor also known to increase DRF (Schredl et al., 2003). Finally, the computation of the hospital DRF only included nights that were explicitly associated with a presence or an absence of dream recall, so nights without a dream recall that were not reported as such by the participants were not considered (21% of nights with an empty dream diary).

Epileptic seizures did not induce an absence of dream recall in this study. Interictal activity, which is often subcontinuous in drug-resistant patients and even activated and more widespread during NREM sleep than during wakefulness (Frauscher et al., 2015; Malow et al., 1998; Bagshaw et al., 2009), did not affect dream recall either, suggesting that its effect is not large enough to induce changes in dream production or memory. To note, the spike index was only computed in a subset of nights; further analyses are needed to confirm

our findings, and may allow to test region-specific hypothesis, as the location of epileptic activity may be critical for influencing dream-related processes.

Regarding dream content, it was not affected by the presence of seizures but by interictal activity. This might suggest that interictal activity, more pervasive than seizures, might interfere with mental content evoked by physiological brain activity during sleep, leading to the incorporation of seizure-related symptoms in dreams. Similar incorporations of external stimuli have been demonstrated in several cases (Solomonova & Carr, 2019) and may also apply to internally-induced stimuli.

We have to acknowledge several limitations to this study. First, results are preliminary, and will need to be confirmed with the analysis of all available data. Second, we could not definitely rule out sleep disorders such as obstructive sleep apnea, which is more common in epilepsy patients (Lin et al., 2017), and which might interact with dream recall (Siclari et al., 2020; Teng et al., 2023). Indeed, 7 patients had abnormal SA-SDQ scores. Third, the spatial sampling bias, inherent to SEEG investigation, prevented us from exploring epileptic activity in the whole brain. However, the targeted regions were the regions most involved in epilepsy, and this approach is the best one for focal exploration of both superficial and deep structures.

As a conclusion, this study suggests that dreaming, as a sleep-related cognitive process, persists in patients with drug-resistant epilepsy, that the effect of a focal seizure on dreaming seems limited, and that interictal activity might influence dream content.

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## Study 3 – Dreaming during Mourning

*The evolution of the mourning process is associated with the evolution of dreams in the first 15 months after the death of a relative*

In preparation

# The evolution of the mourning process is associated with the evolution of dreams in the first 15 months after the death of a relative

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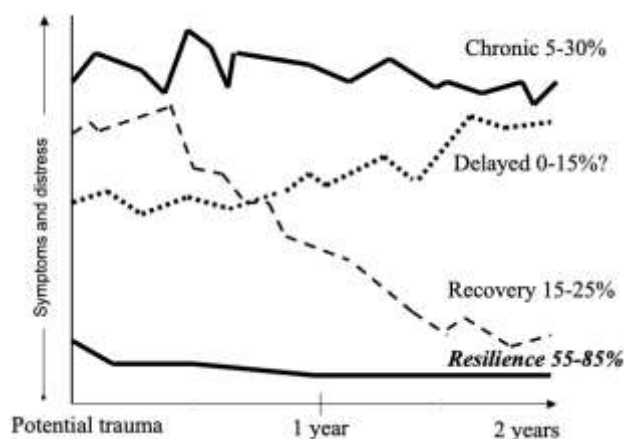
# Introduction

Everyone may or will experience the death of a relative one or several times in a lifetime. While it may represent one of the most difficult hardships, many people receive little help and most don't seek support (Teissier-de Mongolfier, 2010), notably because of the cultural taboo regarding death (Gorer, 1955). It is even more problematic that grief can be accompanied by negative consequences at a physical, psychological and social level (e.g. sleep alteration, De Almeida, 2018; poorer self-reported physical well-being, mental health and social functioning, Liu et al., 2019; work absenteeism and decreased work efficiency, Fox et al., 2013). The stakes of a better understanding of the mourning process and its evolution are both at the individual and the societal levels. It could help to decrease the individual and societal cost of a non-optimal course of the mourning process (bad quality of life, medical care, work absenteeism, supplementary stress and work for members of the family/relatives having potentially adverse consequences on their own lives) by providing tools helping to identify early marker of the mourning process evolution and thereby decreasing the chance of a pathological evolution.

## The mourning process

### The non-pathological course of mourning

Early investigations proposed that mourning involved different and successive emotional stages (e.g. denial, anger, bargaining, depression, acceptance, as proposed by Kübler-Ross, 1969). However more recent studies showed that these stages could be mixed and variable over time (e.g. Shuchter & Zisook, 1993; Schut & Stroebe, 1999; Maciejewski et al., 2007). Some authors consequently updated models and proposed different profiles for the reaction to the death of a relative. Arizmendi & O'Connor (2015) commented that the normal course of mourning ending by its resolution was far from common, only accounting for less than half cases, and identified four typical paths for grieving: *resilient* individuals who show low to no outward grief and distress, *chronic* individuals who show chronic emotional outcries, the *distressed-improved* pattern associated with post-loss life improvements, and the *chronic depression* pattern where grief induces strong depression but more because of pre-loss depression than because of the relative's death. Similarly, Bonanno et al. (2004) identified four possible psychophysiological reactions after a potentially traumatic event, including the same *resilient* and *chronic* paths, with the addition of a *recovery* path with initial impairment and a fast return to normal functioning, and a *delayed* path with later reactions to grief (**Figure 1**).



**Figure 1.** Possible course of psychophysiological reaction to a potentially traumatic event according to Bonanno et al. (2004), adapted from Bonanno et al. (2011).

Despite their differences, the possible courses of mourning show a continuum in the experience of grief, even within one person, ranging from

healthy grief to acute pathological manifestations. These models also stress that reactions to the loss of a close one is highly variable between individuals and specific to each bereaved person (Lotterman et al., 2014).

### Pathological grief

Pathological grief, also referred to as Complicated Grief (CG, Wilson et al., 2022), persistent grief, prolonged grief, or persistent complex bereavement disorder in the DSM-5 and ICD-11 is associated with intense and persistent grief symptoms at least 6 months (ICD-11) or 1 year (DSM-5) post-loss (Szuhany et al., 2021; Lenferink et al., 2021) and can be assessed by a clinical interview and/or thanks to questionnaires such as the Inventory of Complicated Grief (ICG, Prigerson et al., 1995), its revised version (ICG-R, previously Inventory of Traumatic Grief, ITG, Prigerson & Jacobs, 2001), the Prolonged Grief-13 (PG-13, Prigerson et al., 2009) or the Texas Revised Inventory of Grief (TRIG, Faschingbauer, 1981). Thanks to such tools, the incidence of CG has been assessed and results revealed that it may affect a lot of bereaved persons, about 20% according to most studies (20% in Prigerson et al., 1995; 25% in Newson et al., 2011; 15% in Igarashi et al., 2021; 22% in Parro-Jiménez et al., 2021) even if a great variability between studies exists (less than 10% in Kersting et al., 2011; Ito et al., 2012; 60% in Teissier-de Mongolfier, 2010). The issue of CG is all the more concerning that it can result in chronic negative health outcomes such as anxiety, depression, cognitive impairment, feelings of loneliness, social isolation and post-traumatic stress disorder (PTSD; Ghesquiere et al., 2013; Shear et al., 2013), translating to a mourning process that fails to progress and resolve.

There is a widely accepted understanding that the mourning process should ultimately guide individuals to a state of emotional peacefulness through negative emotions integration. This state is frequently associated with the stage of acceptance in Kübler-Ross model of dying (1969). Bereaved persons typically traverse a wide range of emotions, such as sadness which contributes to making meaning of the loss (Bonanno et al., 2008; Bonanno, 2009). Sadness can however become extremely intense and escalate to distress and lose its adaptive nature (Couët-Garand & Lecours, 2019). This psychological distress not only hinders the acceptance process but can also lead to depression (Couët-Garand & Lecours, 2019). On the contrary, some positive emotions can also be experienced during the course of normal grief (Bonanno & Kaltman, 1999; Bonanno et al., 2008). Here again, when positive emotions become too intense, it may be a sign of denial or of a psychiatric response to grief also known as *manic grief* (Bacqué, 2003; Carmassi et al., 2013). In this state, the normally adaptive sadness is replaced by inappropriate excessive joy and excitement (Hanus, 1994), in which case the manic grief can change to *melancholic grief*, a pathological grief with an increased risk of suicide (Freud, 1922). Thus, excessive emotional responses can be an indicator of grief becoming pathological.

### Factors influencing the course of mourning

The mourning process may be influenced by many factors, some of which depending on the bereaved person, some others on the context of the relative's death (e.g. Ringdal et al., 2001a; Mason et al., 2020). For person-dependant parameters, grief intensity has been shown to be higher with pre-existing psychological conditions like anxiety and depression or poor coping skills (Bruinsma et al., 2015; Marques et al., 2013; Ellifritt et al., 2003) and also

for non-pathological personality traits such as insecure attachment styles and high neuroticism (Wijngaards-de Meij et al., 2007; Gegieckaite & Kazlauskas, 2022). Gender differences have also been reported, some studies showing stronger grief intensity in women (Ringdal et al., 2001a; Lawrence et al., 2006; Lundorff et al., 2020; Kersting et al., 2011). It is less clear how the age of the bereaved affects the mourning process. Sanders (1981) identified stronger initial grief in younger widows on several scales of the GEI (an inventory of grief reactions) than matched older widows, who had however a higher grief intensity after 18 months than the younger ones. This result is coherent with the higher likelihood to observe CG in older adults (Ringdal et al., 2001a; Kersting et al., 2011). A curvilinear effect of age has been suggested by Ringdal et al. (2001a), with higher grief reactions for younger and older people than in middle-aged people, although their sample did not allow them to test this effect for younger than 40 years old.

For context-dependant parameters, having a close relationship with the deceased is positively correlated with grief intensity (Smigelsky et al., 2020; Wayment & Vierthaler, 2002; Wijngaards-de Meij et al., 2007), and more reliably so than kinship with the deceased (Fujisawa et al., 2010; Hardison et al., 2005; Ringdal et al., 2001a). The circumstances of the death also affect grief, notably the age of the deceased (Ringdal et al., 2001a; Allen et al., 2013) and the unexpectedness of the death (Wijngaards-de Meij et al., 2005; Fujisawa et al., 2010). Grief is typically increased for young deceased and for persons deceased unexpectedly. Similarly, violent deaths may lead to more difficult grief resolution but results are not all consistent (Keese et al., 2008; Barry et al., 2002; Currier et al., 2006). A lack of resources to confront the death has also been reported as worse for grief resolution (Allen et al., 2013; Vanderwerker & Prigerson, 2004; Kersting et al., 2011).

Only few studies investigated the effect of these parameters on the evolution of the mourning process. Ringdal et al. (2001b) observed a decrease in grief intensity (as measured with the TRIG) over time in the 13 months (1, 3, 6, 13 months) post-loss but no interactions between time and grief modulating parameters (among others age and sex of the bereaved, relationship to the deceased, age and sex of the deceased), i.e. the tested parameters did not induce modulations in the slope of TRIG decrease with time (Ringdal et al., 2001a). Similarly, Tsai et al. (2016) observed a decrease of CG occurrence (measured with the PG-13) over time in the 6 to 24 months post-loss (6, 13, 18, 24 months) and found a faster decrease of grief with social support but no interaction with age of the bereaved. Finally, Wijngaards-de Meij (2005) identified in 219 couples who lost their child a decrease of the ICG in the 6 to 20 months post-loss (6, 13, 20 months). Death unexpectedness also increased the ICG score at 6 months post-loss but not at 13 or 20 months. No correlation was observed with any other tested parameter (among others age and sex of the deceased and of the parents, cause of death, education of the parents). Several other longitudinal studies investigated grief evolution with time (e.g. Barry et al., 2002; Breen et al., 2020) but not possible interactions between risk factors and grief evolution.

Overall, these studies reveal that grief decreases at the very least over the first 13 to 24 months post-loss, and while several factors influence the baseline grief intensity, none affect how fast grief decreases over time except possibly the unexpectedness of the death (Wijngaards-de Meij et al., 2005). Most other studies did not take into account a lot of the presented above risk factors, or supposed them to have an effect by inputting them as confounding factors in their analyses. It is possible that these numerous parameters all interact uniquely with time and confound each other, hiding existing effects that have not been reported yet on the course of grief.

## Dreaming and emotions

About one century and a half of experimental dream reports investigations highlighted the characteristics of dream content and led to propose several possible functions to dreaming (for a review see Ruby, 2011).

A large amount of results showed a thematic continuity between wakefulness thoughts and dreams content, notably for emotions (e.g. Schredl, 2000; Valli et al., 2005; Schredl & Reinhard, 2010; Bulkeley & Kahan, 2008; Gorgoni et al., 2021; Ruby, 2021). This observation led to the continuity hypothesis of dreaming (Schredl & Hofmann, 2003), but also questions whether such continuity reflects a passive or an active mechanism serving a function.

Some authors argued for the latter and proposed that emotions in dreams reflected a functional mechanism, i.e. emotional regulation (e.g. Hartmann, 1996; Levin & Nielsen, 2007; Perogamvros & Schwartz, 2012). Accumulating evidence have now piled up to support this hypothesis (e.g. Cartwright, 1991; Cartwright, Luten, et al., 1998; Cartwright, Young, et al., 1998; Blagrove et al., 2004; Pesant & Zadra, 2006; Malinowski & Horton, 2015; Sandman et al., 2017; Sterpenich et al., 2019; Scarpelli et al., 2019; Lara-Carrasco et al., 2009; Malinowski et al., 2019; Mallett et al., 2021) notably showing that the dreamt version of an episodic memory had a lower emotional intensity than the episodic memory recalled during wake (Vallat et al., 2017).

Several mechanisms have been proposed to support emotional regulation during dreaming. Hartmann (1996) suggested that emotional memories are reactivated during dreaming, where association with various other memories dilutes the intensity of the initial memory and induces the weirdness of dreams. Levin & Nielsen (2007) proposed a similar theory with their neurocognitive model of nightmares. The model states that the recombination of various memories including their emotional load would update and decrease the emotions associated with these memories, effectively leading to emotion regulation. In this model, nightmares would be a consequence of a failure of emotional regulation. We recently suggested that the key mechanism leading to emotional regulation was episodic memory transformation, be it by a change of context, protagonists, perspectives, or by symbolising the associated emotions via a metaphoric representation (Vallat et al., 2017; Ruby, 2021).

These theories are coherent with investigations in the sleep domain since several results support a role for sleep in emotional regulation (Walker & Van Der Helm, 2009; Perogamvros & Schwartz, 2012; Bottary et al., 2023; Meneo et al., 2023). Walker (2009) suggested that emotional memory consolidation involved decoupling memory content and its emotional component, which fits well with the observation that the dreamt version of a memory shows an attenuated emotional intensity (Vallat et al., 2017). Dreams may be the accessible/visible cognitive component of the physiological regulation process of emotions at play during sleep.

According to these theories, one would expect that sleep and dreams play a crucial role after the death of a relative i.e. participate to the good evolution of the mourning process.

## Dreaming during the mourning process

The few existing studies on dreaming during bereavement confirmed that dreaming of the deceased is typical after the death of a relative and suggest a link between dreams of

the deceased (DD) and the evolution of the mourning process (Black et al., 2014, 2016, 2019, 2020; Garfield, 1996; Barrett, 1992; Belicki et al., 2003; Domhoff, 2015; Germain et al., 2013; Wright et al., 2014). Dreaming of the deceased is common in grieving persons, but with various inter-individual frequencies. Among caretakers (N=278) who lost a hospitalised relative, 46.6% reported that they had dreamt at least monthly about the deceased (Wright et al., 2014) and 53 to 75% of the dreams reported by bereaved individuals are some DD according to Black et al. (2019). These results are coherent both with the continuity and the emotional regulation hypotheses of dreaming.

Dreams of the deceased are predominantly positive (Black et al., 2019; Wright et al., 2014), with the deceased coming back to life or being alive, and/or comforting or advising the dreamers. Some DD also show negative themes such as the deceased dying again, being aggressive or ill (Garfield, 1996; Black et al., 2016). An increase of the number of dream characters with time has also been observed in DD by Black et al. (2014) and in dreams of persons with CG by Germain et al. (2013). These results suggest that the reorganization of social links during mourning, which is an important process for an efficient grief outcome (as suggested by Maciejewski et al., 2022), is occurring in dreams and visible in dream reports. It fits with the predictions of the Social Simulation Theory of dreaming, which proposes that offline simulations of behaviour/action in dreams would help to improve, change, or initiate new social behaviors in waking life (Revonsuo et al., 2015).

Several studies attempted to classify DD by content type i.e. back-to-life, advice, dying again, passionate encounter, moving on (for more examples see Garfield, 1996; Barrett, 1992; Belicki et al., 2003; Domhoff, 2015; Black et al., 2016) in an attempt to investigate their evolution through the mourning process. However, results turned out to be only fewly congruent between studies and all attempted replications failed (Belicki et al., 2003; Black et al., 2016). As a consequence, no consensus emerged regarding the evolution of positive (Black et al., 2014; Belicki et al., 2003) and negative (Domhoff, 2015; Belicki et al., 2003) content of DD during the mourning process. Nonetheless, several authors (Garfield, 1996; Domhoff, 2015; Black et al., 2014) suggested that the different stages of grief were associated with specific DD categories.

Importantly, the results presented above issue all from retrospective studies sometimes realised months or years after the relative's death. As a consequence, collected data (dream recall frequency and dream content) may lack precision and suffer from distortion (due to emotional regulation and memory fading with time). Moreover, most of these studies either collected retrospective dream reports and questionnaires from a large population (e.g. Black et al., 2019) or investigated long-term dream diaries from a single person (e.g. Belicki et al., 2003), further limiting their conclusions to a single time point or to a unique case of grief evolution with time. In addition, no studies so far assessed both the evolution with time of dream content and of the mourning process.

Because of these limits, several authors (Wright et al., 2014; Black et al., 2014, 2019) advocated for the use of prospective paradigms to address these shortcomings. Following the latter recommendation, the aim of the present study was to measure prospectively for the first time both the evolution of the mourning process (with regular ICG assessments every 3 months from 2 months to 14 months post-loss and a follow-up assessment at 26 months post-loss) and the evolution of dreams (frequency and content), especially of the deceased, in the 15 months following the death of a relative (thanks to an online questionnaire). What is at stake is a precise and reliable description of the link between dreams and the mourning process in the first year of mourning. Such knowledge is needed to improve, optimize and facilitate care and prevention of complicated grief.

## Objectives and Hypotheses

The aim of the study was twofold. First, we ambitioned to document the mourning process by investigating its evolution over time in the first 15 months with existing scales developed to assess grief, and by testing the effect of several modulating factors of the mourning course on the measured scores of grief and their evolution. Second, we aimed at testing the possible link between the evolution of the mourning process and the evolution of dream content and frequency in the first 15 months after the death of a relative.

Regarding the mourning process, we expected to validate that the ICG score is a sensible tool to assess the evolution of the grief-related emotional state of the bereaved person in the 15 first months after the death of a relative. As for the modulating factors proposed to impact the course of the mourning process, we expected to confirm that increased closeness to the deceased would be associated with an increased ICG score and as a consequence with a longer evolution of the mourning process and/or with more complicated grief. As suggested by the literature, we also predicted increased ICG for unexpected deaths (i.e. accidental, in healthy and in young persons), for young deceased, for high neuroticism scores, and for female versus male bereaved. By contrast, we did not expect the ICG score to be strongly influenced by the age of bereaved individuals.

Regarding the possible link between mourning and dreaming, we hypothesized that the evolution of some emotional aspects of dream content and DD frequency would be correlated to the evolution of ICG across time. We expected 1) more frequent DD for greater ICG scores (in line with both the continuity and the emotional regulation hypothesis of dreaming), 2) to confirm that DD are mainly positive and increase in positivity with time in parallel to the decrease of ICG (in support of the emotional regulation hypothesis). We also expected more helping social interactions and characters in dreams when the ICG score decreases, in support of the emotional regulation and the social simulation hypotheses of dreaming.



# Methods

## Participants

A total of 50 French adults recently bereaved (in the last 3 months) were recruited via web announcement broadcasted on university websites and social media. After inclusion, five of them (3 men and 2 women) quit before the end of the protocol and 45 completed it (35 women, mean age =  $28.1 \pm 9.6$  years old, range: 18-68). For two of them who lost two relatives in the 3-month period before inclusion we considered only the death associated with the greater ICG score in the analyses. The mean delay between the relative's death and inclusion was  $59 \pm 23$  days. Participants had no history of neurological or psychiatric diseases.

The deceased (20 women and 25 men, mean age =  $70.0 \pm 20.8$  years old, range: 21-94) were either grandparents (N=23), parents (N=15), siblings (N=3) or friends (N=4). The cause of death was reported as old age (N=1), disease (17 cancers, 11 infections of which 5 COVID, 3 strokes, 2 heart attacks, 3 neurodegenerative disease), accident (N=5), and suicide (N=3). The reported proximity between the participant and the deceased on a 0-10 scale (0 no link, 10 very close) was  $7.8 \pm 1.6$  on average (range: 3-10). Mean education level was  $3.5 \pm 2.0$  years post-Baccalauréat (range: 0-8) and participants reported at the time of inclusion remembering dreams  $2.8 \pm 2.0$  mornings per week on average (range: 0.1-7).

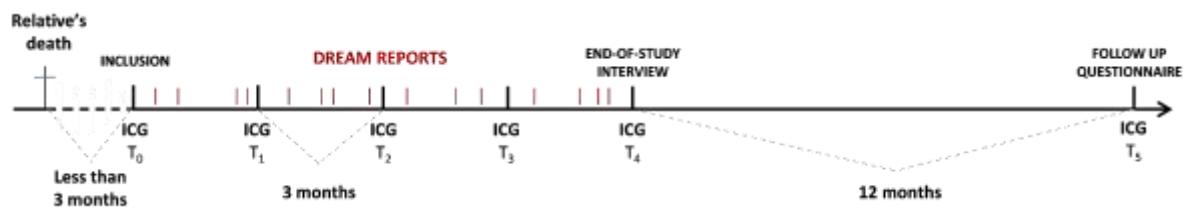
## Procedure

The paradigm is presented in **Figure 2**. Before inclusion, participants were interviewed by a psychiatrist (AN) who controlled for inclusion criteria (no history of neurological or psychiatric disorders), and asked for medical and psychological history (sleep, possible meds), circumstances of the relative's death, relationship with the deceased, and dream recall habits. He also provided participants with an information letter about the study and a consent form to read and sign. The study started after participants were explained how to fill in the online questionnaire designed to collect dream reports and how to complete the ICG questionnaire.

After inclusion, during one year, participants were asked to complete the online dream questionnaire (implemented with Limesurvey GmbH, 2006) whenever they remembered a dream related to the deceased (DD) or a dream in which a character was flying (FD). Even if not mandatory, they were also asked to report other dreams (OD) as often as possible i.e. at least once a week if possible. In addition, ICG questionnaires were to be filled in every 3 months starting at the inclusion i.e. five ICG questionnaires were fulfilled if participants completed the study ( $T_0$  to  $T_4$ ). Reminders were sent before each ICG completion dates, by email and/or by phone.

At the end, participants completed the end-of-study questionnaire (it notably asked whether they agreed to be contacted again in one year for a short follow up questionnaire), the French version of the Big Five Inventory (BFI-Fr, Plaisant et al., 2010), and were encouraged to provide an open-ended feedback on their subjective experience during the study.

One year after the end of the study, participants who agreed to be contacted were sent facultative follow-up retrospective questions about their dreams of the previous year (number and evolution of DD and nightmares) and the current state of their grief (ICG -  $T_5$ ).



**Figure 2. Paradigm.** During the one-year study, dream reports and ICG scores were sent via an online questionnaire accessible either on a computer or a smartphone. Those who agreed to in the end-of-study interview, received a follow-up questionnaire 24 months post inclusion.

## Questionnaires

At inclusion, participants provided information about their deceased relative (age, gender, type of link with the participant - family or friend, duration of the affective link), the circumstances of their relative's death (cause of death, consequence on the participants' daily life, participants' previous encounter with grief), their relationship with him/her (proximity scored on a scale from 0 to 10), and their dream habits (dream recall and nightmare frequency, dreams of the deceased before and after his/her death).

The current grief state and intensity was measured at inclusion ( $T_0$ ) and every 3 months ( $T_1$  to  $T_4$ ) with the French version of the Inventory of Complicated Grief, which participants could complete online (Prigerson et al., 1995; translated to French by Bourgeois, 2002; validated in French by Teissier-de Mongolfier, 2010). The ICG questionnaire comprises 19 items assessing the emotional state of the respondent regarding his/her relative death and its consequences on his/her daily life. Each question is answered on a scale going from 0 ("never") to 4 ("always"), and a total score can be computed by summing the scores to each question (total score range: 0-76, showing an excellent internal consistency). Prigerson et al. (1995) suggested a cutoff score of  $\geq 26$  to be indicative of CG, although several studies used a cutoff of  $\geq 30$  to remove borderline CG cases (e.g. Bui et al., 2015; Germain et al., 2013). The medical recommendations regarding the delay post-loss to assess possible complicated grief is minimum 6 months in ICD-11 and 1 year in DSM-5.

The end-of-study questionnaire asked the participants to assess the percentage of their remembered dreams that they reported in the study for DD, FD and OD (i.e. they were asked to answer 80% if they reported 8 of their 10 remembered DD). The questionnaire also asked the frequency of nightmares in the year of the study, and about possible help used by the participant to ease their grief and mourning process (bereaved support group, psychotherapy, medication). To estimate more reliably the DRF of each participant in the year of the study, the individual percentages of reported DD, FD and OD were used to compute a corrected number of DD, FD and OD for each participant. At the same time, we assessed five dimensions of the participants personality using the French version of the Big Five Inventory (BFI-Fr, Plaisant et al., 2010), with total scores ranging from 0 to 5: Extraversion (vs introversion), Agreeableness (vs antagonism), Conscientiousness (vs lack of direction), Neuroticism (vs emotional stability), and Openness (vs closedness) to experience. The BFI-Fr has excellent internal consistency and presents similar mean scores as those obtained in Spanish and American equivalent populations, with the Spanish and American version of the BFI respectively.

Participants who agreed to during the end-of-study questionnaire were contacted by email to complete a follow-up questionnaire 24 months post-inclusion. The questionnaire asked the participants to assess the number of DD, of FD and nightmares they had in the last 12 months. They were also asked about any evolution of their DD content, and about additional help sought to ease their mourning process. They were finally asked whether they felt that their mourning process had progressed in the last 12 months, and if so, to precise if it was in a positively or negative direction.

### Dream collection

Participants were asked to report all their recalled DD and FD. FD were initially selected as a control condition since they were not expected to be related with the mourning process. They presented the advantage to be : 1) often positive (Schredl, 2011; Picard-Deland et al., 2020) similarly to DD (Black et al., 2019; Wright et al., 2014), which provided the additional benefit to focus the participants not only on the sad topic of death, 2) not very frequent (Schredl & Piel, 2007; Schredl, 2011) which made it feasible to add the request to report all of them in addition to all DD. OD had never been collected so far in addition to DD in previous studies and were also used as a control condition. Such reported other dreams (neither DD nor FD) nevertheless had the limitation to be a possibly limited and freely selected by the participants (according to unknown rules) subset of all participants OD.

For each dream reported using the online questionnaire, participants indicated the date of the morning they had the dream memory, wrote an as detailed as possible description of their dream memory (they had been asked to do so just after awakening), scored the intensity of positive (0-10 scale), negative (0-10 scale) emotions and of fear (0-10 scale) in their dream memory, and whether the dream woke them up or not.

For DD and FD, they also scored how much they had a feeling of control in the dream (0-10 scale), how bizarre the dream was (0-10 scale), how much the dream grouped together elements (persons, actions, places) usually segregated (in time and space) in waking life (0-10 scale).

For DD, participants also had to tell how much the dream was related to the deceased (0 no relation, 10 strongly related), in which context the deceased appeared (dying, burial, funeral, resurrection, life before/after death...) and whether, as a whole, the dream left them a positive or a negative impression. Note that the two participants who lost two relatives were asked to report all dreams related to any of their related deceased as DD.

For FD, they reported who was flying (themselves or another character), and if themselves, the reason why they were flying (for fun, or with a specific goal in mind) and how (using wings, by flapping arms, levitating above the ground without moving limbs, making large leaps on the ground, aboard a flying machine, or other).

### External dream scoring

The dream-related emotional information scored by the participants was limited (positive and negative emotions, fear) to keep the task manageable in the long term. For this reason, we did not systematically ask participants to score any specific emotions for each dream (except for fear). However, positive/negative emotions and fear may be insufficiently specific emotional parameters to investigate the evolution of grief. For this reason, we also used external scoring to assess dream content regarding specific emotions that may be

involved in and evolve during the mourning process. Given the available literature on mourning and dreaming, we chose to assess the following emotions and emotionally related parameters in dream reports: *Sadness - Happiness*, *Distress - Peacefulness*, *Emotion evolution through the dream*, *Amount of characters*, *Discomfort - Comfort brought by the dream characters*.

*Sadness* and *Happiness* were scored on a single -5 to 5 scale (-5: extreme sadness adapted to the situation, may cry; 0: none or balanced happiness and sadness; 5: intense happiness with overflowing emotions). Sadness is appropriate in grief as long as it is not overwhelming, as it allows realisation and progressive acceptance of the death (Bonanno, 2010). Happiness is commonly present in DD (e.g. Black et al., 2019).

*Distress* and *Peacefulness* were also scored on a single -5 to 5 scale (-5: despair, panic, hopelessness; 5: peace of mind, calmness, looking forward to the future). It is widely accepted that peacefulness is a positive state of mind associated with acceptance of the death and indicative of grief resolution (e.g. acceptance stage of model of Kübler-Ross, 1969). On the contrary distress is a violent, negative emotion that reflects difficulty to sort one's emotions. Persistent distress has also been associated with CG by preventing acceptance of the death (Couët-Garand & Lecours, 2019).

*Initial* and *Final dream emotions* of the dreams were scored on two separate -5 to 5 scales (-5: negative emotions; 0: no or neutral emotions; 5: positive emotions) and subtracted to give a *Dream emotion evolution* score (-10 to 10). Cartwright and colleagues suggested that negative emotions in dreams of the end of the night indicate an incomplete process of emotion regulation (Cartwright, Lutten, et al., 1998; Cartwright, Young, et al., 1998).

The *Amount of dream characters* was scored on a 0 to 4 scale (0: none; 1: one; 2: two or three; 3: small group; 4: crowd), and the *Comfort brought by the dream characters* on a -5 to 5 scale (-5: feeling out of place, alone, targeted against; 5: helping, comforting characters, feeling at ease). As compared to norms, in dreams of persons with CG more family characters and fewer aggressions were observed, and grief intensity was negatively correlated with friendliness of dream characters (Germain et al., 2013). Black et al. (2014) also found an increasing number of familiar characters in DD with time in the first years after the death of a relative. These results suggest that social interactions in dreams may play a role in emotion regulation during mourning notably by making the bereaved person experience positive emotions with other people than the deceased.

Each parameter was scored by two judges (AdIC and JP) after a training session on unrelated dreams. Judges were blind to the dream date and author, and dreams to score were grouped by author. The idea was to make available to the judges the intra-individual variability in dream content. To assess the evolution of dream content between inclusion and the end of the study, we selected after exclusion of the very first and very last dreams, the two first DD and two first OD of the first semester and the two last DD and two last OD of the second semester (when possible). To further assess the evolution of dream content across the whole year within-subject, we randomly selected and scored 8 OD and up to 8 DD (including the dreams previously selected), balanced across all trimesters, with a target of 2 dreams per trimester. All participants (who all reported at least 1 DD in each semester) were considered for the first analysis. For the second analysis, only the 39 participants with at least 8 OD were included in the analysis of OD, while all participants were considered for the analysis of DD to take into account as much inter- and intra-individual variability as possible in DD. A total of 318 dreams (154 DD, 164 OD) were scored for the first analysis and 251

additional dreams for the second analysis (92 DD, 159 OD), where a total of 558 dreams were considered (246 DD, 312 OD). In fine, a total of 569 dreams were scored (246 DD, 323 OD).

## Statistical analyses

Bayesian statistics were used for all presented analyses for their multiple advantages compared to frequentist statistics (Wagenmakers et al., 2018). Bayesian inference builds evidence for or against the alternate hypothesis (and thus allows rejecting the alternative hypothesis), this evidence can be quantitatively interpreted (contrary to the p-value threshold in frequentist analyses), and prior knowledge can be integrated in the analysis. Moreover, selection of an appropriate prior removes the multiple-comparison problem from Bayesian analyses (Gelman et al., 2012).

The Bayes Factor computed with Bayesian statistics is an estimator of the level of evidence for an alternative hypothesis against the null hypothesis. A  $BF_{10}$  between 1 and 3 indicates weak evidence for the alternate hypothesis, between 3 and 10 positive evidence, between 10 and 100 strong evidence and above 100 decisive evidence (Lee & Wagenmakers, 2014).

All correlation analyses were conducted with non-parametric Bayesian Spearman tests. We used a beta prior with a width of 0.3 to account for the higher probability of small correlation coefficients. Simple correlations were conducted in JASP (*version 0.16.3.0*) while multilevel correlations (*see section below*) were conducted in R.

Bayesian repeated-measure ANOVA were conducted in JASP (*version 0.16.3.0*) with default parameters and were followed by an analysis of effects. Models containing an effect (factor or interaction) were compared to equivalent models without that effect. The result of this analysis provided a  $BF_{inclusion}$  for each individual factor and interaction, which is a measure of their contribution to all tested models (i.e. variance explanation).

## *Grief during the study*

To assess the evolution of the ICG across time and the effect of possible modulating factors, we used a Bayesian repeated-measure ANOVA with as within-subject factor *Time* (0, 3, 6, 9 and 12 months) and as between-subject factors *Sex* (M, F) and *Age* of the participant (18 to 68), *Age of the deceased* (21 to 94), *Proximity* with the deceased (0-10), *Neuroticism* score (1-5), and *Death-Expectedness* (Low, High). Only simple interactions between time and each of these factors were included in the analysis.

Moreover, we investigated the evolution of the ICG score for Complicated Grief cases (CG) and Non-Complicated Grief (NCG) as defined with the ICG score at 14 months 1) with the original criterion of Prigerson et al. (1995;  $ICG \geq 26$ , CG26) and, 2) with a more conservative criterion used in several other studies ( $ICG \geq 30$ , CG30; e.g. Bui et al., 2015; Germain et al., 2013). For these two analyses, we conducted a Bayesian repeated-measure ANOVA with the within-subject factor *Time* and the between-subject factor *Grief-Type* (resp. CG<sub>26</sub>, NCG and CG<sub>30</sub>, NCG).

### *Dreams during the study*

We similarly evaluated 1) the evolution of the number of dreams (DD, OD, FD) with a Bayesian repeated-measure ANOVA with as within-subject factor *Time* (*Trimester 1, 2, 3 or 4*), and 2) the evolution of dream content with within-subject factors *Time* (*Semester 1 or 2*) and *Dream-Type* (DD, OD).

### *Relation between mourning evolution and dreaming*

While questionnaire-based studies often make use of cross-sectional correlations, results obtained at the level of the group do not necessarily reflect intra-individual processes (Hamaker, 2012). On the other hand, correlations between individual-specific changes are more appropriate to characterise within-subject relationships but are statistically inefficient as they make use of only a subset of the available data. In contrast, multilevel techniques provide a statistically powerful approach to investigate within-person processes while retaining generalizability at the population level.

Here we used multilevel correlations to assess the relationships between grief - as indexed by ICG scores - and dreams frequency and characteristics, both self-reported and rated by experimenters. Given that the ICG was administered at fixed intervals whereas dreams were spontaneously reported at irregular time points, we clustered all available dreams by trimester so that ICG scores could be correlated with dreams either preceding them or following them. Lagged correlations provide a hint at causal relationships insofar as they measure the association between variables that are temporally ordered by construction.

In practice, dreams characteristics were averaged based on the chosen method of aggregation and data were rank-transformed. This transformation allowed us to interpret results as Spearman correlation coefficients, which quantify monotonic rather than merely linear associations and are more robust to outliers. Then, taking advantage of the fact that the correlation coefficient is equivalent to the standardised regression coefficient in a simple linear model, the relationship between the two variables was assessed using a mixed model with random intercepts by participants. We used the implementation of this pipeline available in the R *correlation* package (Makowski et al., 2020).

# Results

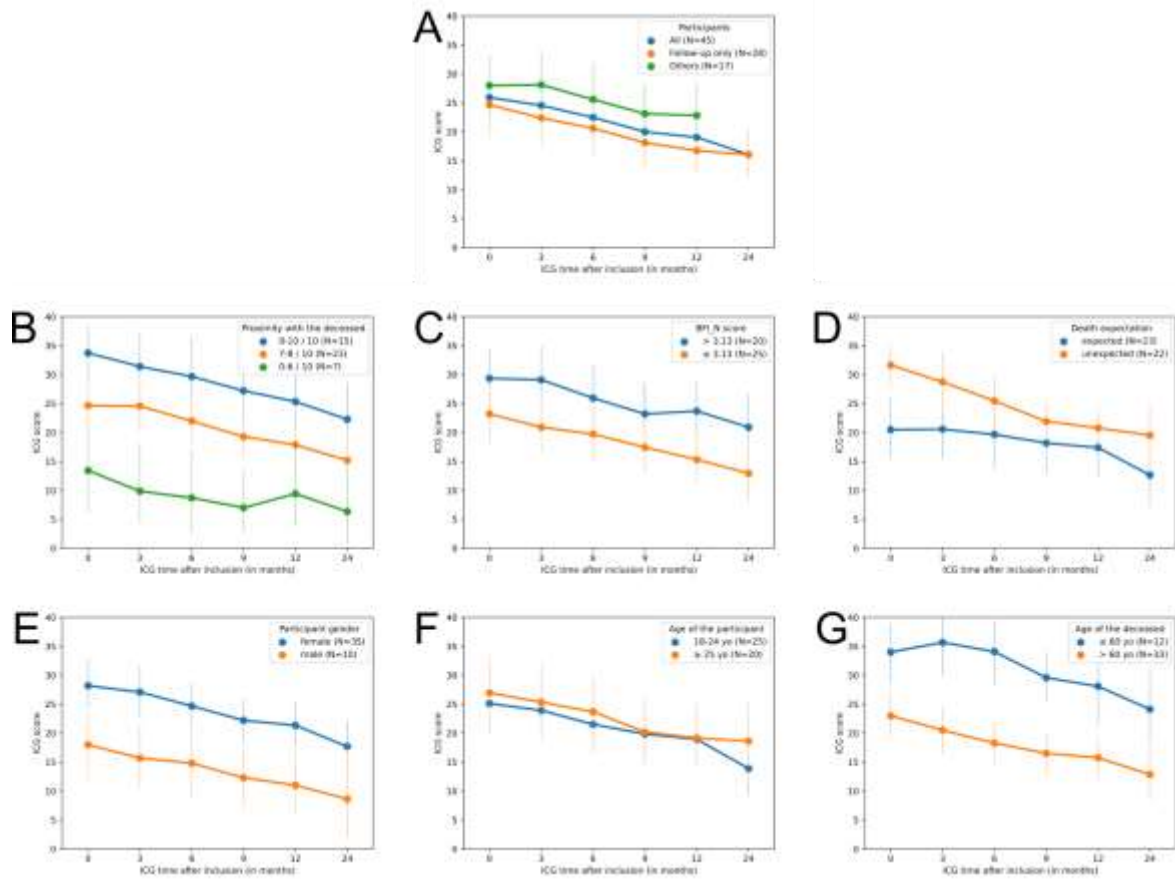
## 1) Evolution of the mourning process

Modulations of the ICG score were evaluated with a repeated-measure Bayesian ANOVA with within-subject factor *Time* and between-subject factors *Sex<sub>P</sub>* (sex of the participant), *Age<sub>P</sub>* (age of the participant), *Age<sub>D</sub>* (age of the deceased), *Proximity* (proximity with the deceased), *BFI<sub>N</sub>* (Neuroticism score of the BFI), *Death-Expectedness*, along with their interaction with the factor *Time* (**Figure 3**).

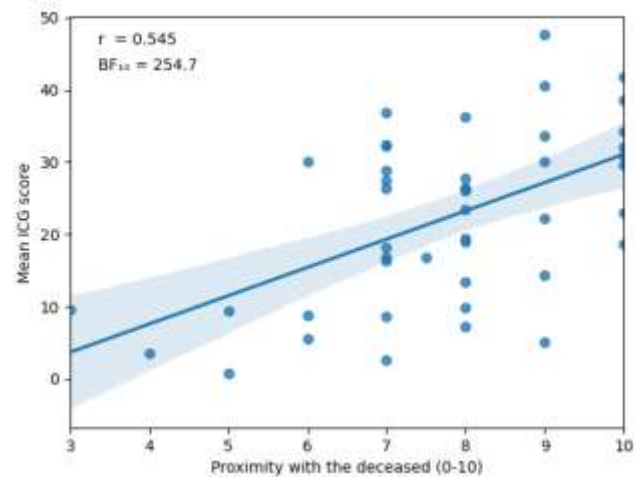
The best model presented an effect of *Time*, *Age<sub>D</sub>*, *Death-Expectedness*, *Proximity*, *BFI<sub>N</sub>* and an interaction between *Time* and *Death-Expectedness* (decisive evidence:  $BF_{10} = 5e17$ ). The analysis of effects confirmed decisive evidence for *Time* ( $BF_{inc} = 6e9$ ), for *Proximity* ( $BF_{inc} = 572$ ) and for the interaction between *Time* and *Death-Expectedness* ( $BF_{inc} = 245$ ), as well as strong evidence for *Age<sub>D</sub>* ( $BF_{inc} = 15.1$ ), positive evidence for *BFI<sub>N</sub>* ( $BF_{inc} = 3.3$ ), and weak evidence for *Death-Expectedness* ( $BF_{inc} = 1.9$ ) and for *Sex<sub>P</sub>* ( $BF_{inc} = 1.1$ ). The ICG score was higher for closer relatives (B), for younger relatives (G), for unexpected deaths (D), in women as compared to men (E), and for participants with higher neuroticism scores at the BFI (C). ICG also decreased over time (A), and faster so for unexpected deaths (D).

Interestingly, there was also strong evidence for an absence of effect of *Age<sub>P</sub>* ( $BF_{inc}=0.310$ , F) and weak to decisive evidence against the interactions between *Time* and *Sex<sub>P</sub>* ( $BF_{inc}=0.075$ , E), *Time* and *Age<sub>P</sub>* ( $BF_{inc}=0.020$ , F), *Time* and *Age<sub>D</sub>* ( $BF_{inc}=0.002$ , G), *Time* and *Proximity* ( $BF_{inc}=0.001$ , B), and *Time* and *BFI<sub>N</sub>* ( $BF_{inc}=6e-4$ , C).

**Figure 4** shows the Spearman correlation between the mean ICG score ( $T_0$ ) and the proximity score ( $r = 0.552$ ,  $BF_{10}=508$ ). Similar observations were made for ICG scores at all time points (not shown here;  $BF_{10} \geq 24$ ).



**Figure 3.** ICG score evolution with time after the death of a relative and modulating factors (vertical bars represent standard deviation). A) ICG evolution with time in all participants, those who filled in the ICG two years after their inclusion and those who did not. The following modulating factors of ICG are represented: proximity with the deceased (B), BFI neuroticism score (C), death expectedness (D), sex of the participant (E), age of the participant (F), age of the deceased (G).

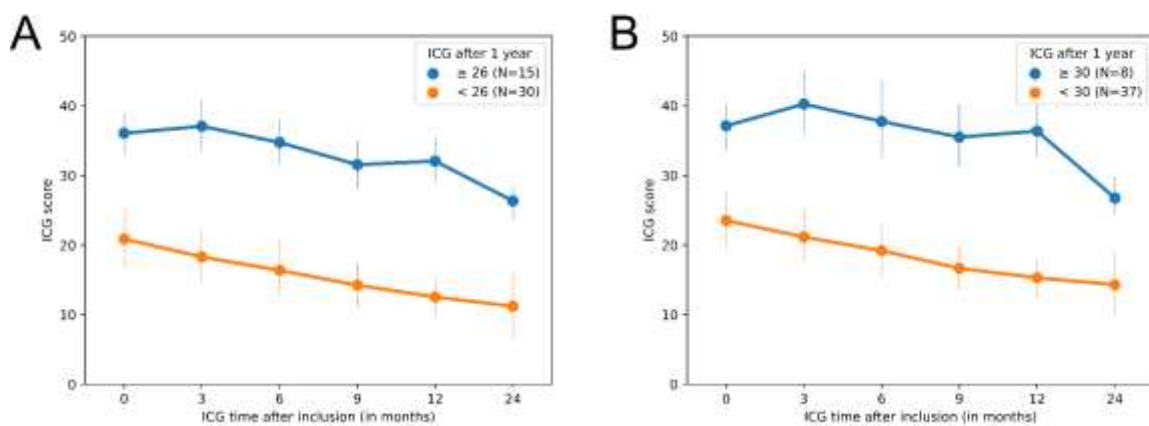


**Figure 4.** Mean ICG score as a function of the proximity with the deceased. ICG and proximity scores are positively correlated: the closer to the deceased, the higher the ICG score. Similar correlations were observed for all individual ICG scores ( $T_0$  to  $T_4$ ).



Using a cutoff ICG score of 26 (Prigerson et al., 1995) after one year of participation ( $426 \pm 24$  days  $\approx$  14 months post-death) resulted in 15 cases (33%) of Complicated Grief ( $CG_{26}$ ) in our sample. At a clinical level, the level of ICG score (i.e. grief intensity) but also the slope of its evolution across time (i.e. grief persistence) are both important parameters to consider regarding the diagnosis of complicated grief. We thus tested whether this slope differed in the two groups ( $CG_{26}$  and NCG) thanks to a Bayesian ANOVA with within-subject factor *Time* and between-subject factor *Grief-Type*. The best model ( $BF_{10}=3 \times 10^{15}$ ) included the factors *Time* ( $BF_{inc}=8 \times 10^9$ ) and *Grief-Type* ( $BF_{inc}=3 \times 10^5$ ), but not their interaction: it showed a decreasing ICG score as time passes and a higher score for  $CG_{26}$  cases.

Using a cutoff ICG score of 30 (e.g. Bui et al., 2015; Germain et al., 2013) after one year of participation resulted in 8 cases (18%) of Complicated Grief ( $CG_{30}$ ). With this threshold, we applied again the previously described ANOVA. This time, the best model contained all factors and their interaction ( $BF_{10}=2 \times 10^{13}$ ). The analysis of effects showed an effect of *Time* ( $BF_{inclusion}=9 \times 10^9$ ), of *Grief-Type* ( $BF_{inclusion}=621$ ) and of their interaction ( $BF_{inclusion}=3.1$ ), with a slower decrease for  $CG_{30}$  cases than for the other ones (**Figure 5**).



**Figure 5.** Evolution of the ICG score across time for non-pathological (orange) and complicated (blue) griefs, when CG is defined by a cutoff score of 26 ( $CG_{26}$ , A) or 30 ( $CG_{30}$ , B) at 14 months post-loss.

## 2) Evolution of dreams during the mourning process

### Descriptive statistics

A total of 2224 dream reports from 45 bereaved participants were collected. On average, participants reported  $49.4 \pm 42.8$  dreams during the year of the study ( $13.1 \pm 15.2$  DD,  $35.4 \pm 34.2$  OD,  $1.4 \pm 2.3$  FD). Few FD were reported (with 24 people not reporting a single FD, and only 1 person reporting at least one FD every trimester), which jeopardised their use as a control condition. Instead, we used OD as a control condition. For the two participants who lost two relatives during the 3-month period before inclusion, DD were more frequently related to the deceased with the highest ICG score at inclusion (15 DD for ICG 34 vs 3 DD for ICG 13; and 32 DD for ICG 34 vs 9 DD for ICG 17). As nightmares can be defined as negative dreams awakening the dreamer, we also considered dreams that led to an awakening with a negative intensity greater or equal to 6/10 as nightmares. Participants

reported on average  $5.4 \pm 4.9$  dreams that met these criteria during the year of the study. The reported dreams were on average  $111 \pm 124$  words long ( $152 \pm 153$  for DD,  $94 \pm 107$  for OD,  $144 \pm 114$  for FD). Participants reported more dreams of their deceased relative during the study ( $13.1 \pm 15.2$ ) than during the year preceding their death ( $4.3 \pm 8.4$ ,  $BF_{10} = 33007$ ). Finally, participants reported in average having thought of the deceased the day before the dream for  $57.1 \pm 36.5\%$  of the DD (and for  $66.3\%$  of all reported DD).

The validity of the scales for judge-rated dream content was assessed with correlations between self-scores (intensity of fear, positive and negative emotions) and the average of the two judges scores. Results revealed that the dreamers and the judges scores were significantly correlated (**Table 1**). To assess the scales reliability, the two judges scores were compared with the Intraclass Coefficients (ICC) “two-way random effects, consistency, multiple raters/measurements”, also called ICC(3,k), or the ICC “two-way random effects, consistency, single rater/measurement”, also called ICC(3,1) (Koo & Li, 2016). ICC(3,k) provides the reliability when using the scores from multiple scorers, as is usually done in research, while ICC(3,1) better represents the reliability for single scorers, e.g. clinicians evaluating patients. For multiple-rater ICC, all scales showed good to excellent reliability ( $ICC > 0.85$ ). For single-rater ICC, all scales showed good reliability (ICC between 0.75 and 0.9) except for the *Distress-Peacefulness* scale, which only showed moderate reliability ( $ICC = 0.700$ ) (**Table 1**). For all subsequent analyses, the scores of the two judges were averaged. Descriptive stats of the self-rated and judge-rated scores of DD and OD are reported in **Table 2**.

	Validity analysis			Reliability analysis	
	Positive emotions	Negative emotions	Fear	ICC(3,k)	ICC(3,1)
Sadness - Happiness	0.474 ***	-0.48 ***	-0.206 ***	0.865 ##	0.762 ##
Distress - Peacefulness	0.422 ***	-0.61 ***	-0.448 ***	0.823 ##	0.700 #
Dream initial emotions	0.432 ***	-0.552 ***	-0.352 ***	0.895 ##	0.810 ##
Dream final emotions	0.484 ***	-0.627 ***	-0.407 ***	0.906 ###	0.829 ##
Number of dream characters	-	-	-	0.859 ##	0.753 ##
Interactions with dream characters	0.496 ***	-0.628 ***	-0.4 ***	0.868 ##	0.766 ##

**Table 1.** Validity and reliability of the dream content scales. Validity analyses were conducted with frequentist Spearman correlations (\*\*\*:  $p < 0.001$ ). Reliability analyses were assessed with Intra-Class Correlations (ICC): a score below 0.5 indicates poor reliability, between 0.5 and 0.75 moderate reliability (#), between 0.75 and 0.9 good reliability (##) and above 0.9 excellent reliability (###).

	scale	DD	OD
Self-rated scales	Positive emotional intensity (0-10)	4.5 ± 2.8	3.9 ± 2.7
	Negative emotional intensity (0-10)	3.7 ± 3.0	3.4 ± 3.0
	Fear intensity (0-10)	1.8 ± 2.5	2.1 ± 2.8
	Proportion of awakenings (%)	26.9 ± 44.4	19.5 ± 39.6
	Feeling of Control (0-10)	2.0 ± 2.3	-
	Bizarreness (0-10)	3.8 ± 2.9	-
	Incorporation of unrelated waking-life elements (0-10)	3.2 ± 3.0	-
Judge-rated scores	Sadness–Happiness scale (-5-5)	0.2 ± 2.0	0.2 ± 1.4
	Happiness intensity (0-5)	1.1 ± 1.3	0.5 ± 1.0
	Sadness intensity (-5-0)	-1.0 ± 1.5	-0.4 ± 1.0
	Distress–Peacefulness scales (-5-5)	-0.3 ± 1.7	-0.8 ± 1.6
	Peacefulness intensity (0-5)	0.7 ± 1.1	0.4 ± 0.9
	Distress intensity (-5-0)	-1.1 ± 1.2	-1.1 ± 1.3
	Initial emotions intensity (-5-5)	0.0 ± 2.3	-0.5 ± 1.8
	Positive initial emotions intensity (0-5)	1.5 ± 1.5	0.9 ± 1.3
	Negative initial emotions intensity (-5-0)	-1.4 ± 1.5	-1.2 ± 1.2
	Final emotions intensity (-5-5)	-0.3 ± 2.4	-0.8 ± 2.2
	Positive final emotions intensity (0-5)	1.4 ± 1.5	0.9 ± 1.4
	Negative final emotions intensity (-5-0)	-1.7 ± 1.7	-1.6 ± 1.6
	Evolution of emotions within the dream (-10-10)	-0.3 ± 2.4	-0.3 ± 1.6
	Positive evolution of dream emotions intensity (0-10)	0.9 ± 1.4	0.5 ± 1.1
	Negative evolution of dream emotions intensity (-10-0)	-1.3 ± 2.0	-0.8 ± 1.2
	Number of dream characters (0-4)	2.1 ± 0.9	2.0 ± 1.0
	Interactions with dream characters intensity (-5-5)	-0.1 ± 2.2	-0.7 ± 2.0
	Positive interactions with dream characters intensity (0-5)	1.3 ± 1.5	0.9 ± 1.3
Negative interactions with dream characters intensity (-5-0)	-1.4 ± 1.5	-1.5 ± 1.5	

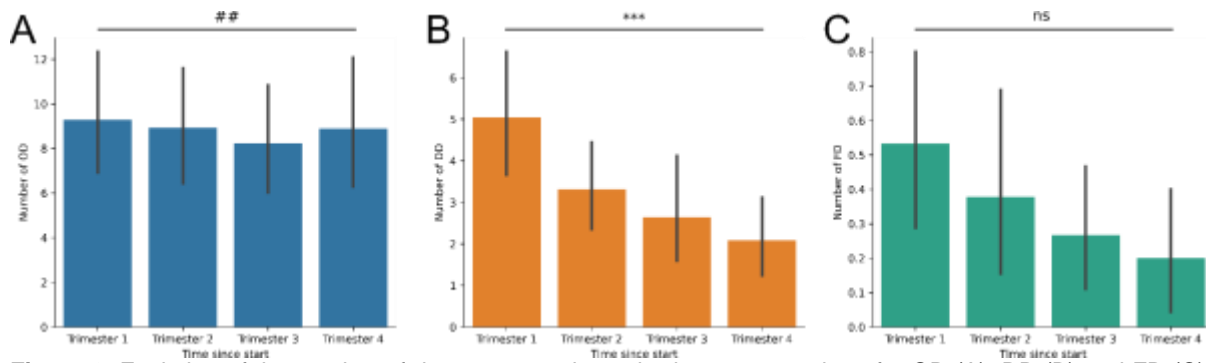
**Table 2.** Self-rated and judge-rated scores (mean between scorers) for DD and OD.

In the end-of-study questionnaire, the self-estimated rate of reported remembered dreams was  $93.6 \pm 9.5\%$  for DD,  $96.4 \pm 16.5\%$  for FD and  $65.2 \pm 24.2\%$  for OD, which suggested that participant had understood and followed the instruction to give priority to the report of DD and FD. We used these estimations to compute a total number of remembered dreams, i.e.  $66.0 \pm 52.8$  per participant ( $13.9 \pm 16.4$  DD,  $51.0 \pm 43.6$  OD,  $1.5 \pm 2.5$  FD). Note that the numbers don't exactly add up to the total number of dream reports since some of them were both DD and FD. A subpart of the participants ( $N=25$ ) were also asked to report at 12 months post inclusion how many nightmares they had during the study. They reported  $11.8 \pm 10.1$  nightmares in average, including  $3.0 \pm 6.9$  that were related to the deceased. They generally enjoyed the DD they had ( $25/43$ , 2 participants did not answer). Most participants considered the study helpful or without influence on their mourning process (6 "not helpful at all", 26 "maybe a little helpful", 7 "probably, yes", 6 "definitely, yes"), and 11 of them sought external support for their grief (bereaved group, psychologist, medication, energy treatments, shiatsu massages, hypnosis, physiotherapist, sport competitions). At the end of the study (12 months post-inclusion), average BFI scores were  $3.6 \pm 0.6$  (BFI-O),  $3.7 \pm 0.6$  (BFI-C),  $3.3 \pm 0.8$  (BFI-E),  $4.0 \pm 0.5$  (BFI-A) and  $3.1 \pm 0.8$  (BFI-N).

The 24-month-post-inclusion follow-up questionnaire was completed by 32 participants. They reported that during the 12 preceding months, they had  $8.7 \pm 20.8$  DD and  $1.3 \pm 3.7$  FD. They also reported  $9.6 \pm 11.3$  nightmares (including  $0.3 \pm 0.9$  that were related to the deceased according to  $N=23$  participants). Among the 25 participants who reported that they had at least 1 DD in the previous year, 13 observed an evolution in the content of their DD: they were more normal and similar to memories ( $N=5$ ), more positive ( $N=6$ ), and less emotionally intense ( $N=5$ ). Most participants ( $26/32$ ) also reported a positive evolution of their mourning process (no change:  $N=5$ ; negative evolution:  $N=1$ ). All participants who did not seek external support during the study did not seek it during the following year.

### Dreams frequency across time

To test the effect of time on the amount of dream reports we used a Bayesian ANOVA with the within-subject factor *Time* (*Trimester 1, 2, 3 or 4*) for OD, DD and FD (**Figure 6**). For OD there was strong evidence for the null model ( $BF_{10}=0.053$ ), i.e. participants reported as many OD in all trimesters. For DD there was decisive evidence for the model with the factor Time ( $BF_{10}=1.6 \times 10^6$ ), showing a decrease in DD number over time. For FD there was weak evidence for the model with factor Time ( $BF_{10}=1.11$ ), suggesting a decrease of FD over time.



**Figure 6.** Evolution of the number of dream reports in each trimester over time, for OD (A), DD (B) and FD (C). ##,  $1/10 \leq BF_{10} < 1/3$ ; \*\*\*,  $BF_{10} > 100$ ; ns,  $1/3 < BF_{10} < 3$ .

## Dreams content across time

Regarding dream content, we used Bayesian ANOVA with factors *Time* and *Dream-Type* on all dreams reported, to investigate the possible evolution of DD and OD self-reported characteristics across time. Note that as the *feeling of control*, the *impression left by the dream*, the *bizarreness* and the *incorporation of unrelated waking-life elements* were reported only for DD, the factor *Dream-Type* was not tested for these parameters. For the dream content characteristics assessed by judges, Bayesian ANOVA were conducted on the first two and last two dreams of the year reported by participants, and the bipolar scales (*Happiness-Sadness*, *Peacefulness-Distress*, *positive/negative initial, final or differential emotions*, *positive/negative interactions*) were separately investigated as half-scales to test for the involvement of each parameter. **Table 3** reports the best model and the contribution of each factor as indicated by the  $BF_{inclusion}$  for each ANOVA. **Figure 7** represents the emotional content of OD and DD across time.

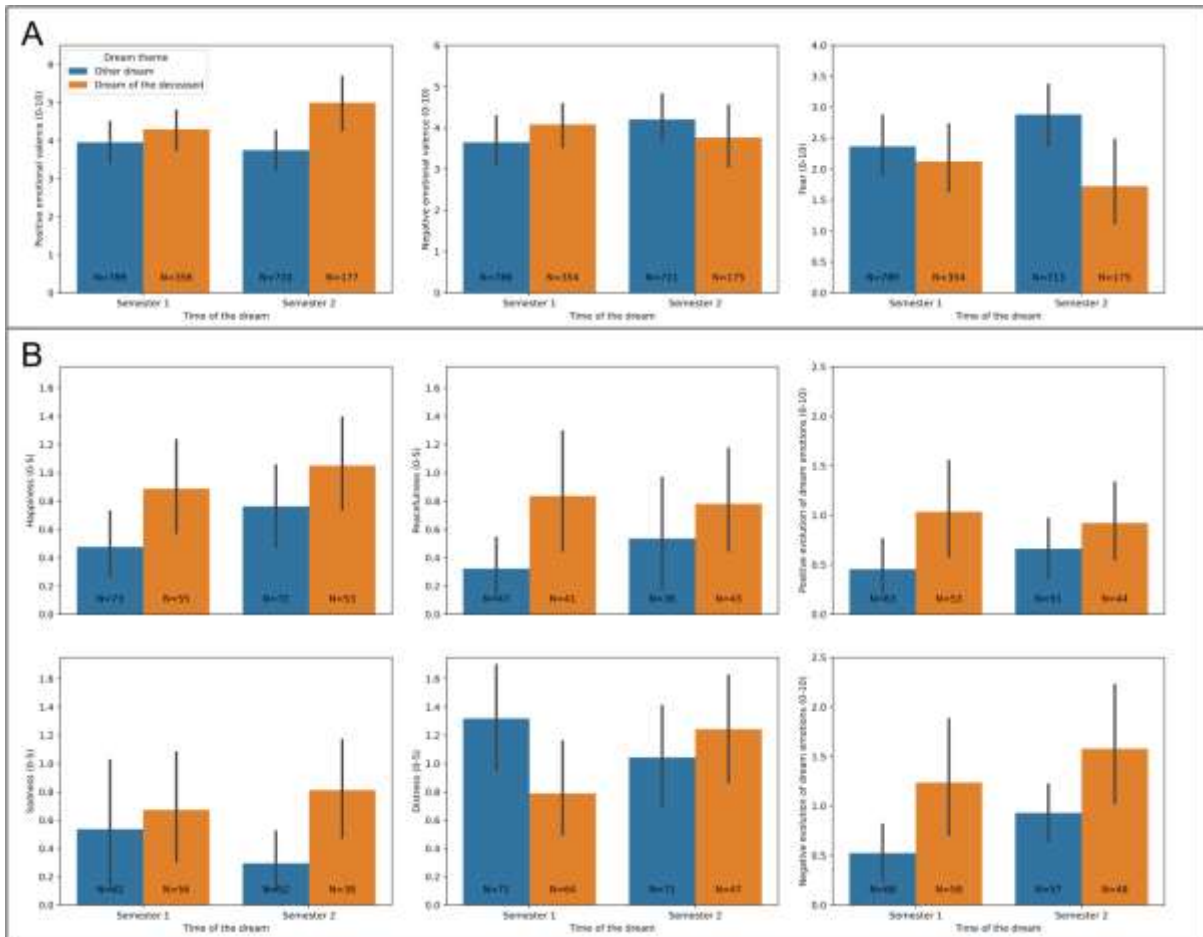
We observed strong evidence for an effect of *Dream-Type* on self-scored positive emotional intensity ( $BF_{10}=13.7$ ), as well as positive evidence for an effect of *Dream-Type* on self-scored fear intensity ( $BF_{10}=9.3$ ) and on judge-scored Happiness ( $BF_{10}=9.9$ ), Sadness ( $BF_{10}=4.5$ ) and negative evolution of the dreams ( $BF_{10}=3.3$ ). Compared to OD, DD presented less fear, more happiness and more sadness, and they tended to become more negative through the dream than OD. For all other parameters the best model was either the null model or supported with weak evidence ( $BF_{10} \leq 1.5$ ).

We similarly compared the intensity of self-rated positive compared to negative emotions in DD and in OD with Bayesian paired t-tests, independently of the subject. Positive emotions were rated more intense than negative emotions in both DD ( $4.5 \pm 2.8$  vs  $3.7 \pm 3.0$ ;  $BF_{10} = 35$ ) and OD ( $3.9 \pm 2.7$  vs  $3.4 \pm 3.0$ ;  $BF_{10} = 84$ ). We further separated between non-pathological grievers (non-CG<sub>26</sub> cases, N=15), who had similarly more positive than negative emotions in DD ( $4.6 \pm 2.7$  vs  $3.3 \pm 2.9$ ;  $BF_{10} = 474$ ) and in OD ( $3.8 \pm 2.6$  vs  $3.2 \pm 2.9$ ;  $BF_{10} = 894$ ), and CG<sub>26</sub> cases (N=26), who showed strong evidence for an absence of difference between positive and negative emotions in both DD ( $4.5 \pm 2.8$  vs  $4.2 \pm 3.0$ ;  $BF_{10} = 0.096$ ) and OD ( $4.1 \pm 2.9$  vs  $4.1 \pm 3.1$ ;  $BF_{10} = 0.067$ ).

	Best model	Factor contribution
Positive emotional intensity	Dream-Type $BF_{10} = 13.70$	$BF_{inc}(\text{Dream-Type}) = 14.16$ $BF_{inc}(\text{Time}) = 0.303$ $BF_{inc}(\text{Dream-Type*Time}) = 1.339$
Negative emotional intensity	<i>Null model</i>	$BF_{inc}(\text{Dream-Type}) = 0.166$ $BF_{inc}(\text{Time}) = 0.196$ $BF_{inc}(\text{Dream-Type*Time}) = 0.728$
Difference between Positive and Negative emotions	<i>Null model</i>	$BF_{inc}(\text{Dream-Type}) = 0.577$ $BF_{inc}(\text{Time}) = 0.168$ $BF_{inc}(\text{Dream-Type*Time}) = 1.560$
Fear intensity	Dream-Type $BF_{10} = 9.260$	$BF_{inc}(\text{Dream-Type}) = 9.245$ $BF_{inc}(\text{Time}) = 0.185$ $BF_{inc}(\text{Dream-Type*Time}) = 1.340$
Proportion of awakenings	Dream-Type + Time $BF_{10} = 1.481$	$BF_{inc}(\text{Dream-Type}) = 1.498$ $BF_{inc}(\text{Time}) = 1.006$ $BF_{inc}(\text{Dream-Type*Time}) = 0.406$
Feeling of control	<i>Null model</i>	$BF_{inc}(\text{Time}) = 0.235$
Global impression left by the dream	<i>Null model</i>	$BF_{inc}(\text{Time}) = 0.600$
Bizarreness intensity	<i>Null model</i>	$BF_{inc}(\text{Time}) = 0.239$
Incorporation of unrelated waking-life elements	<i>Null model</i>	$BF_{inc}(\text{Time}) = 0.300$
Happiness intensity	Dream-Type $BF_{10} = 9.845$	$BF_{inc}(\text{Dream-Type}) = 9.519$ $BF_{inc}(\text{Time}) = 0.281$ $BF_{inc}(\text{Dream-Type*Time}) = 0.315$
Sadness intensity	Dream-Type $BF_{10} = 4.453$	$BF_{inc}(\text{Dream-Type}) = 4.421$ $BF_{inc}(\text{Time}) = 0.153$ $BF_{inc}(\text{Dream-Type*Time}) = 0.211$
Peacefulness intensity	Dream-Type $BF_{10} = 1.356$	$BF_{inc}(\text{Dream-Type}) = 1.304$ $BF_{inc}(\text{Time}) = 0.233$ $BF_{inc}(\text{Dream-Type*Time}) = 0.433$
Distress intensity	<i>Null model</i>	$BF_{inc}(\text{Dream-Type}) = 0.216$ $BF_{inc}(\text{Time}) = 0.169$ $BF_{inc}(\text{Dream-Type*Time}) = 3.530$
Positive initial emotions intensity	Time $BF_{10} = 1.153$	$BF_{inc}(\text{Dream-Type}) = 0.979$ $BF_{inc}(\text{Time}) = 1.018$ $BF_{inc}(\text{Dream-Type*Time}) = 0.618$
Negative initial emotions intensity	<i>Null model</i>	$BF_{inc}(\text{Dream-Type}) = 0.168$ $BF_{inc}(\text{Time}) = 0.154$ $BF_{inc}(\text{Dream-Type*Time}) = 0.892$
Positive final emotions intensity	Time $BF_{10} = 1.066$	$BF_{inc}(\text{Dream-Type}) = 0.492$ $BF_{inc}(\text{Time}) = 0.978$ $BF_{inc}(\text{Dream-Type*Time}) = 0.293$
Negative final emotions intensity	<i>Null model</i>	$BF_{inc}(\text{Dream-Type}) = 0.156$ $BF_{inc}(\text{Time}) = 0.161$ $BF_{inc}(\text{Dream-Type*Time}) = 0.303$

Positive evolution of dream emotions intensity	Dream-Type $BF_{10} = 1.332$	$BF_{inc}(\text{Dream-Type}) = 1.295$ $BF_{inc}(\text{Time}) = 0.197$ $BF_{inc}(\text{Dream-Type*Time}) = 0.281$
Negative evolution of dream emotions intensity	Dream-Type $BF_{10} = 3.339$	$BF_{inc}(\text{Dream-Type}) = 3.172$ $BF_{inc}(\text{Time}) = 0.655$ $BF_{inc}(\text{Dream-Type*Time}) = 0.198$
Number of dream characters	<i>Null model</i>	$BF_{inc}(\text{Dream-Type}) = 0.233$ $BF_{inc}(\text{Time}) = 0.128$ $BF_{inc}(\text{Dream-Type*Time}) = 0.182$
Positive interactions with dream characters intensity	<i>Null model</i>	$BF_{inc}(\text{Dream-Type}) = 0.716$ $BF_{inc}(\text{Time}) = 0.526$ $BF_{inc}(\text{Dream-Type*Time}) = 0.327$
Negative interactions with dream characters intensity	<i>Null model</i>	$BF_{inc}(\text{Dream-Type}) = 0.195$ $BF_{inc}(\text{Time}) = 0.148$ $BF_{inc}(\text{Dream-Type*Time}) = 0.485$

**Table 3.** Results of the ANOVAs testing the effect of time on self-reported characteristics of dream content (9 first lines) and the effect of time on the characteristic of dream content assessed by the judges.



**Figure 7. (A)** Semester-averaged scores of positive and negative emotional valences and of fear (assessed by dreamers) for DD and OD across time. **(B)** Semester-averaged scores of Happiness, Sadness, Peacefulness, Distress, and Positive and Negative evolution of dream emotions (assessed by judges) for DD and OD across time.

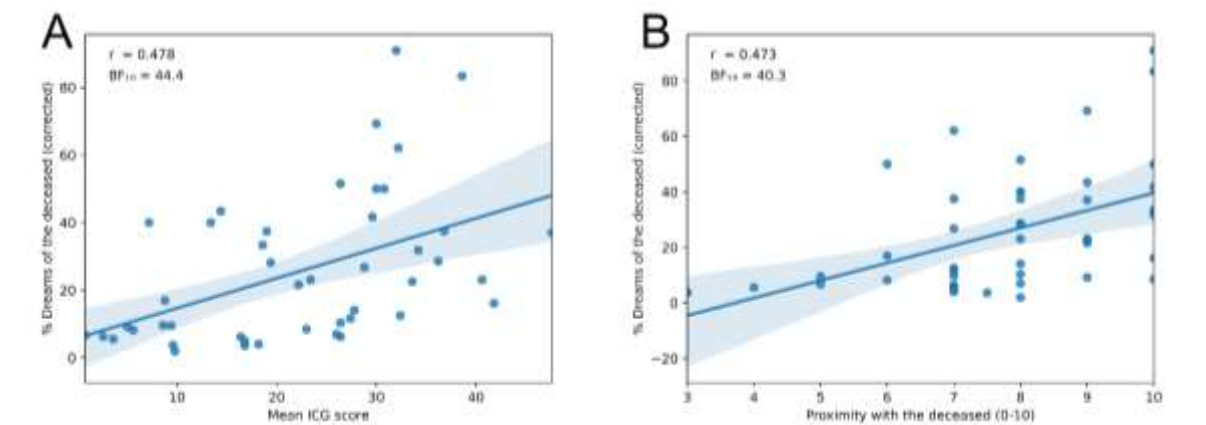
### 3) Coevolution of dreams and mourning

#### a) Relation between ICG and amount of DD

##### *Inter-individual analysis*

We investigated the association between DD frequency and grief by running correlations between the percentage of DD during the study and 1) the mean ICG score, and 2) the proximity with the deceased score. As the number of dreams is highly dependent on DRF, we used the corrected percentage of DD, computed as the number of remembered DD (as opposed to reported) divided by the total number of remembered dreams (numbers of remembered dreams are computed based on the self-estimation by participants of their reported/remembered dream ratio in the end-of-study questionnaire).

**Figure 8A** shows the positive correlation between the corrected percentage of DD and the mean ICG score ( $T_0$  to  $T_4$ ), which is supported by strong evidence ( $BF_{10} = 44.4$ ,  $r = 0.478$ ). **Figure 8B** shows the positive correlation between the corrected percentage of DD and proximity with the deceased, which is supported by strong evidence ( $BF_{10} = 40.3$ ,  $r = 0.473$ ).

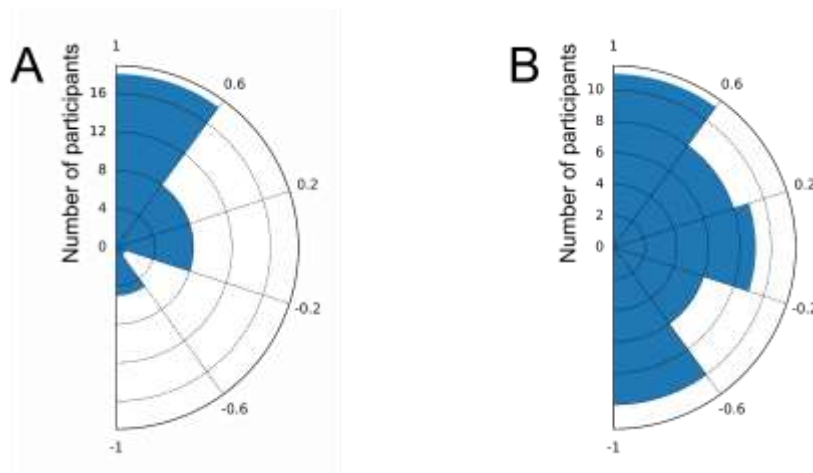


**Figure 8.** Correlations between the corrected percentage of DD and **(A)** the mean ICG score and **(B)** the proximity with the deceased score.

##### *Intra-individual analysis*

Secondly, we used multilevel Bayesian correlations to account for both intra- and inter-individual variability and fluctuations in both DD/OD recall frequency and grief intensity. Multilevel correlations between the number of DD in a trimester and the next ICG score supported a positive correlation with decisive evidence (**Figure 9A**,  $BF_{10} = 2208$ ,  $r = 0.313$ ). On the contrary, there was strong evidence for an absence of correlation between the number of OD in a trimester and the next ICG score (**Figure 9B**,  $BF_{10} = 0.187$ ,  $r = 0.017$ ). Similar results were obtained when correlating the number of DD in a trimester ( $BF_{10} = 8961$ ;  $r = 0.333$ ) and the number of OD in a trimester ( $BF_{10} = 0.294$ ;  $r = 0.069$ ) with the previous ICG score but are not represented here.





**Figure 9.** Distribution of the correlation coefficients of all within-subject correlations between the amount of DD and the next ICG score **(A)** and between the amount of OD and the next ICG score **(B)**.

## b) Relation between ICG and dream content

### *Between-subject analyses*

We tested the relation between dream content and grief with a similar method as the one used to test the relation between the amount of DD and grief. We used Bayesian correlations to compare the mean ICG score ( $T_0$  to  $T_4$ ) to the average self-rated and judge-rated scores of dream content. For self-rated scores all reported dreams were used, and for judge-rated scores 8 OD and up to 8 DD were randomly chosen (balanced across trimesters when possible, see Methods section) and scored.

Results are reported in **Table 4**. There was weak evidence for and against a correlation between any parameter and the mean ICG score for OD ( $0.351 \leq BF_{10} \leq 1.220$ ) and for DD ( $0.351 \leq BF_{10} \leq 2.921$ ). It should be noted that for DD the level of evidence for the correlations with negative valence ( $BF_{10}=2.109$ ), Sadness-Happiness ( $BF_{10}=2.348$ ), and Distress-Peacefulness ( $BF_{10}=2.921$ ) is higher, albeit still being weak evidence.

<i>Correlation with mean ICG</i>	<b>Dreams of the Deceased (DD)</b>	<b>Other Dreams (OD)</b>
Positive emotional intensity	0.172 $BF_{10}=0.617$	0.139 $BF_{10}=0.505$
Negative emotional intensity	0.302 $BF_{10}=2.109$	0.005 $BF_{10}=0.351$
Difference between Positive and Negative emotions	-0.094 $BF_{10}=0.415$	0.089 $BF_{10}=0.408$
Fear intensity	0.091 $BF_{10}=0.410$	0.066 $BF_{10}=0.381$
Feeling of control	-0.007 $BF_{10}=0.351$	-

Global impression left by the dream	-0.211 <i>BF</i> <sub>10</sub> =0.827	-
Bizarreness intensity	0.279 <i>BF</i> <sub>10</sub> =1.602	-
Incorporation of unrelated waking-life elements	0.054 <i>BF</i> <sub>10</sub> =0.371	-
Sadness – Happiness intensity	-0.311 <i>BF</i> <sub>10</sub> =2.348	-0.153 <i>BF</i> <sub>10</sub> =0.545
Distress – Peacefulness intensity	-0.327 <i>BF</i> <sub>10</sub> =2.921	-0.268 <i>BF</i> <sub>10</sub> =1.220
Dream initial emotions intensity	-0.246 <i>BF</i> <sub>10</sub> =1.129	-0.133 <i>BF</i> <sub>10</sub> =0.496
Dream final emotions intensity	-0.126 <i>BF</i> <sub>10</sub> =0.474	-0.205 <i>BF</i> <sub>10</sub> =0.737
Evolution of emotions within the dream	0.118 <i>BF</i> <sub>10</sub> =0.457	-0.192 <i>BF</i> <sub>10</sub> =0.680
Number of dream characters	0.057 <i>BF</i> <sub>10</sub> =0.374	0.268 <i>BF</i> <sub>10</sub> =1.214
Interactions with dream characters intensity	-0.254 <i>BF</i> <sub>10</sub> =1.222	-0.225 <i>BF</i> <sub>10</sub> =0.850

**Table 4.** Bayesian between-subject correlations and their level of significance (*BF*<sub>10</sub>) between the mean ICG score and the mean dream content scores for DD and OD (self-rated scores: lines 1 to 8, judge-rated scores: lines 8 to 14).

#### *Multilevel analyses*

We also used multilevel Bayesian correlations to account for both inter- and intra-individual variability and fluctuations in DRF and grief intensity (**Table 5**). For self-ratings, we correlated the average score in each trimester and for each type of dream (DD or OD) with the following ICG score. For judge-ratings, we correlated the average scores from the randomly selected scored dreams in each trimester and for each type of dream (DD or OD) with the next ICG score.

For OD, there was weak to positive evidence for an absence of correlation between any score and the next ICG score (*BF*<sub>10</sub> ≤ 0.349). For DD, there was not more evidence for a correlation between the Happiness-Sadness score and the next ICG score than evidence against it (*BF*<sub>10</sub> = 1.018) while there was weak to positive evidence against all other tested correlations (*BF*<sub>10</sub> ≤ 0.445).

Similar multilevel correlations were also carried with the preceding ICG score. There was weak to positive evidence for an absence of correlation for all tested parameters, both for DD (*BF*<sub>10</sub> ≤ 0.705) and for OD (*BF*<sub>10</sub> ≤ 0.614).

<i>Correlation with next ICG</i>	<b>Dreams of the Deceased (DD)</b>	<b>Other Dreams (OD)</b>
Positive emotional intensity	-0.029 <i>BF</i> <sub>10</sub> =0.218	0.086 <i>BF</i> <sub>10</sub> =0.349
Negative emotional intensity	-0.017 <i>BF</i> <sub>10</sub> =0.209	-0.011 <i>BF</i> <sub>10</sub> =0.192
Difference between Positive and Negative emotions	-0.006 <i>BF</i> <sub>10</sub> =0.266	0.040 <i>BF</i> <sub>10</sub> =0.221
Fear intensity	0.098 <i>BF</i> <sub>10</sub> =0.437	-0.034 <i>BF</i> <sub>10</sub> =0.209
Feeling of control	-0.010 <i>BF</i> <sub>10</sub> =0.206	-
Global impression left by the dream	-0.075 <i>BF</i> <sub>10</sub> =0.311	-
Bizarreness intensity	-0.077 <i>BF</i> <sub>10</sub> =0.321	-
Incorporation of unrelated waking-life elements	0.036 <i>BF</i> <sub>10</sub> =0.224	-
Sadness – Happiness intensity	-0.146 <i>BF</i> <sub>10</sub> =1.018	-0.034 <i>BF</i> <sub>10</sub> =0.222
Distress – Peacefulness intensity	-0.032 <i>BF</i> <sub>10</sub> =0.220	-0.005 <i>BF</i> <sub>10</sub> =0.196
Dream initial emotions intensity	-0.099 <i>BF</i> <sub>10</sub> =0.445	-0.037 <i>BF</i> <sub>10</sub> =0.222
Dream final emotions intensity	-0.037 <i>BF</i> <sub>10</sub> =0.225	-0.006 <i>BF</i> <sub>10</sub> =0.196
Evolution of emotions within the dream	0.064 <i>BF</i> <sub>10</sub> =0.225	0.019 <i>BF</i> <sub>10</sub> =0.202
Number of dream characters	-0.027 <i>BF</i> <sub>10</sub> =0.216	-0.050 <i>BF</i> <sub>10</sub> =0.236
Interactions with dream characters intensity	-0.091 <i>BF</i> <sub>10</sub> =0.367	-0.017 <i>BF</i> <sub>10</sub> =0.201

**Table 5.** Bayesian correlations and their level of significance (*BF*<sub>10</sub>) between the next ICG score and the dream content scores for DD and OD (self-rated scores: lines 1 to 7, judge-rated scores: lines 8 to 14).

## Discussion

Thanks to a prospective study, we investigated the evolution of the mourning process and the evolution of dreams content and frequency (notably dreams about the deceased), and their possible relationship during the 14 first months of bereavement in 45 persons.

The observed impact on ICG of the modulating factors of grief investigated here led us to recommend the use of an ICG threshold at 30 at 12 months post-loss and to take into account the slope of the ICG evolution across time and/or the context of the relative's loss (e.g. proximity to the deceased, death expectedness) to adequately set the diagnosis of CG.

Regarding dreaming, we could objectivate that the number of dreams incorporating a person increased after the death of the person and then decreased with time (OD did not decrease with time). In addition, multilevel analyses revealed for the first time decisive evidence for a correlation between the amount of DD and the next ICG score (**Figure 9**), suggesting a meaningful link between emotional regulation and DD. Finally, we replicated the mainly positive nature of DD and showed that whereas the intensity of negative emotions is usually greater than the intensity of positive emotions in dreams (Röver & Schredl, 2017), it was the other way around for persons with NCG only (N=30). These results suggest that a compensatory mechanism during sleep and dreaming (sadness during wake compensated by positive emotions during sleep) participates to emotional regulation, i.e. to the positive evolution of the mourning process. These results validate and encourage the use of dreams in a clinical setup to assess and optimize the evolution of the mourning process in bereaved persons.

### ***Evolution of grief according to time and several modulating factors***

We used the ICG score (Prigerson et al., 1995) at several time points to assess grief intensity and the evolution of the mourning process (**Figure 3**). This scale has been designed and used as a diagnostic tool, several months or years after a relative's death, to detect patients suffering from CG. However, the ICG score evolution across time has been rarely investigated so far and may add important information to help the diagnosis of CG. Contrary to most studies, we used a prospective design which did not focus only on death that happened in hospitals (causes of death were diverse), the bereaved were younger than usually in previous studies (median age = 24 years old), and we considered the possible influence of commonly reported risk factors of CG (sex and age of the bereaved, age of the deceased, proximity with the deceased, neuroticism, death expectedness) on the ICG score and its evolution.

As observed in previous studies, we found that the ICG score was higher for closer relatives (e.g. Wayment & Vierthaler, 2002), younger relatives (e.g. Ringdal et al., 2001a), and for participants with a higher neuroticism scores at the BFI (e.g. Wijngaards-de Meij et al., 2007). Not expecting the death and being a woman also tended to increase the ICG score, which is also in line with previous results (Wijngaards-de Meij et al., 2005; Fujisawa et al., 2010; Kersting et al., 2011). The weak effect of death expectedness could be explained by the fact that death unexpectedness is mainly captured by the death at a young age whose effect is clearly significant, as this effect was found by Wijngaards-de Meij (2005) in a study of parents who lost a child. Moreover, ICG scores significantly decreased over time as observed in previous studies measuring grief with ICG or other scales (e.g. Ringdal et al.,

2001b; Wijngaards-de Meij et al., 2005; Tsai et al., 2016) which confirms that the ICG scale is sensible to the evolution of the emotional state of the bereaved persons across the mourning process. Only death expectedness showed an interaction with time i.e. a faster decrease of ICG for unexpected death than for foreseeable death (**Figure 3**). This effect comes from the fact that the main difference between expected and unexpected death is the ICG score at the time of death rather than the speed of the mourning process, as if the grief and mourning process started at the time of death for unexpected deaths, and before the death for foreseeable deaths. It fits with a concept known as anticipatory grief (Coelho & Barbosa, 2017), corroborated by the results of Wijngaards-de Meij et al. (2005). The absence of any other interaction (with sex and age of the bereaved, age of the deceased, proximity with the deceased, and neuroticism) confirms the findings of Ringdal et al. (2001a) despite including supplementary common risk factors of CG.

Complicated grief is defined as a slow or non-evolutive mourning process, with symptoms affecting the bereaved persons' quality of life. One may thus expect to objectivate a slower evolution of ICG in CG than in non-pathological grief. In our sample, a difference of the ICG evolution slope can be seen between non-pathological grief and CG, when CG has been defined using a threshold of 30 at 14 months post-loss. No significant difference of the ICG evolution slope between CG and non-pathological grief has been observed when using a threshold of 25 at 14 months post-loss. Those results suggest that a threshold at 30 may be more specific and more clinically pertinent to diagnose CG than a threshold at 25. As the slope i.e. the evolutive character of grief intensity is a central notion of CG, it also seems pertinent to measure ICG at several time points (e.g. 6 months and 12 months post-loss) before reaching a diagnosis. Indeed, in our sample, when the 26 threshold is used, 3 bereaved persons show a final ICG score between 25 and 30 but also a regular decrease of their ICG. Such pattern may highlight an intense mourning process taking time because a lot has to be processed instead of a pathological process.

Finally, the context of the relative's death, and notably the level of proximity between the bereaved and the deceased seems to be critical to take into account before reaching a decision. Indeed, an ICG score between 25 and 30 at 6 months may convey very different situations if the deceased was very close or important to the bereaved or if he/she was not (or if he/she died unexpectedly). As ICG scores are typically higher for closer deceased and decrease faster for unexpected death, an ICG at 30 six months post-loss if the bereaved and the deceased were very close and/or if the deceased died unexpectedly may indicate a healthy ongoing mourning process, whereas an ICG at 30 six months post-loss may be understood as a risk sign for CG if the bereaved and the deceased were not very close and/or if the loss was foreseeable.

In conclusion, our results suggest to use an ICG threshold at 30, measured at least 12 months post-loss, while considering the slope of the ICG evolution between at least 2 time points and the main modulating factors (e.g. proximity to the deceased, death expectedness) before reaching a decision for the diagnosis of CG. Even if a person is not diagnosed with CG, support during this difficult period will anyways contribute to a more favourable mourning process and should be considered.

### ***Dreaming during the mourning process***

In this study we separately investigated dreams of the deceased (DD) and other dreams (OD). Previous studies of dreaming during the mourning process generally investigated only DD (e.g. Black et al., 2016, 2019; Belicki et al., 2003; Wright et al., 2014) or

the last dream remembered (Germain, 2013). Our unique approach allowed us to observe a specific decrease in the number of DD but not in the number of OD in the first 14 months of mourning. Such decrease in DD paralleled the decrease in ICG scores, as well as within-subject DD-specific content changes across the year of participation.

While participants reported an average retrospective DRF of 2.8 dreams per week at inclusion, they sent an average of 0.95 dreams per week during the study. Both the retrospective and prospective DRF are higher than expected (Schredl, 2008), which is at least partly explained by the fact that the study's ads mentioned dreaming. It led to recruitment biases towards individuals interested in dreaming, who were consequently expected to show a high DRF (it has been shown that interest in dreams is positively correlated with DRF, Schredl et al., 2003). As could be also expected, the prospective DRF was lower than the retrospective DRF since participants were clearly instructed that they did not have to report all their remembered dreams but rather about once a week if possible. Even with this reasonable request of dream report frequency, there was a risk that the long duration of the study induced reporting fatigue and decrease over time (Schredl, 2002). We thus discovered with interest that the report frequency of OD remained stable during the year of the study, which argues for a stable involvement of the participants and a compliant application of the instructions over time. On the contrary the number of reported DD decreased over time, suggesting a time course specific to DD and potentially related to the ongoing mourning process leading to a decrease in grief intensity (as evidenced by ICG scores also decreasing with time).

This hypothesis was supported by results both at the between-subject level and at the within-subject level. First, according to a retrospective assessment (by the participants at inclusion) of the frequency of dreams involving the deceased before his/her death, DD frequency clearly increased after the death of participants' relatives. We also identified between subjects a positive correlation between the proportions of DD reported in the year of the study and the mean ICG score. Finally, multi-level correlations confirmed that at the within-subject level, the number of DD but not of OD correlated with the next ICG score during the year of participation. This result confirms and extends those of a previous retrospective study reporting an influence of grief intensity on the number of DD reported in the month before (Black et al., 2019). It is also coherent with studies suggesting that dreams express the dreamer's emotional state (Hartmann, 1996; Malinowski & Horton, 2015; Ruby, 2021) and observations that in psychotherapies, dreams can be used to identify the most important issues (Pesant & Zadra, 2004), as DD represent a large proportion of the reported dreams (26%) and as their number covaries with the ICG score. Overall, our results evidence for the first time a clear and reliable link between grief intensity and DD frequency which opens an avenue for the use of dreams at the clinical level notably to assess and follow grief intensity evolution across time.

Regarding dream content, we investigated self-rated emotional assessment of dream content and we also used or developed and validated rating scales to measure subcategories of positive and negative emotions specifically related to mourning: happiness-sadness, peacefulness-distress, the evolution of emotion across the dream, and the number of dream characters and the support they provided. We confirmed previous observations that DD were more positive than negative (Wright et al., 2014; Black et al., 2019) and we further showed that it was the case only for non-pathological grief. Furthermore, we evidenced for the first time that DD were more positive than OD. This effect was significant for the self-rated positive emotion scale and for the happiness but not for the peacefulness scores assessed by judges. As home dreams in non-bereaved persons typically show equal

self-ratings of positive and negative emotions or more negative than positive emotions (Vallat et al., 2017; Plailly et al., 2019; Fosse et al., 2001; Schredl & Doll, 1998; Röver & Schredl, 2017; Nielsen et al., 1991; Schredl & Reinhard, 2010), the positivity of DD argues for a regulation mechanism compensating for the grief-related sadness and having a soothing effect (25/43 participants reported to appreciate having DD). Nonetheless, this interpretation fits with the fact that participants who reached the threshold of complicated grief at 14 months post-loss did not show a positivity bias in their dreams. It should however be noted that the difference between positive and negative emotions did not predict the evolution of the ICG and did not differ between DD and OD. Finally, we also identified lower self-rated fear levels and more judge-rated sadness in DD than in OD. This new result is interesting since sadness is considered to be part of the mourning process, by turning attention inward, promoting acceptance, updating cognitive structures, inducing social comfort (Bonanno et al., 2008).

Despite these differences between DD and OD, we did not observe any significant self-rated or judge-rated emotional dream content evolution over time or any convincing correlation between emotional dream content evolution and ICG evolution across time. The difference in sadness between DD and OD contrasts with the absence of an association with the evolution of the ICG, and an existing relationship may be identified by using more subjects and/or dreams. Among judge ratings, there was only weak evidence for an increase in happiness when the ICG decreases. The weakness of the effect could be due to participants under-representing their positive dream emotions in dream reports (Sikka et al., 2014; Röver & Schredl, 2017), potentially concealing an actual effect of dream happiness on the mourning process. Some authors previously proposed an evolution of specific emotional dream contents during the mourning process although no clear effect was evidenced (Garfield, 1996; Domhoff, 2015; Black et al., 2014).

These results bring new evidence for an involvement of dreaming in emotion regulation. On the one hand, participants recalled thinking about the deceased the day before for approximately 66.3% of the dreams. This result is only partly coherent with the continuity hypothesis of dreaming (Schredl & Hofmann, 2003), since more than 30% of DD were not associated with any deceased-related thoughts the day before. Nevertheless, conscious thoughts may not be necessary to trigger the incorporation of an emotional memory into dreams. In addition to previous studies showing associations between dream emotions and ongoing preoccupations (e.g. Cartwright, 1991; Vallat et al., 2017), we found that the mourning process was associated with an increased frequency of dreams with the deceased relative. The association between the mourning process and dream content is supported by the more positive than negative dreams of non-pathological griever compared to complicated grief cases. The higher positive than negative self-rated emotions of dreams in non-CG participants, in line with previous studies (Wright et al., 2014; Black et al., 2019), argues for a compensation mechanism being part of the emotional regulation processes taking place during sleep and dreams (Vallat et al., 2017; Ruby, 2021), rather than continuity between wake and dreams.

### ***Strengths and Limitations***

Our study is the first prospective study of dreaming during mourning, with a systematic collection of dreams of the deceased and most of the other dreams right after waking up in 45 participants. Previous studies were all retrospective, either collecting the last dream of the deceased in a large sample (e.g. Black et al., 2016, 2019, 2020; Wright et al.,

2014) or a dream diary of a single person (Black et al., 2014; Belicki et al., 2003). In comparison to previous studies, this allowed us to test not only for the evolution of dream characteristics over time but also to correlate dream characteristics to the evolution of the mourning process.

While a similar study has never been conducted before and offers new insights in the mourning process and the dreams that follow a relative's loss, our investigation would have welcomed a higher number of participants to be more representative of the general population. As there is not a single course of normal grief (Arizmendi & O'Connor, 2015), previous studies of the course of mourning recruited hundreds of participants (N=183 in Ringdal et al., 2001b; N=219 in Wijngaards-de Meij et al., 2005; N=216 in Tsai et al., 2016). However, these studies were less demanding, consisting only in punctual questionnaires. On the contrary, our participants were asked a continuous involvement during a year, making it not easy to recruit (the inclusion of 45 participants spanned 30 months).

As the study was already very demanding, participants were only asked to rate their dreams on three emotional scales: positive and negative emotions, and fear. While this data is already unique in the field of dreaming during mourning, we further investigated sub-specific emotions reported as involved in mourning by establishing external rating scales, in line with several previous analyses. The excellent validity and reliability of the scales supported this approach. As previous studies (Sikka et al., 2014; Röver & Schredl, 2017) identified an underestimation of dream emotions by external ratings compared to self-ratings, especially regarding positive emotions, some of our results (notably the absence of relation between DD content and the mourning process) may have been different had the participants themselves evaluated these sub-emotions.

The percentage of reported versus remembered dreams was lower for OD than for DD, which may have led to a biased conclusion regarding OD content. Despite this, the high proportion of reported OD (65% in averaged based on the end-of-study questionnaire) and their stability over time suggest that they were reasonably representative of all OD. We asked fewer questions about OD than about DD for feasibility reasons (to not overload the participants; Bernstein & Belicki, 1996; Schredl, 2002), preventing from more content comparisons between OD and DD.

Finally, bereavement can last years or even never end, yet this study only investigated dreams of the deceased in the first 14 months of the mourning process. Belicki et al. (2003) did not notice any obvious change in dream categories in a widower 16-year long dream journal (N=106 dreams) and suggested that dreams of the deceased followed the cyclic, non-uniform progression of grief, in opposition to the classical stages model of grief. On the contrary, Domhoff (2015) identified in a widower 22-year long dream journal (N=143 dreams) a decreasing number of resurrection, reassuring and illness dreams and increasingly aggressive and negative dreams. Because of the uniqueness of each grief, it's difficult to generalise the conclusion reached from these two cases without a more systematic evaluation, which is hard to conduct on more than 1 year. Nevertheless, the first 14 months of grief seem to be very significant for the mourning process, since the ICG score decreased between 14 and 26 months as much as in a single trimester of the year of our study. This suggests that our results are informative of a significant part of the mourning process.

### ***Perspectives***

As DD present unique characteristics compared to OD, it would seem reasonable to use these dreams as a tool to work on the mourning process, especially in people suffering



from CG. The use of dreams in therapies can bring several benefits (Pesant & Zadra, 2004: better insight, more trust in the psychiatrist, better communication...) and few studies were carried out in the case of grief therapies, showing benefits only on some aspects of the therapy (Hill et al., 2000; Moss, 2002; Begovac & Begovac, 2012; Noronha, 2014). We suggest that a long-term therapy focusing more on DRF and content of DD may facilitate the mourning process, for instance by using the presence of DD as a marker of current grief state. As DD are more positive than OD, it would be interesting to investigate whether CG cases following Imagery Rehearsal Therapy (IRT) could strengthen the role of positivity in these dreams and therefore improve their mourning process. This technique, which consists in visualising dreams and imagining an alternate outcome to their story, has been successfully applied to recurrent nightmares treatment by removing their negative emotions (e.g. Krakow & Zadra, 2010), and even more so when IRT was combined with Targeted-Memory Reactivation (Schwartz et al., 2022). Similar benefits could apply to DD: as these dreams possess the common theme of the deceased, presence of the deceased could be associated with positive dream stories and potentially contribute to the mourning process. Moreover, as IRT is an indirect modification of dreams but not of the mourning process, it would confirm that dreams have a causal role in emotion regulation during the mourning process.

### ***General conclusion***

In this study we confirmed the role of several factors (proximity with the deceased, age of the deceased, neuroticism) on grief intensity and of the expectedness of the death on its course in the first 14 months post-loss. The ICG score decreased all the more that the frequency of dreams of the deceased decreased as well. Dreams of the deceased were frequent, more positive, happier, less fearful, and less sad than other dreams. They were also more positive than negative in people with a non-complicated grief, but equally positive and negative in complicated grief.

A better understanding of the mourning process is an essential step toward a better care of grieving people, especially those at risk of developing complicated grief. In this sense, dream evaluations and systematic grief assessments with questionnaires such as the ICG appear to be cost-effective and time-efficient methods to evaluate the progression of grief, especially with the likely involvement of dreaming in emotion regulation processes. As a final note, if 20% of the population suffers from complicated grief, then among the current French population of 68 million inhabitants, no less than 13.6 million people are affected, with negative consequences on their health, their productivity and their happiness. More systematic assistance is necessary to assist through this wide-spread issue, for instance with regular grief assessments with questionnaires and the more common use of psychotherapy, where dreams may be used as well.

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## IV. General discussion

## Summary of the results

### Memory, attention and dream recall frequency

One of the aims of this thesis was to examine the cognitive and neurophysiological traits associated with inter-individual variations in DRF. Existing literature has already identified the involvement of several factors and neurophysiological activities, although the involvement of several of them remained unclear. Based on this literature, we conducted a study targeting the role of auditory working memory and attention in DRF, both at the behavioural and at the neurophysiological scale, by comparing the abilities at wake of low and high frequency dream recallers.

### Evidence for behavioural differences of attention but not memory between LR and HR

In the study 1a, we used a cognitively demanding task (MEMAT) to test whether the increased neurophysiological components of top-down and bottom-up attention in HR (Ruby et al., 2022) would result in decreased behavioural performance in a challenging context, and to confirm whether STM abilities were associated with DRF. Memory difficulty did not affect differently LR and HR in this task, supporting our hypothesis of an absence of influence of STM abilities on DRF. The studies which have assessed the influence of STM abilities during wake on DRF led mainly to negative results and inconsistencies (Blain, de la Chapelle, et al., 2022) so far, with an absence of a clear effect of both visual and auditory short-term memory abilities. Our results confirm these previous results showing the absence of a strong link between working memory abilities during wake and DRF. One explanation is that memory abilities during sleep, during wakefulness, and during the sleep-wake transition do not necessarily correlate, although no study tested this hypothesis to the best of our knowledge. As an alternative explanation, rather than the STM abilities, we propose that what matters for dream recall is the ability of the short-term memory content to survive the sleep-wake transition. Abrupt awakenings favour such survival (Shapiro et al., 1965; Goodenough et al., 1965), which may explain that HR with their more reactive brain (Eichenlaub, Bertrand, et al., 2014; Ruby et al., 2013, 2022) awaken more sharply than LR, which would favour a frequent survival of STM content. Little sleep inertia in HR, as well as a quick reinstatement of functional connectivity at awakening, may also favour a short and efficient transition between sleep and wakefulness, giving more chances for STM content to stay available (Vallat et al., 2020).

Indeed, HR showed more impairment to hard-to-ignore distractors than LR in our study, evidencing an impact on performance of the increased bottom-up attentional abilities in HR. As expected, HR demonstrated fewer available resources when the task complexity increased which resulted in more impairment than in LR in such challenging conditions.

Results argue thus in favour of the hypothesis that due to increased bottom-up and top-down processes (Ruby et al., 2022), HR would be less likely to maintain an efficient balance between bottom-up and top-down processes when the task difficulty increases. The fact that HR showed worse overall performance than LR supports a global increased difficulty to suppress distractors in HR when conditions are demanding.

To summarize, we demonstrated differences in attentional performance between LR and HR thanks to the use of a challenging paradigm. MEMAT enabled us to evidence a high distractibility in HR hampering performance when conditions are challenging. The fact that we compared LR and HR with extremely low and high DRF, combined with the previously ambiguous literature, confirms that any difference in auditory short-term memory between LR and HR is very unlikely, or at most consists in a very small effect.

### HR and LR differ in filtering cerebral processing

The cerebral correlates of MEMAT in LR and HR have been investigated in Study 1c (re-analysis of the data of the study 1b, to compare LR and HR). We identified increased differences between the ERFs to to-be-attended and to-be-ignored stimuli in the right auditory cortex between 225 and 275ms post stimulus onset in LR compared to HR. In other words, LR better differentiated between relevant and irrelevant stimuli at the neurophysiological scale than HR. This result explains the better overall performance of LR as compared to HR. It suggests that an increased processing of irrelevant stimuli in HR would hamper their ability to sufficiently dissociate between relevant and irrelevant stimuli at the cerebral level. This result confirms the higher brain reactivity of HR compared to KR observed in several studies (Eichenlaub, Bertrand, et al., 2014; Ruby et al., 2013, 2022).

### Dream recall and dream content in epilepsy

We also investigated how dreaming differed from healthy populations in a neurological condition, epilepsy, using both a large scale, systematic questionnaire study in a wide population of patients (Study 2a), and electrophysiological investigations in patients with drug-resistant epilepsy (Study 2b). We further questioned the influence of epileptic, internally-generated stimuli on dream content, which remained scarcely investigated.

As we presented in our review of dreaming in epilepsy, in the introduction of this thesis, there is a bidirectional interaction between epilepsy and sleep – and potentially also

dreaming. Studying dreaming in epilepsy is therefore a relevant approach to improve our understanding of both dreaming and epilepsy. We explored the influence of epilepsy-related activity on dream recall in one behavioural study (questionnaires, 2a) and one SEEG study (2b). The Studies 2a and 2b are still undergoing analyses because of delaying circumstances (delayed inclusions in Montreal due to the Covid-19 pandemic, and drastic reduction in hospital activity due to staff shortages in the post-pandemic period), but the preliminary results are already very informative about dream frequency and content in this population.

DRF was high in the two studies, i.e. in Study 2a, where epileptic patients (N=84) were systematically asked retrospectively about their dreams, and in Study 2b, where drug-resistant epileptic patients (N=24) implanted with depth electrodes kept a dream diary during their stay at the neurological hospital, and this high value was not explained by age or gender. The weekly DRF (about 2 dreams recalled per week) was similar as in a previous study with epileptic patients (Bentes et al., 2011), and twice as high as in the general population (0.8 dream recalled per week in a representative German sample, Schredl, 2008). These authors compared the DRF of patients with epilepsy to that of a control group and found decreased DRF in patients. However, their control group had a very high DRF as compared to that of the general population, possibly due to uncontrolled parameters such as interest in dreams and openness to experience (the two parameters are associated with increased DRF, Schredl et al., 2003). We thus confirm previous results showing that epileptic patients have a DRF at about 2 dreams recalled per week and conclude, contrary to what has been previously written, that epileptic patients do not show a decreased DRF, but on the contrary show an increase of dream recall quite coherent with the increase in intra-sleep wakefulness induced by the epileptic activity.

Several studies have pointed toward a positive effect of nocturnal awakenings on DRF in healthy populations (Schredl et al., 2003; Vallat, Lajnef, et al., 2017), and this effect was close to significance in epileptic patients (Study 2a). Furthermore, a similar effect was observed in Study 2b, as the subjective number of awakenings correlated positively with DRF. The increased intra-sleep wakefulness of epileptic patients has been repeatedly reported before, and this effect may contribute to explain the elevated DRF in epilepsy patients. Here again, the significance of these results is limited by the preliminary state of the studies (N=84 in Study 2a), although we can reasonably expect them to be confirmed with the full expected samples (N=300 in Study 2a). Interestingly, the observed associations with DRF were limited to subjective – and not objective – awakenings. Previous studies in healthy subjects reported objective intra-sleep wakefulness, but the observed increased number of long awakenings (>120s) in those with a high DRF (Vallat, Lajnef, et al., 2017) may be close to what is considered a subjective awakening since conscious awakenings typically necessitate about 2 min of wakefulness (Campbell & Webb, 1981; Winser et al., 2013). An investigation of long objective awakenings in epileptic patients may thus reconcile results from different field

possibly confirming a correlation between long objective awakenings and DRF, which we hope to do thanks to the automated scoring of the sleep recordings in Study 2b.

We expected epileptic activity to influence DRF by possibly fragilizing the short-term memory of the dream and/or by stimulating or disturbing regions involved in dream recall or production such as the TPJ or the MPFC. We estimated the influence of epileptic seizures and of interictal activity on DRF in the Studies 2a and 2b. None of the tested variables (subjectively reported sleep seizures in Study 2a, and objective sleep seizures and interictal activity in Study 2b) covaried with DRF. Here again, these results are preliminary and may not reflect the actual impact of epilepsy on dreaming. They however suggest that epileptic activity itself is not responsible for the increased DRF of epileptic patients, but that the pathology would rather impact DRF through the epilepsy-related increase of intra-sleep wakefulness, which in turn would increase DRF. Note also that one cannot exclude that two opposite effects coexist: epilepsy activity increasing intra-sleep wakefulness (promoting dream recall), and also disturbing dream short-term memory (suppressing dream recall), which would result in variable effects across patients notably depending on the localization of the epileptic focus. The preliminary state of the analysis does however not allow to draw this conclusion yet. Interestingly, the Study 2a evidenced a negative effect of epilepsy duration on DRF, which suggests a progressive degradation of the brain function involved in DRF and therefore point towards a long-term influence of epilepsy on DRF.

The original nature of these studies, even if some results are preliminary, brought unique evidence pointing toward similar mechanisms of dream recall in epileptic and healthy populations, except for the added long-term influence of seizures on the brain. Further confirmation will however prove necessary, which we hope to achieve in the next months.

Regarding dream content, in the study 2a, we systematically asked patients undergoing a medical consultation to fulfill a questionnaire about their dreams, and notably whether they had dreams in which they had seizures, symptoms of their seizures, or staging the consequences of their epilepsy on their daily life. While most of the patients did not report any of these epilepsy-related features in their dreams, some of them often experienced epilepsy-related dreams. This result could be explained by the fact that epilepsy symptoms and consequences are very present in the daily life of the patients. As a consequence, both the continuity hypothesis and the emotional regulation hypothesis of dreaming would predict an incorporation of the epilepsy-related features of daily life into dreams. However, this result may also suggest that in some cases epileptic activity can influence dream content. This assertion received further support from the belief held by several patients that their dreams of seizures were concomittent to actual seizures, based on identification of usual seizure symptoms and/or observations from relatives.

We tested this hypothesis by investigating nightly ictal and interictal activity and incorporations of epilepsy-related elements in dream content in the Study 2b. We recruited 24

epileptic patients in a hospital setting while they were implanted with depth electrodes for presurgical evaluation of their epilepsy. In this context, patients who had a seizure during the night did not report more epilepsy-related dream content than after nights with no seizure. On the contrary, sleep-related interictal activity during the whole night correlated with the presence of epilepsy-related dream content. We supposed that epileptic seizures induced such strong stimulations that the patient would wake up and/or forget the dream, preventing any potential incorporation in dream content. On the contrary, the weaker but persistent spiking activity would induce small changes in brain activity, and/or fragments of epilepsy-related symptoms, which would lead to their incorporation in dream content. In this sense we extend the findings of Speth & Speth (2016), who found increased motor dream imagery when conducting transcranial stimulations of the motor cortex, by suggesting all brain regions can be stimulated by weak currents and induce stimulus-related dream content.

While these findings are very interesting in the context of the formation of dream content, we hope to be able to confirm these findings with the full target populations as soon as possible.

## Dream recall and dream content during the mourning process

One of the questions that this thesis addressed was the association between dreaming and emotion regulation. As sleep is known to play a role in emotion regulation, and based on a large body of investigations, dreams have also been proposed to play this role, notably by incorporating the object of the regulation processes. We thus conducted a prospective, one-year long study of dreaming during the mourning process to confirm this association.

In Study 3, we evaluated the evolution of the mourning process across time, how dreams of the deceased differed from other dreams, and how these dreams coevolved with the mourning process. Such a large-scale and intensive study of both grief and dreams has never been conducted, bringing a large improvement of our knowledge about dreaming. We first confirmed the involvement of several risk factors in the course of the mourning process (age of the deceased, proximity with the deceased, neuroticism, expectation of the death). We showed that the number of dreams of the deceased decreased over time contrary to other dreams and followed the evolution of the grief intensity. This finding confirms that grief-specific dream content follows the grief state at wake, and furthermore that the intensity of emotional waking-life events predicts their incorporation in dreams. By contrast, we could not identify a significant correlation between dream emotional features (positive, negative, other emotions) and the grief intensity at wake as measured every 3 months with the ICG. This result would suggest a non-specific regulation process occurring during sleep, where the intensity of the



emotional memory influences only its incorporation rate rather than the intensity of the alteration of the memory during the dream. In other words, the emotional intensity of the memory would lead to an incorporation (or not), but the actual regulatory processes would not be visible in the dream emotions. Alternatively, more statistical power may have been needed to observe such an effect. We further identified differences in the emotions present in dreams of the deceased compared to other dreams, which we identified through both self-ratings (positive emotions, fear) and external ratings obtained by two scorers (happiness, sadness). The increased positive emotions (and specifically happiness) and sadness and the decreased fear in dreams of the deceased seems to translate the combined emotions of a happy reunion and the sad reminder of the loss. Importantly, this result suggests a combination between the negative theme of the death and the positive emotions originating from other memories, in a recombination of memories operated by the dream and proposed to contribute to emotion regulation processes (Levin & Nielsen, 2007). Furthermore, positive and negative emotions were not different in DD and in OD in participants reaching the threshold of pathological (complicated) grief at 14 months post-death but not in the NCG participants. We interpreted the positivation of dreams as a mechanism serving emotional regulation. It should be noted that the author is currently involved in an ongoing systematic evaluation of positive and negative emotions in dreams, which will allow to confirm the unique nature of the emotional balance in bereavement situations.

In short, the large collection of dreams gathered in this mourning population supports a dynamic contribution of this negative event to the formation of dream content, which would reflect the underlying emotion regulation processes. This study therefore brings an additional argument for the role of dreaming in emotion regulation. Furthermore, the number of dreams of the deceased significantly predicted the evolution of the mourning process, which suggests either that dreams participate to the emotional regulation of grief or that dreams are a good indicator of the mourning process. As a consequence, therapies using dreams may be especially helpful in bereaved participants, both to assess the evolution of the mourning process and to improve it if it is not evolving enough. By focusing on the proportion of dreams of the deceased compared to other dreams, a rapid evaluation of the grief intensity and its evolution seems possible. This prospective use of dreams will need further investigation to prove usefulness in clinical practice.

## Update of the comprehensive model of dream recall proposed by Vallat in 2017

In order to integrate the conclusions of this thesis in the existing literature about dreaming, we summarized our results in an extended version of the integrative model of dream recall proposed by Vallat (2017) that includes both our results regarding dream recall and regarding dream content (Figure 12).

The amount of dreams of the deceased in our study predicted the state of the mourning process, and their frequency was elevated all along the study (27% of all collected dreams). Continuity of dream content with the waking life has been evidenced numerous times, especially for emotional memories, it was thus expected that grief-related memories and thoughts would be incorporated into dream content. This result is especially coherent with the RAM model of sleep/dreaming, according to which emotional memories are preferentially tagged and processed during sleep and dreaming. Emotion regulation processes taking place during sleep would imply an expression or a modification of grief-related memories and thoughts (i.e. the target of the regulatory process) in the dream experience (Ruby 2021). As saliency of dreams has been suspected to increase dream recall, the emotion regulation processes at play during sleep and dreaming would then participate to the increased recall of the deceased-related dreams. Likewise, the epileptic activity during sleep may evoke seizure-like symptoms incorporated into dream content to maintain the sleep continuity, as has been observed for external stimuli just below the awakening intensity threshold (e.g., incorporation of the alarm clock in dreams).

We further refined the role of cognitive abilities in dream recall. Previous studies and our results support increased bottom-up and top-down attentional processes in HR compared to LR, associated with structural and functional brain differences. During sleep, top-down attention would draw the focus of the dreamer to the dream experience, and when waking up, this phenomenon would prevent other thoughts or stimuli to erase short-term memory or to interfere with the encoding process in long-term memory. This effect could also explain the influence of interest in dreams on the DRF, as motivation was shown to increase top-down attention related to the object of the motivation (Bourgeois et al., 2016). On the other hand, bottom-up attention contributes to the elevated brain reactivity of HR and therefore to increasing intra-sleep wakefulness, leading to increased opportunities to gain consciousness and encode in long-term memory the short-term memory of a dream (Vallat, Lajnef, et al., 2017). Elevated focus on salient dream content would also increase dream recall. By contrast, short-term auditory memory capacity during wake appears to have no or little relation with DRF. Previous hypotheses stated that a larger short-term memory would contribute to a better recall, which wasn't supported by experimental evidences. One hypothesis is that the ability to preserve dream memories when waking up (i.e. resisting to interfering thoughts/stimuli),

which is mediated by top-down attentional abilities, may be more important than the amount of information stored in short-term memory for dream recall. Previously reported differences in sleep inertia between LR and HR may also contribute to encoding and/or recall differences in DRF, by allowing HR to access their dream memories faster/better than LR. Further studies will be necessary to confirm these hypotheses.

As HR present higher bottom-up attentional abilities, they appear more sensitive to external stimuli during sleep, leading to increased intra-sleep wakefulness. We confirmed this effect in two epileptic populations, which both showed a higher-than-average DRF, and where subjectively rated nocturnal awakenings correlated with their DRF. As these studies are still ongoing, we could not confirm yet whether this effect was specifically associated with the number of long awakenings as shown in previous studies. However, long awakenings are more likely to be remembered (e.g., Winser et al., 2013), so future analyses with the complete dataset might confirm this observation.

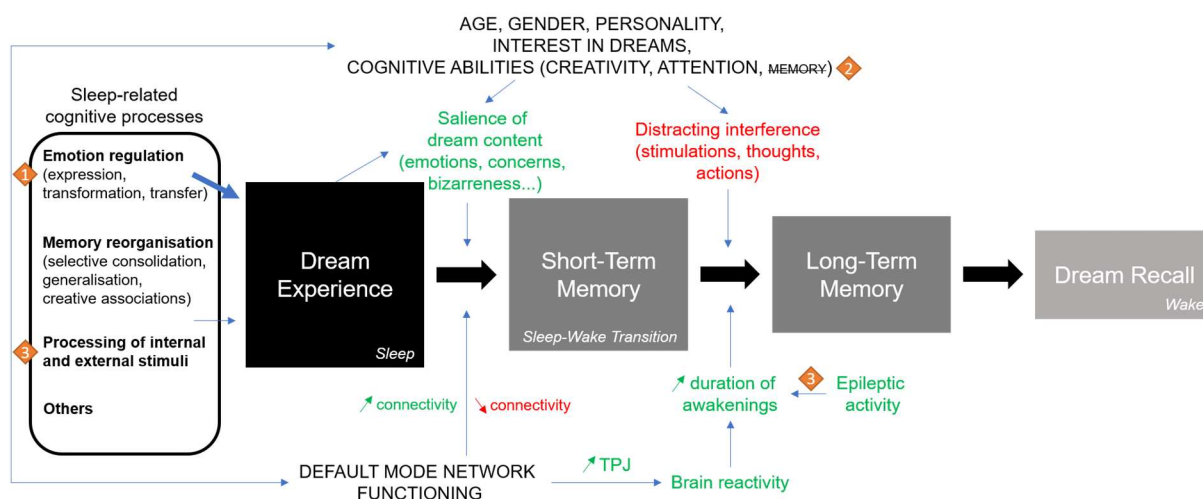


Figure 12 – An extended model of dreaming, based on the integrative model of dream recall of Vallat (2017). In green: factors reinforcing the dream recall/experience; in red: factors preventing dream recall. Orange diamonds indicate the study of the current thesis supporting an effect.

## General conclusion

The work conducted throughout this manuscript allowed us to address several remaining questions in the study of the functions, content, and recall of dreams. In an effort to improve our understanding of dreaming, we investigated healthy populations and patients with a neurological disease, in home and lab environments, with normal or mourning circumstances. We first investigated the role of several factors of DRF in healthy and epileptic populations. We disproved any role of auditory short-term memory in dream recall abilities whereas the role of attentional abilities was confirmed at the behavioral and neurophysiological levels in healthy populations. While preliminary, the investigation of epileptic patients revealed similar factors of DRF as in a healthy population (intra-sleep awakenings), and no signs so far of an alteration of short-term memory processes during sleep. The direct influence of epileptic activity on DRF remains to be confirmed but is promising based on the currently identified influence of epilepsy duration on DRF. On the other hand, our results show that dreams contain memories associated with concurrent brain activity and processes, such as emotion regulation processes and epileptic activity. Moreover, dream content appears to reflect the efficiency of these mechanisms. Based on the findings of the current thesis, and as a summary of our work, we proposed an update of the model of dream recall proposed by Vallat (2017) to include the factors of DRF and of dream content we studied (Figure 12). The conclusion of this thesis, which is a new page in the timeless book of dream research, contributes to a better understanding of dreaming. We earnestly hope that the insights gained from these studies will catalyze and inform future research endeavors, and someday, lead to illuminating findings in the grand field of dream research.

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