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# Sensory Disconnection and Dreaming:
## The Functional and Phenomenological Impact of Sensory Stimulation During Sleep

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&
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**By**
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*À Maëlle*

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# Abbreviations

| | |
|---|---|
| CD | Contentful Dream |
| CLMM | Cumulative Link Mixed Model |
| DLQ | Dream Lucidity Questionnaire |
| DMN | Default Mode Network |
| ECG | Electrocardiography |
| EEG | Electroencephalography |
| E/I | Excitation/Inhibition |
| EMG | Electromyography |
| EOG | Electrooculography |
| (e)KC | (Evoked) K-Complex |
| (f)MRI | (Functional) Magnetic Resonance Imaging |
| GLMM | General Linear Mixed Model |
| ICA(A) | Independent Component (Analysis) |
| IRASA | Irregularly Resampled Auto-Spectral Analysis |
| LD | Lucid Dream |
| LRLR | Left-Right-Left-Right |
| ND | No Dream |
| NREM | Non-Rapid Eye Movement |
| N1/2/3 | Non-Rapid Eye Movement 1/2/3 |
| PRISMA | Preferred Reporting Items for Systematic Reviews and Meta-Analyses |
| PGO | Ponto-Geniculo-Occipital |

| | |
|---|---|
| PSG | Polysomnography |
| REM | Rapid Eye Movement |
| SDDC | Stimulus-Dependent Dream Change |
| SSILD | Senses Initiated Lucid Dreaming |
| SVLD | Signal-Verified Lucid Dream |
| SWS | Slow-Wave Sleep |
| SWA | Slow-Wave Activity |
| TMR | Targeted Memory Reactivation |
| TLR | Targeted Lucidity Reactivation |
| tACS | Transcranial Alternating Current Stimulation |
| tDCS | Transcranial Direct Current Stimulation |
| TMS | Transcranial Magnetic Stimulation |
| WD | White Dream |
| ΔS | Stimulus-Dependent Aperiodic Slope Variation |

# **Abstract** (English)

Sleep is often perceived as a state of disconnection from the environment. Yet, accumulating evidence suggests that the brain can monitor and process external stimuli even while asleep. The accompanying subjective experiences, commonly referred to as dreams, are also thought to be influenced by sensory perceptions. However, the precise mechanisms through which sensory stimulation affects dreaming activity remain largely unknown.

This work seeks to address this gap through a comprehensive, multi-faceted approach. It begins with a systematic review of the existing literature on the influence of sensory stimulation on dreams, uncovering key findings and identifying current limitations in the field. Following this, an experimental study investigates the use of multimodal sensory stimulation to enhance dream lucidity during REM sleep, highlighting the potential of sensory-based protocols for facilitating real-time communication with dreamers and objectively exploring perceptual awareness during sleep. Finally, the relationship between multimodal stimulation during NREM sleep and EEG aperiodic activity is empirically explored, indicating that aperiodic spectral slopes may serve as informative markers of subjective sleep experiences.

By integrating theoretical, experimental, and analytical perspectives, this work aims to deepen the understanding of how external stimuli influence consciousness during sleep. The findings contribute to the growing body of knowledge on the dynamic interplay between the sleeping brain and sensory stimulation, offering valuable insights into how these interactions shape our dreams.

# **Abstract** (Italiano)

Il sonno è spesso percepito come uno stato di disconnessione dall'ambiente circostante. Tuttavia, un numero crescente di studi suggerisce che il cervello sia in grado di monitorare e processare stimoli esterni anche durante il sonno. Le esperienze coscienti che lo accompagnano, comunemente denominate sogni, sembrano anch'esse essere influenzate dalle percezioni sensoriali. Tuttavia, i meccanismi precisi attraverso i quali la stimolazione sensoriale influenza l'attività onirica rimangono in gran parte sconosciuti.

Questa tesi cerca di colmare tale lacuna attraverso un approccio comprensivo e diversificato. Si apre con una revisione sistematica della letteratura scientifica esistente sull'influenza della stimolazione sensoriale sui sogni, evidenziando le principali scoperte e identificando le attuali limitazioni nel campo. Successivamente, viene riportato uno studio sperimentale che indaga l'uso della stimolazione sensoriale multimodale per incrementare le possibilità di raggiungere stati di lucidità onirica durante il sonno REM. Tale studio dimostra il potenziale dei protocolli di induzione basati sui sensi per facilitare la comunicazione in tempo reale con i sognatori e per valutare oggettivamente la percezione sensoriale durante il sonno. Infine, si esplora empiricamente la relazione tra stimolazione multimodale durante il sonno NREM e l'attività aperiodica dell'EEG. I risultati suggeriscono che la variazione della pendenza dello spettro aperiodico in funzione della stimolazione sensoriale rappresenta un marcatore informativo delle esperienze soggettive durante il sonno.

Integrando prospettive teoriche, sperimentali e analitiche, questo lavoro mira ad approfondire la comprensione di come gli stimoli esterni influenzino la coscienza durante il sonno. Complessivamente, questa tesi apporta un sostanziale contributo alle attuali conoscenze sulla relazione tra il cervello dormiente e la stimolazione sensoriale, offrendo preziose intuizioni su come queste interazioni modellino i nostri sogni.

# **Abstract** (Nederlands)

Slaap wordt vaak gezien als een toestand van ontkoppeling van de omgeving. Toch suggereert toenemend bewijs dat de hersenen in staat blijven om externe stimuli te monitoren en te verwerken, zelfs tijdens de slaap. De bijbehorende subjectieve ervaringen, die gewoonlijk worden aangeduid als dromen, worden waarschijnlijk ook beïnvloed door zintuiglijke waarnemingen. De precieze mechanismen waarmee zintuiglijke stimulatie de droomactiviteit beïnvloedt, blijven echter grotendeels onbekend.

Dit werk tracht deze kennisklоof te dichten door middel van een uitgebreide, veelzijdige benadering. Het begint met een systematische review van de bestaande literatuur over de invloed van zintuiglijke stimulatie op dromen, waarbij belangrijke bevindingen worden onthuld en huidige beperkingen in het veld worden geïdentificeerd. Vervolgens wordt in een experimentele studie het gebruik van multimodale zintuiglijke stimulatie onderzocht om de helderheid van dromen tijdens de REM-slaap te vergroten. Deze studie benadrukt het potentieel van op zintuigen gebaseerde protocollen voor het faciliteren van real-time communicatie met dromers en het objectief verkennen van perceptueel bewustzijn tijdens de slaap. Ten slotte wordt de relatie tussen multimodale stimulatie tijdens de NREM-slaap en EEG-aperiodische activiteit empirisch onderzocht, wat aangeeft dat aperiodische spectrale hellingen informatieve markers kunnen zijn van subjectieve slaapervaringen.

Door theoretische, experimentele en analytische perspectieven te integreren, beoogt dit werk een dieper inzicht te geven in hoe externe stimuli het bewustzijn tijdens de slaap beïnvloeden. De bevindingen dragen bij aan de groeiende kennis over de dynamische interactie tussen het slapende brein en zintuiglijke stimulatie, en bieden waardevolle inzichten in hoe deze interacties onze dromen vormgeven.

# Chapter 1.
# General Introduction

Sleep is a ubiquitous phenomenon observed across the entire animal kingdom, signifying its fundamental importance despite the inherent vulnerability it imposes due to diminished behavioural reactivity (Cirelli & Tononi, 2008; Peigneux, Laureys, Delbeuck, et al., 2001). The critical nature of sleep is underscored by the myriad pathologies associated with its deprivation, which, in severe cases, can result in fatality (Cortelli et al., 1999; Irwin, 2015; Luyster et al., 2012). The necessity of sleep for maintaining health is unequivocal, although its multifaceted functions remain the subject of ongoing investigation. Decades of research have indicated that sleep facilitates energy restoration, supports immune function and metabolic clearance, and is crucial for emotional regulation, cognition, and brain plasticity (Hobson, 1990; Siegel, 2005; Zielinski et al., 2016).

Phenomenologically, sleep is often accompanied by subjective conscious experiences known as dreams (Siclari et al., 2013). The scientific study of dreams has evolved significantly since their initial psychodynamic conceptualization as a reflection of the subconscious mind (Freud, 1997), yet their precise role remains elusive. Some neuroscientists propose that dreams are epiphenomena of underlying brain activity, lacking specific adaptive value (Domhoff & Schneider, 2018; Flanagan, 1995; Hobson et al., 1998; Hobson & McCarley, 1977). Others argue that dreaming serves several functions, including memory and learning, emotional regulation, predictive processing, and threat and social simulation (Bucci & Grasso, 2017; Cartwright et al., 1998; Crick & Mitchison, 1983; Desseilles et al., 2011; Hoel, 2021; Llewellyn, 2015; Nielsen et al., 2004; Perogamvros et al., 2013; Revonsuo, 2000; Samson et al., 2023; Scarpelli et al., 2019; Tuominen et al., 2019; Valli & Revonsuo, 2009; Walker & van der Helm, 2009).

Regardless of the perspective, these conscious experiences offer valuable insight into the ongoing processes of the sleeping brain, representing a highly valuable resource for cognitive neuroscience (Malinowski & Horton, 2021; Wamsley, 2013). Although dreams have been somewhat sidelined within sleep research due to their inherent subjective and volatile nature, there is growing interest in understanding their essence, particularly how and why these conscious experiences arise during a state of apparent disconnection from the environment.

## 1.1. A Brief Historical Account of Sleep Research

Modern sleep research began nearly a century ago with Berger's pioneering recordings of brain electrical activity, which revealed clear differences between sleep and wakefulness (H. Berger, 1929). This breakthrough soon led to the electroencephalographic (EEG) characterization of a set of recurrent activity patterns observed during sleep (Loomis et al., 1935). Shortly after, the same group provided the first experimental evidence of sensory perturbations on sleep EEG, introducing the concepts of arousal and stimulus-dependent changes, including the appearance of large reactive slow-waves, which they termed K-complexes (Davis et al., 1939; Loomis et al., 1937).

A few years later, in 1953, Aserinsky and Kleitman described the occurrence of periods of increased ocular motility during sleep, marking the discovery of the rapid eye movement (REM) sleep stage (Aserinsky & Kleitman, 1953). The high dream recall frequency following awakenings from REM sleep led to the belief that dreaming was exclusively linked to this stage. Around the same time, Jouvet's work in cats played a significant role in further characterizing REM sleep, noting that it was accompanied by total muscle atonia (Jouvet et al., 1959, 1960). It was also confirmed that sleep stages alternate in cyclic patterns, revealing the ultradian nature of sleep (Hartmann, 1966), with each cycle lasting about 90 minutes and repeating four to six times per night (Colten et al., 2006; Nielsen, 2011).

The rapidly accumulating evidence in this burgeoning field necessitated the standardization of definitions and terminology for the various neurophysiological states that had been discovered, resulting in the creation of the first sleep staging manual (Kales & Rechtschaffen, 1968). Since then, technical advances have enabled finer characterization of the physiological correlates of each stage, particularly with the advent of polysomnography (PSG). By combining EEG, electrooculogram (EOG), electromyogram (EMG), and electrocardiogram (ECG) measurements, PSG has become the gold standard of sleep research. As a result, sleep scoring rules have progressively evolved to incorporate these advances, providing a comprehensive framework for studying sleep (e.g., Berry et al., 2017; Iber, 2007).

To set the stage for this dissertation, a brief overview of the current understanding of sleep architecture and its key concepts will be provided, with a focus on their relationship to environmental disconnection and subjective experiences. Following this, various approaches to the scientific study of sleep consciousness will be summarized, highlighting the challenges associated with its investigation. Finally, the rationale for selecting sensory stimulation as the method of exploration will be explained.

## 1.2. The Patterns of Sleep: Structure, Sensory Disconnection, and Associated Subjective Experiences

### 1.2.1. REM Sleep

REM sleep constitutes approximately 20% of total sleep time and is predominantly observed in the final third of the night, with its proportion increasing across successive sleep cycles (Carskadon & Dement, 1989; Dement & Kleitman, 1957). It is distinguished by low-amplitude, irregular, high-frequency brain activity, along with periods of marked rapid eye movement. The desynchronized EEG activity pattern of REM sleep closely resembles that observed during wakefulness yet occurs alongside muscular atonia. This earned REM

sleep the designation of 'paradoxical' sleep (Jouvet, 1965; Jouvet et al., 1959).

Other typical EEG features of REM sleep include the presence of theta activity (4-8 Hz) and the so-called 'sawtooth' waves (2-5 Hz; Bernardi et al., 2019; Colten et al., 2006). The latter have been hypothesized to be related to the occurrence of pontogeniculo-occipital (PGO)-like waves (Frauscher et al., 2020), identified in animal studies and correlating in humans with large bursts of activity from the pons to the lateral geniculate nucleus, occipital cortex, and other cortical and limbic regions (Arnulf, 2011; Callaway et al., 1987; Fernández-Mendoza et al., 2009; Gott et al., 2017; Peigneux, Laureys, Fuchs, et al., 2001).

Functional neuroimaging studies revealed that REM sleep is associated with higher metabolic activity in the anterior cingulate cortex, amygdala, parahippocampal gyrus, thalamic nuclei, dorsal midbrain, and pontine tegmentum, along with decreased activity in the dorsolateral prefrontal cortex, precuneus, and specific parietal and posterior cingulate regions (Braun, 1997; Maquet et al., 1996; Miyauchi et al., 2009; Peigneux, Laureys, Fuchs, et al., 2001).

Although signs of sensory processing are present during REM (Bastuji et al., 1995; Bastuji & García-Larrea, 1999; C. Chen et al., 2016; Nashida et al., 2000; Perrin et al., 1999, 2000, 2002; Ruby et al., 2013), arousal thresholds—defined as the propensity to exhibit signs of arousal or wake up in response to stimulation—remain relatively high during this stage (Bonnet et al., 2007; Bonnet & Moore, 1982; Busby et al., 1994; Rechtschaffen et al., 1966), further highlighting the paradoxical nature of this particularly active but disconnected state. This is also reflected in the subjective perception of sleep depth, which is highest during REM compared to all other stages (Stephan et al., 2021).

However, it is crucial to note that REM sleep is a quite heterogeneous stage that can be divided into phasic and tonic periods, depending on the presence or absence of phasic events, including eye movement bursts and muscular twitches (Corsi-Cabrera et al., 2008;

Simor et al., 2020; Wehrle et al., 2007). Tonic REM has been associated with higher alpha and beta power over frontocentral regions, while higher gamma and low-frequency oscillations are more prominent during phasic periods (Simor et al., 2016, 2019). Interestingly, arousal thresholds seem to vary depending on this, with reduced sensory-dependent responses and higher thresholds during phasic than tonic REM (Andrillon et al., 2017; Ermis et al., 2010; Price & Kremen, 1980; Sallinen et al., 1996; Takahara et al., 2002, 2006; Wehrle et al., 2007). Therefore, tonic and phasic periods are suggested to serve distinct functions within REM sleep, potentially representing online and offline states that correspond to external and internal attentional orientation, respectively (Simor, Bogdány, et al., 2021; Simor et al., 2020).

Regarding conscious experiences, early research on REM sleep highlighted that most awakenings from this stage result in dream reports (Dement & Kleitman, 1957). In fact, up to 80% of REM awakenings are accompanied by vivid dreams, often featuring bizarre, complex scenes with strong emotional and social content (Foulkes, 1962; Hobson et al., 2000; Martin et al., 2020; Nielsen, 2000). The presence of such immersive dreaming activity has been proposed to contribute to the limited sensory processing observed during REM sleep (Nir & Tononi, 2010). These rich internal conscious experiences likely compete with external stimuli, providing a plausible explanation for the high degree of sensory disconnection associated with this stage.

Although still debated, phasic activity and PGO-like waves have been suggested as contributors to the generation of oneiric hallucinatory content and as modulators of behavioural responsiveness and cortical processing of external stimuli during REM sleep (Andrillon & Kouider, 2020; Ermis et al., 2010; J.-X. Gao et al., 2023; Hobson, 2009a; Hong et al., 1997; Miyauchi et al., 2009). Additionally, bursts of phasic eye movements during REM have been shown to correspond—at least partially—to gaze orientation within dream experiences, supporting the 'scanning hypothesis' (Arnulf, 2011). Notably, the parallel between dreaming activity and bodily movements is also observed in patients

who physically enact their dreams due to failures in the typical REM-associated muscular inhibition (Arnulf, 2012).

The functions attributed to REM sleep and dreams include roles in procedural and associative memory (Konkoly et al., 2023; Rasch & Born, 2013), abstraction and generalization of previously learned concepts (Pereira et al., 2023; Sterpenich et al., 2014), emotional processing (Desseilles et al., 2011; Sterpenich et al., 2009), prospective coding (Hobson et al., 2014; Llewellyn, 2015), and social and threat simulation (Revonsuo, 2000; Valli et al., 2005; Valli & Revonsuo, 2009; Zadra et al., 2006). These functions are well-aligned with the underlying brain activation patterns observed during REM sleep, particularly the activation of limbic structures and the deactivation of the prefrontal cortex (Scarpelli et al., 2015). Moreover, the complex associative content and the strong emotional and social nature of dream activity during REM sleep reflect and potentially support these proposed functions.

### 1.2.2. NREM Sleep

Non-REM (NREM) sleep is characterized by slower brain activity and increased neural synchrony relative to wakefulness and REM sleep (Carskadon & Dement, 1989). Neuroimaging studies show that NREM sleep is accompanied by a decrease in metabolic activity across wide cortical regions, including the frontal, parietal, temporal, and occipital visual and associative areas, as well as thalamic regions (Braun, 1997; Nofzinger et al., 2002). In contrast, relative increases in metabolic activity have been observed in the dorsal pontine tegmentum, basal forebrain, hypothalamus, ventral striatum, anterior and posterior cingulate cortex, precuneus, insula, primary somatosensory and motor cortices, as well as in the amygdala, hippocampal, and parahippocampal areas (Maquet, 2010; Nofzinger et al., 2002).

Based on PSG measurements, NREM sleep was initially classified into four stages by Rechtschaffen and Kales (1968), each characterized by progressively slower and more ample EEG patterns, along with lower arousal and higher subjective sleep depth (Bonnet et

al., 2007; Bonnet & Moore, 1982; Busby et al., 1994; Stephan et al., 2021). More recently, the two deepest stages were merged into a single stage, now referred to as N3 (Iber, 2007). This progression in sleep depth is accompanied by a reduction in signal complexity (Bandt, 2017; Burioka et al., 2005; González et al., 2022; Nicolaou & Georgiou, 2011; Schartner et al., 2017) and decreased functional connectivity between large-scale resting-state networks (Kung et al., 2019; Tagliazucchi, von Wegner, Morzelewski, Brodbeck, Borisov, et al., 2013; Tagliazucchi, von Wegner, Morzelewski, Brodbeck, Jahnke, et al., 2013; Tarun et al., 2021). These changes parallel the gradual loss of consciousness observed across NREM stages, aligning with the information integration theory, which posits that a system's capacity to integrate information determines its potential to support conscious subjective experiences (Kung et al., 2019; Nemirovsky et al., 2023; Tononi, 2004; Tononi et al., 2016).

#### 1.2.2.1. N1

Stage N1 (or NREM 1) is often considered a transitional state from wakefulness to sleep. Often relatively short in duration, this period is marked by a progressive decrease in EEG amplitude and frequency, shifting from alpha dominance (8-12 Hz) to slower theta (4-8 Hz) waves, with patterns of slow rolling eye movements (Dauvilliers & Billiard, 2004; Dement & Kleitman, 1957). During this phase, subjects often report having hallucinatory-like perceptual experiences, often including visual imagery, called 'hypnagogia' (Foulkes & Vogel, 1965).

Hypnagogic episodes are characterized by the original association of seemingly unrelated concepts, during which individuals are still somehow able to process and even respond to environmental stimuli (see Ghibellini & Meier, 2023 for a review). In fact, N1 has been described as a state of heightened creativity and problem-solving (Lacaux et al., 2021), which can be modulated by the presentation of sensory cues (Haar Horowitz et al., 2018, 2020, 2023).

#### 1.2.2.2. N2

N2 (or NREM 2) is the most prominent sleep stage, accounting for about half of total sleep time (Carskadon & Dement, 1989). It is

characterized by a background of low-amplitude mixed frequencies with a gradual increase in slow-wave activity (SWA; 0.5-4 Hz), overlaid with the hallmarks of this stage: sleep spindles and K-complexes (Bernardi et al., 2017; Colrain, 2005; Davis et al., 1939). Sleep spindles are fast bursts of waxing and waning waves oscillating in the sigma frequency range (12-16 Hz), reflecting thalamocortical interactions. They play a crucial role in synaptic plasticity, learning, and memory, and their presence has been linked to greater resilience against external sensory perturbations (Antony et al., 2019; Buzsáki, 1998; Cairney et al., 2018; Dang-Vu et al., 2011; Fernandez & Lüthi, 2019; Ulrich, 2016). K-complexes, on the other hand, are large, sharp slow waves (< 2 Hz) that occur either spontaneously or in response to external stimuli (Bernardi et al., 2017; Davis et al., 1939; Halász, 2005; Steriade & Amzica, 1998). They are thought to serve a dual function of environmental monitoring and sleep protection, as they represent reactive events while sharing the same physiological generation mechanism as sleep slow waves (Andrillon & Kouider, 2020; Czisch et al., 2002, 2009; Jahnke et al., 2012).

The presence of physiological markers associated with sensory stimulation during N2 sleep suggests that the brain continues to process external information in this stage. The nature of the stimuli plays a critical role in shaping the brain's response, with novel and salient information triggering specific activation patterns (Ameen et al., 2022; Bastuji & García-Larrea, 1999; Ibáñez et al., 2006; Moyne et al., 2022; Perrin et al., 1999, 2000, 2002; Portas et al., 2000; Ruby et al., 2008; Strauss et al., 2015). Furthermore, complex task-relevant EEG responses have been observed even in the absence of conscious awareness (Andrillon et al., 2016; Kouider et al., 2014; Legendre et al., 2019), indicating that higher-order cognitive and sensory processing mechanisms remain active during this stage. Recent studies suggest that fluctuations in these EEG responses may also translate to overt behavioural reactions, even without conscious appraisal or sleep disruption (Türker et al., 2023).

Regarding dreams, reported rates vary significantly across studies, although it is generally accepted that subjective experiences are relatively frequent during N2 sleep, with about half of awakenings resulting in conscious recall (Nielsen et al., 2001; Siclari et al., 2013). The content of these N2 reports tends to be shorter and more thought-like rather than perceptual, often incorporating a higher proportion of episodic memory fragments compared to REM dreams (Baylor & Cavallero, 2001; Siclari et al., 2013; Stickgold et al., 1994). Notably, NREM stages, including N2, have been consistently associated with memory processing, largely due to hippocampal neural replay events thought to be crucial for memory consolidation (Wamsley & Stickgold, 2011). These replay events have been proposed as potential mechanisms for the incorporation of memories into ongoing dream experiences (Picard-Deland et al., 2023; Wamsley, Perry, et al., 2010; Wamsley, Tucker, et al., 2010).

#### 1.2.2.3. N3

N3 (or NREM 3), also sometimes referred to as slow-wave sleep (SWS) or deep sleep, represents the most globally synchronized state (Guo et al., 2022; Steriade, 1993). This stage is most prevalent during the early sleep cycles and gradually diminishes as the night progresses, becoming less frequent or even absent in the later hours of sleep (Dement & Kleitman, 1957; Iber, 2007). During N3, the EEG is dominated by high-amplitude delta activity (0.5 - 4 Hz), with increased SWA, particularly in frontal regions (Bernardi et al., 2017; Dijk, 2009; Finelli et al., 2001). This reflects a generalized state of neuronal bistability, where cortical neurons oscillate spontaneously between active (up-state) and silent (down-state) periods (Steriade, 2003; Steriade et al., 2001).

Down-states are believed to impair information integration, a process essential for both consciousness and the effective processing of external stimuli (Andrillon et al., 2016; Massimini et al., 2005; Pigorini et al., 2015; Schabus et al., 2012). Hence, neuronal bistability acts as a cortical gating mechanism, restricting sensory processing and leading to higher arousal thresholds and deeper sleep (Andrillon et al., 2016).

These low levels of information integration may help explain why dream reports are infrequent upon awakening from N3, with only 20% of awakenings yielding a dream report (Siclari et al., 2013). The low dream recall frequency associated with this stage might be further compounded by the negative effects of increased sleep inertia on recall abilities (Hobson, 2009a).

Functionally, N3 sleep has been associated with learning, cerebral restoration, and recovery functions, with its characteristic SWA representing a main marker of sleep pressure (Born, 2010; Dijk, 2009; Tamaki et al., 2013; Walker, 2009; Girardeau & Lopes-dos-Santos, 2021). The synaptic homeostasis hypothesis provides an explanatory framework, postulating that sleep facilitates the downscaling of synaptic strength (Cirelli & Tononi, 2008). According to this hypothesis, SWA drives the downregulation of previously strengthened synaptic connections, ultimately supporting memory consolidation by enhancing the signal-to-noise ratio between significant learning-related neural activations and irrelevant ones. Additionally, SWA is believed to play a crucial role in information transfer from the hippocampus to the cortex, indicating memory consolidation processes beyond synaptic weakening mechanisms (Fujisawa & Buzsáki, 2011).

### 1.2.3. REM-NREM Alternation

The ultradian sleep process determines the cyclic alternation of REM and NREM stages throughout sleep (Hobson & Pace-Schott, 2002). Ultradian cycles were originally thought to be driven by the reciprocal interaction between a REM-on cholinergic system, located in the pontine reticular formation, and a REM-off monoaminergic system, mainly distributed over the locus coeruleus and dorsal raphe nuclei (Hobson, 1992; Hobson & Pace-Schott, 2002; Le Bon, 2020; McCarley & Hobson, 1975; Merica & Fortune, 2004). Since, evidence for a GABAergic REM-suppressing system has extended and updated this view (S.-H. Park & Weber, 2020; Weber et al., 2018), indicating the occurrence of a complex interaction among excitatory, inhibitory, and autoregulatory circuits involving a large panel of neurotransmitters,

including GABA, glutamate, dopamine, orexin, and histamine (Hobson & Pace-Schott, 2002; Le Bon, 2020; S.-H. Park & Weber, 2020).

The structure of ultradian cycles fluctuates throughout the night, with early cycles characterized by deeper and longer NREM stages and later cycles featuring lighter sleep with a higher prevalence of REM stages (Feinberg & Floyd, 1979; Hartmann, 1968; Le Bon et al., 2001, 2002). REM dreams are generally more frequent, longer, more vivid, complex, perceptual, bizarre, and emotional than those during NREM (R. Fosse et al., 2004; Foulkes, 1962; Kales et al., 1967; Martin et al., 2020; Nielsen, 2010; Wamsley et al., 2007). However, evidence suggests that stage-dependent differences in dream recall, length, and complexity diminish across cycles, with NREM and REM reports becoming increasingly similar as the night progresses (Antrobus et al., 1995; Chellappa et al., 2011; Chellappa & Cajochen, 2013; Cicogna et al., 1998; R. Fosse et al., 2004; Malinowski & Horton, 2014c; Montangero & Cavallero, 2015; Nielsen, 2011; Wamsley et al., 2007). Interestingly, within cycles, dream recall appears to follow opposite U-shaped patterns: for NREM sleep, increased recall occurs at the beginning and end of the stage, while in REM sleep, higher content recall is noted in the middle parts of the stage (Hobson et al., 2000; Nielsen, 2010; Stickgold, 2001).

Although the roles of REM and NREM sleep have traditionally been evaluated separately, their recurrent alternation suggests that the typical NREM-REM sequentiality may have an inherent functional significance. It is proposed that NREM sleep primarily processes previously encoded memories, while the subsequent REM sleep stage facilitates their integration and generalization into existing memory networks (Ficca et al., 2000; Giuditta, 2014; Pereira & Lewis, 2020; Satchell et al., 2024). This sequential hypothesis aligns well with the observed changes in dream content throughout the night, where early dreams tend to be more closely related to wake-like and episodic memories, while later dreams become increasingly emotional and associative (Malinowski & Horton, 2021).

### 1.2.4. Sleep-Wake Regulation

At a larger scale, the alternation between stable periods of sleep and wakefulness is governed by a 'flip-flop' switch, orchestrated by the hypothalamus (Saper et al., 2005, 2010). This switch operates through a mutually inhibitory circuit that balances wake-promoting structures, primarily driven by the reticular activating system (Moruzzi & Magoun, 1949), against sleep-promoting structures, with the ventrolateral preoptic nucleus playing a central role (Saper et al., 2005). The flip-flop switch enables rapid transitions between wakefulness and sleep, modulated by several interrelated mechanisms.

The most widely accepted model of sleep regulation is the two-process system (Borbély, 2066, 2022; Borbély & Achermann, 1999). This model involves the homeostatic process 'S,' which represents the accumulation of sleep pressure during wakefulness, and the circadian process 'C,' which regulates daily fluctuations in physiological activation. Sleep pressure, reflected by an increase in SWA, dissipates as sleep progresses. High sleep pressure is associated with higher subjective sleepiness and changes in brain activity including increases in delta and theta power and decreases in alpha activity during wakefulness (De Gennaro et al., 2007; Finelli et al., 2000, 2001; Snipes et al., 2023), along with increased slow-wave density, amplitude, and steepness during subsequent sleep (Achermann et al., 1993; Beersma, 1998; Bersagliere & Achermann, 2010; Borbély & Achermann, 1999; Riedner et al., 2007). Homeostatic sleep pressure also influences the ultradian sleep cycle, affecting the proportions of NREM and REM sleep within each cycle, particularly following sleep deprivation (Beersma et al., 1990; Borbély et al., 1981; Dijk & Beersma, 1989; Endo et al., 1998). High sleep pressure tends to extend NREM sleep duration in the first cycle, while lower sleep pressure is associated with longer REM phases (Cajochen et al., 2024).

The circadian process 'C' is driven by the central circadian clock in the suprachiasmatic nucleus of the hypothalamus, which is synchronized by external light. The suprachiasmatic nucleus, along

with peripheral pacemakers, regulates various physiological processes, including hormonal cycles, blood pressure, and body temperature (Borbély et al., 2016; Mohawk et al., 2012; Richards & Gumz, 2012). While no definitive EEG marker of circadian drive has been established, spindle frequency appears to follow the timing of the 'C' process, with higher spindle frequencies observed in early and late-night cycles, as well as during daytime naps (Bódizs et al., 2022, 2024).

Interestingly, circadian influences have been posited as a candidate for the modulation of dream activity during sleep, promoting - along with ultradian mechanisms - the required levels of cortical activation for the emergence of consciousness. This is supported by studies showing that stage-dependent differences in dream content and length tend to dissipate across the night, with NREM and REM reports becoming highly comparable in moments of stronger circadian wake drive, namely during early morning and day naps (Antrobus et al., 1995; Chellappa et al., 2009; Chellappa & Cajochen, 2013; Cicogna et al., 1998; R. Fosse et al., 2004; Malinowski & Horton, 2021; Montangero & Cavallero, 2015; Nielsen, 2011; Wamsley et al., 2007).

Recently, processes S and C have been reinterpreted as representing two distinct forms of homeostasis. Process S is thought to involve reactive homeostasis, encompassing the restorative functions of sleep for metabolism, immunity, and cognition. This is aligned with the prevalence of slow-wave NREM sleep during the first part of the night, which is often accompanied by thought-like conscious experiences that tend to contain episodic and autobiographical memories (Baylor & Cavallero, 2001; Cavallero et al., 1990; Nielsen & Stenstrom, 2005; Simor et al., 2023). In contrast, process C would reflect predictive homeostasis, which prepares the brain for subsequent waking periods during the later hours of sleep. This process is associated with a relative increase in REM sleep and intense embodied dreaming featuring complex and associative content, namely including future-oriented elements (Simor et al., 2023; Wamsley, 2013).

Beyond the two-process mechanism, sleep regulation is also influenced by allostatic load, which refers to the body's adaptive response to stress (McEwen, 2000, 2006; Saper et al., 2005). High levels of allostatic load can disrupt sleep homeostasis, leading to various sleep disturbances (Juster & McEwen, 2015; Radwan et al., 2021) that, in turn, affect subjective experiences during sleep (Nofzinger et al., 2004; Werner et al., 2016). A notable example of this is the detrimental effect of the COVID-19 pandemic on sleep and dreaming activity, illustrating how environmental stressors can alter these patterns across the general population (Conte et al., 2022; Gorgoni et al., 2022; Jahrami et al., 2021; Scarpelli, Nadorff, et al., 2022; Simor, Polner, et al., 2021).

In summary, sleep is a complex process shaped by multiple interdependent factors, resulting in a highly variable and dynamic state, both physiologically and phenomenologically. The interaction of these factors directly influences vigilance and sleepiness during wakefulness (Ruby et al., 2024), as well as consciousness and arousability during sleep (Achermann et al., 1995; Akerstedt & Folkard, 1996; Borbély & Achermann, 1992; Cajochen et al., 2014), contributing to significant variations in subjective experiences throughout the sleep-wake cycle. However, emerging evidence suggests that these processes may be more nuanced than previously thought, often involving localized rather than system-wide modulations, offering a more detailed understanding of how sleep is regulated.

### 1.2.5. Local Sleep Regulation

Sleep has traditionally been regarded as a generalised state, viewed in contrast to wakefulness (Avvenuti & Bernardi, 2022; Nobili et al., 2012; Siclari & Tononi, 2017). However, sleep hallmarks such as slow waves and spindles appear to be temporally and topographically heterogeneous, with regional differences suggested to reflect intrinsic variations in vulnerability to sleep pressure, wakefulness-dependent use, or a combination of both (Bastuji et al., 2020; Bernardi et al., 2017; Huber et al., 2004, 2006; Jang et al., 2022; Kattler et al., 1994; Krueger & Obäl Jr., 1993; Murphy et al., 2011; Nir et al., 2011; Nobili et al., 2011).

Research has shown that changes in SWA following sleep deprivation are not uniformly distributed across the scalp: they increase most significantly in frontal regions, with minimal changes in posterior areas (De Gennaro et al., 2001; Finelli et al., 2001). Moreover, studies have demonstrated that brain regions heavily used during wakefulness—such as those involved in tasks requiring extensive practice—exhibit increased SWA during subsequent sleep, while other regions show no significant changes in activity (Huber et al., 2004; Hung et al., 2013; Murphy et al., 2011). This experience-dependent fatigue is also linked to the emergence of local sleep-like slow waves during wakefulness, which are thought to reflect neuronal sleep need. Notably, the presence of these waves correlates with task-related behavioural errors and attentional lapses (Andrillon et al., 2021; Andrillon & Oudiette, 2023; Avvenuti et al., 2021; Avvenuti & Bernardi, 2022; Bernardi et al., 2015; Hung et al., 2013; Van Dongen et al., 2011).

These observations suggest that sleep and wakefulness are not merely opposing states but can coexist simultaneously. Interestingly, intrusions of sleep-like activity during wakefulness, and vice versa, have been linked to the nature of concurrent subjective experiences (Siclari & Tononi, 2017). For instance, periods of mind-wandering or mind-blanking have been associated with sleep-like brain activity during wakefulness, resulting in decreased behavioural performance (Andrillon et al., 2019; Jubera-Garcia et al., 2021; Poh et al., 2016). Conversely, wake-like activity during sleep has been linked to dreaming (Siclari et al., 2017), and is believed to contribute to parasomnias, including sleepwalking, confusional arousals, and sleep terrors (Andrillon & Oudiette, 2023; Castelnovo et al., 2016, 2018; Cataldi et al., 2024; Idir et al., 2022; Stephan et al., 2021; Terzaghi et al., 2009, 2012).

Thus, sleep and wakefulness appear to be locally regulated, with specific patterns of brain activity directly impacting behavioural responsiveness, arousal thresholds, and sensory disconnection (Andrillon et al., 2016; Kouider et al., 2014; Legendre et al., 2019; Tamaki et al., 2016; Türker et al., 2023), while also influencing

subjective experiences (Mainieri et al., 2021; Ruby et al., 2024; Siclari et al., 2017; Stephan et al., 2021; Uguccioni et al., 2013). Consequently, sleep may be regarded as a naturally fluctuating state with 'fluid boundaries' (Sarasso et al., 2014) existing on a continuum from highly synchronized to highly heterogeneous brain activity, the specificities of which define the nature of the accompanying conscious experiences.

## 1.3. Studying Sleep Consciousness

### 1.3.1. Defining Dreams

The varied terminology used to refer to sleep conscious experiences and the numerous attempts to characterise dreams across the literature highlight the complexity of this task (Nielsen, 2000; Pagel et al., 2001). Although these differences might seem trivial, they have significantly impacted dream research, as recall rates and reported content are heavily influenced by the chosen definition. Some researchers consider dreams as the highly perceptual, emotional, and often bizarre immersive experiences typically associated with REM sleep (Domhoff, 2022; Hobson et al., 2000; Hobson & Stickgold, 1994; Windt, 2020), contrasting with the less vivid, more thought-like subjective experiences reported during NREM sleep (Foulkes, 1962; Hobson & Stickgold, 1994). However, this dissertation adopts a more inclusive view: dreams are understood to encompass all types of conscious experience during sleep, from simple thoughts and static images to complex, movie-like scenarios (Nir & Tononi, 2010; Siclari et al., 2013, 2017; Wong et al., 2020).

The diverse nature of dreams has led to the development of various models to explain their origin. The initial 'REM-dream isomorphism' view, which equated dreaming with REM sleep, was challenged by evidence that dreaming can also occur without REM sleep (Oudiette et al., 2012; Solms, 2000; Suzuki et al., 2004). This led to the proposal of new dream generation mechanisms. The 'two-generator' model posited that REM and NREM dreaming arise from distinct, stage-specific processes (Hobson et al., 2000; Hobson &

McCarley, 1977). In contrast, 'one-generator' models suggested that dreaming relies on a single underlying mechanism, with qualitative differences depending on stage-dependent levels of cognitive and memory access (Antrobus, 1983, 2000; Foulkes, 1985; Koulack & Goodenough, 1976). Over time, several variations and reinterpretations of these models have emerged, including the 'covert-REM' model (Nielsen, 2000), the 'Activation-Input-Modulation' model (Hobson, 2009b; Hobson et al., 2000), and the 'dual rhythm model' (Wamsley et al., 2007), among others.

Despite these efforts, the specific mechanisms underlying the emergence of dreams remain largely unknown, mirroring the broader mystery of consciousness itself (Chalmers, 1997; Nagel, 1974). The debate over stage-dependent differences between REM and NREM conscious experiences continues, yet there is growing consensus that dreaming is shaped by local neural activity patterns rather than being solely determined by the global state of sleep or arousal (Andrillon & Oudiette, 2023; Desseilles et al., 2011; Fazekas & Nemeth, 2018). Recent advances in neuroscience and increasingly sophisticated methodologies have rekindled interest in understanding the neural underpinnings of dreaming, progressively bridging the gap between the neurophysiological and phenomenological aspects of sleep.

#### 1.3.1.1. The Neural Correlates of Dreaming

The neural correlates of dreaming have been explored from various perspectives, with research converging on a set of common substrates, particularly the medial prefrontal cortex and the temporo-parieto-occipital regions. Early insights into the brain regions involved in dreaming, beyond those related to REM sleep (Braun, 1997; Dang-Vu et al., 2010; Desseilles et al., 2011; Maquet et al., 1996, 2005), stemmed from clinical observations. These studies found that specific localized brain injuries, especially in the temporal posterior areas and ventromedial frontal regions, were associated with the alteration or cessation of dreaming activity (Bischof & Bassetti, 2004; Cathala et al., 1983; Murri et al., 1984; Solms, 1997, 2000).

Other researchers have placed dreaming along a continuum with mind-wandering—those moments of waking spontaneous thought during which attention is internally oriented, also known as daydreaming (Christoff et al., 2016; Domhoff, 2011; Domhoff & Fox, 2015; Fox et al., 2013). This conceptualization underscores the significant involvement of the default-mode network (DMN) during periods of mind-wandering and, to an even greater extent, during REM sleep, proposing the DMN as the neural substrate for internally generated conscious experiences (Chow et al., 2013; Domhoff, 2019). Moreover, the DMN has also been shown to maintain its functional connectivity during NREM sleep, though it progressively disintegrates in deeper stages (Horovitz et al., 2007; Larson-Prior et al., 2009; Sämann et al., 2011). Key DMN hubs, including the medial prefrontal cortex, precuneus, temporo-parietal junction, and posterior cingulate cortex, have been linked to spontaneous thoughts about the present and future self (Andrews-Hanna et al., 2010; Domhoff & Fox, 2015). However, this viewpoint tends to narrow the concept of dreams to the most vivid and immersive forms of sleep mentation—those "*enhanced forms of spontaneous thought that can be characterized as an 'embodied simulation'*" (Domhoff, 2019), contrasting with the broader definition of dreaming embraced by much of the dream research community and adopted in the present work.

While the previously mentioned accounts relied on retrospective and indirect associations, the advent of neuroimaging techniques, including high-density EEG and functional magnetic resonance imaging (fMRI), has enabled more empirical approaches to characterizing the neural correlates of dreaming. Some researchers have tried to elucidate trait-like characteristics relating to individual dream recall frequency, showing that high dream recallers present higher intra-sleep wakefulness and increased brain reactivity to external stimulation, both during wakefulness and sleep, compared to low recallers (Eichenlaub, Bertrand, et al., 2014; Moyne et al., 2022; Ruby et al., 2022; Vallat, Lajnef, et al., 2017; van Wyk et al., 2019). Good dream recallers also present higher white-matter density in the medial

prefrontal cortex, increased resting state regional cerebral blood flow over the temporo-parietal junction and prefrontal cortex during sleep, and greater DMN connectivity upon awakening relative to low recallers (Eichenlaub, Nicolas, et al., 2014; Vallat et al., 2018, 2020).

Another area of research investigates the relationship between EEG pattern variations occurring just before awakening and the conscious experiences reported immediately afterward. REM dream recall has been associated with specific changes in EEG activity, including decreases in delta and increases in theta oscillations in frontal areas, as well as alterations in alpha and beta activity (Chellappa et al., 2011; Esposito et al., 2004; Marzano et al., 2011; Ruby, 2020; Scarpelli, Bartolacci, et al., 2020; Scarpelli et al., 2015; Siclari et al., 2017; Takeuchi et al., 2003). During NREM sleep, dreaming has also been linked to higher levels of brain activation, evidenced by reduced low-frequency activity and increased high-frequency activity, particularly in parieto-occipital regions (Chellappa et al., 2011, 2012; D'Atri et al., 2019; Esposito et al., 2004; Scarpelli, D'Atri, et al., 2020; Scarpelli et al., 2017; Siclari et al., 2017, 2018; Takeuchi et al., 2003; Williamson et al., 1986; J. Zhang & Wamsley, 2019).

While the literature lacks complete consistency, some common patterns have emerged in recent years. Notably, increased high-frequency activity and/or decreased SWA seem to differentiate conscious from unconscious experiences in both NREM and REM sleep. Recent work has highlighted the significance of brain activity changes in a specific 'posterior cortical hot zone'—encompassing low- and high-level sensory areas, the precuneus, posterior cingulate, and retrosplenial cortex—in distinguishing between dream experiences and periods without dreams (Siclari et al., 2017). Instead, the recall of dream content appears to be associated with heightened high-frequency activity in medial and lateral frontoparietal areas compared to cases of no recall (Siclari et al., 2017).

Brain activity patterns also seem to reflect qualitative differences in dream content. During REM sleep, thought-like content correlates with high-frequency activity in frontal regions, while

perceptual content is linked to high-frequency activity in parieto-occipital regions (Siclari et al., 2017). Moreover, the incorporation of recent waking life experiences into dreams is associated with increased frontal theta activity during REM (Eichenlaub et al., 2018). Furthermore, structural variations in the amygdala, medial prefrontal cortex, and hippocampus have been related to qualitative differences regarding the length, bizarreness, vividness, and emotional tone of individual dream reports (De Gennaro et al., 2011, 2016).

Interestingly, functional neuroimaging studies have demonstrated the potential for decoding dream content, with visual dream perceptions predicted from neural activity based on previous wake-like measurements or deep neural network-driven feature-level representations (Horikawa et al., 2013; Horikawa & Kamitani, 2017). Waking and sleeping EEG activity related to specific subjective content have also been shown to overlap, with observations of increased activity in the fusiform face area when dreaming about faces, in the Wernicke area for speech-related dreams (Siclari et al., 2017), and increased frontal alpha asymmetry linked to higher levels of dream anger (Sikka et al., 2019).

#### 1.3.1.2. The Special Case of Lucid Dreaming

Among the various types of dream experiences, one stands out for its significance in the scientific study of sleep consciousness and its relevance to this dissertation: lucid dreams (LDs). Dream lucidity is defined as a state of awareness about the dreaming state, in contrast to the typical obliviousness of oneiric experiences (Baird, Mota-Rolim, et al., 2019). This awareness indicates the presence of logical, reflective, and higher-order metacognitive abilities that usually fade away during REM sleep—the stage where most lucid experiences occur (Baird, Mota-Rolim, et al., 2019; Filevich et al., 2015; Kahan & LaBerge, 1994).

This enhanced cognitive appraisal of the ongoing conscious state has been associated with the unusual activation of the precuneus, frontopolar, and dorsolateral prefrontal cortex during lucid dreaming, regions that are otherwise relatively deactivated during REM sleep

(Dresler et al., 2012). Moreover, the cuneus, precuneus, and temporo-parieto-occipital regions appear to be even more active during lucid than non-lucid REM sleep, potentially reflecting the higher vividness and perceptual intensification of lucid compared to non-lucid dreams (Dodet et al., 2015; Dresler et al., 2012). Frequent lucid dreamers also present increased resting-state functional connectivity between frontopolar and temporo-parietal areas (Baird et al., 2018).

Scalp EEG studies showed that lucidity is associated with increases in frontal gamma and parietal beta power and decreased delta activity compared to non-lucid REM (Baird, Mota-Rolim, et al., 2019; Dodet et al., 2015; Holzinger et al., 2006; Voss et al., 2009). These observations have led some to suggest that lucid dreaming represents a transitional state combining wake-like and sleep-like features (Hobson, 2009b; Voss et al., 2009), while others defend that lucidity is a particularly active form of REM sleep (Baird et al., 2022; Dodet et al., 2015).

Phenomenologically, LDs are also characterized by the ability to access waking memories and exert volitional control over certain aspects of the dream (Dresler et al., 2014; Erlacher, 2009; Mallett, 2020; Voss et al., 2013). These features enable the execution of predefined tasks while dreaming, making lucidity particularly valuable for the neurocognitive study of sleep consciousness. In fact, lucid dreamers can signal their awareness by performing actions that translate into measurable behaviours, such as specific eye movements or changes in respiration patterns. This ability provides an objective temporal marker for the onset of lucidity and dream control, as well as a means of communication between the dreamer and the external world (Konkoly et al., 2021; LaBerge et al., 1981; Oudiette et al., 2018). Moreover, lucid control over the dream allows for measuring the neural correlates of specific dreamed actions, with evidence suggesting significant overlap between the brain areas activated during these dreamt actions and those engaged in similar behaviours while awake (Dresler et al., 2011; Erlacher et al., 2003; Erlacher & Schredl, 2008).

These attributes can also be leveraged in more applied research, particularly within the clinical field. Indeed, lucid dreaming shows promise as a treatment for insomnia, nightmare disorders, and related symptoms (de Macêdo et al., 2019; Ellis et al., 2021a; Ouchene et al., 2023; Spoormaker & van den Bout, 2006). Additionally, lucidity may be harnessed in motor and sports sciences, as studies suggest that practicing specific movements during LDs may lead to improvements in wakeful performance (Erlacher & Schredl, 2010; Schädlich & Erlacher, 2018). Given its considerable potential and relatively rare spontaneous occurrence (Saunders et al., 2016), various lucid dream induction techniques have been developed over the years. These methods range from cognitive training and sensory stimulation to brain stimulation and pharmacological interventions, though success rates vary widely, indicating substantial room for improvement (Oldoni et al., 2024; Stumbrys et al., 2012; Tan & Fan, 2023).

### 1.3.2. Methods for Studying Dreams

Since dreams are not directly observable, their study relies on the recollection and reporting of dream memories, which are accessed in a different vigilance state than the one in which they originated (Nemeth, 2022; Rosen, 2013; Schwartz & Maquet, 2002; Wamsley, 2013). This reliance on indirect measures introduces several limitations and potential biases, making it essential to adopt careful methodological considerations and remain vigilant about possible confounding factors when investigating the phenomenon of dreaming.

#### 1.3.2.1. Approaches to Dream Collection and Analysis

Dream reports can be collected using various methods. Retrospective methods ask participants to estimate the frequency and quality of their past dream experiences, whereas prospective approaches involve maintaining a dream diary or collecting reports during experimental sleep studies. Home-based prospective methods tend to yield higher dream recall frequencies than retrospective ones, likely due to better accuracy and recall, but they require greater compliance and motivation from participants (Aspy, 2016; Aspy et al., 2015; Nemeth,

2022; Zadra & Robert, 2012). Alternatively, prospective dream reports can be obtained in a laboratory setting using serial awakening paradigms, which have proven effective in collecting multiple dream reports within short time intervals (Noreika et al., 2009; Schoch et al., 2019; Siclari et al., 2013).

Compared to home-based methods, serial awakening studies in the lab provide greater control over the timing and conditions of awakening and reporting. This controlled environment allows for the integration of dream collection with neurophysiological measurements and more sophisticated experimental designs, such as sensory or brain stimulation paradigms (Zadra & Domhoff, 2017). However, laboratory paradigms come with their own set of challenges, including significant effort and cost. Additionally, dreams collected in such a controlled setting often differ qualitatively from those recorded at home: they tend to be less emotional and are more likely to include elements related to the laboratory or experimental environment (Picard-Deland et al., 2023; Picard-Deland, Nielsen, et al., 2021; Schredl, 2008; Sikka et al., 2018; Stickgold et al., 1994; Valli et al., 2023).

Once dream reports are collected, they can be analysed to extract various measures, which can be divided into quantitative and qualitative aspects of oneiric activity. Quantitative measures typically focus on the incidence and frequency of dream reports, with dream recall frequency being the most common metric (Beaulieu-Prévost & Zadra, 2007; Blagrove & Pace-Schott, 2010; Schredl, 2007; Schredl et al., 2003; Zadra & Robert, 2012). In contrast, qualitative features are assessed using scales and structured questionnaires or through analysis of free dream reports. Structured questionnaires limit the scope of information to predefined categories (Schredl, 2010), while free reports offer a more comprehensive view but require rigorous processing to extract comparable measures. These measures might focus on structural aspects, such as report length or total word count, or on the semantic features of the reported content (Elce et al., 2021).

Traditionally, content analysis has relied on standardized coding systems, like the Hall and Van de Castle system (1966) or the

factored scale by Hauri and colleagues (1967), which categorize dream elements into thematic dimensions (Domhoff & Schneider, 2008; Pesant & Zadra, 2006). However, manual rating methods are often limited by their reliance on predefined structures and the potential interpretative biases introduced by external raters (Schredl & Doll, 1998; Sikka et al., 2014). These limitations can be addressed with computational linguistics tools, which offers promising, objective, replicable, and automated approaches to dream content analysis (Elce et al., 2021; Pennebaker et al., 2015; Schwartz & Maquet, 2002).

#### 1.3.2.2. Factors Influencing Dream Recall & Content

Various factors have been identified as influential in determining dream recall. Personal traits, such as gender and age, along with psychological and cognitive characteristics like openness to experience, absorption, thought suppression, visual imagery, creativity, verbal fluency, attitudes toward dreams, and a tendency for mind-wandering, all play a significant role in how frequently dreams are remembered (Beaulieu-Prévost & Zadra, 2007; Blagrove & Pace-Schott, 2010; Elce et al., 2024; Malinowski, 2015; Mangiaruga et al., 2018; Nielsen, 2012; Schredl, 2010; Schredl & Reinhard, 2008; Zadra & Robert, 2012). In addition to these individual differences, situational factors such as the sleep stage, timing and mode of awakening, sleep quality, the salience and bizarreness of the dream, and the presence of distracting information upon awakening can significantly affect the degree to which a dream is recalled (Cipolli et al., 1993, 2015; Cohen, 1974, p. 197; Cohen & Wolfe, 1973; Nemeth, 2023; Parke & Horton, 2009; Pivik & Foulkes, 1968; Schredl & Fulda, 2005).

Regarding dream content, the ongoing psychological and emotional state of the subject greatly influences the quality and content of dream reports, in line with the 'continuity hypothesis' between waking and dreaming (Pesant & Zadra, 2006; Schredl & Hofmann, 2003). This hypothesis is supported by numerous observations indicating that our dreams are closely related to our daily lives, personal experiences, and concerns, contrary to the common belief that dreams are predominantly bizarre (Domhoff, 2007; Hall, 1953;

Revonsuo & Salmivalli, 1995). Consequently, dreams can serve as valuable tools for evaluating an individual's psychological well-being, as many psychiatric disorders are associated with alterations in dream quality or frequency (Armitage et al., 1995; del Giudice et al., 2022; Hadjez et al., 2003; Hartmann, 1998; Kramer & Roth, 1973; Levin & Nielsen, 2007; Schredl & Engelhardt, 2001; Spoormaker et al., 2006; Stompe et al., 2003; Wittmann et al., 2007; Zanasi et al., 2008, 2011).

Studies exploring the relationship between dream content and waking experiences have also shown that dream memory sources follow specific timelines. Variations in the temporal remoteness of dream memories occur overnight, with later awakenings incorporating more distant memories (Malinowski & Horton, 2021; Picard-Deland et al., 2022). Over a broader timescale, dreams tend to incorporate elements from the previous day—known as 'day residues'—or from the previous week (5-7 days prior), following the 'dream-lag effect' (Blagrove, Henley-Einion, et al., 2011; Nielsen et al., 2004; Nielsen & Powell, 1989, 1992; Powell et al., 1995). Day residues are predominantly observed during light NREM sleep and, when they involve recently learned tasks, are associated with improved subsequent performance, potentially reflecting memory consolidation processes (Fogel et al., 2018; Hudachek & Wamsley, 2023; Plailly et al., 2019; Schoch et al., 2019; Stickgold, 2000; Wamsley, Perry, et al., 2010; Wamsley, Tucker, et al., 2010). In contrast, delayed incorporation is more frequent in REM dreams and often involves significant or emotionally salient events, emphasizing the emotional regulation function of REM sleep (Battaglia et al., 1987; Blagrove, Fouquet, et al., 2011; Eichenlaub et al., 2019, p. 201; Nielsen et al., 2004; Nielsen & Powell, 1992; Vallat, Chatard, et al., 2017; van Rijn et al., 2015).

#### 1.3.2.3. Open Issues & New Directions in Dream Research

The body of evidence on the building blocks of dream content primarily stems from two main approaches. The first involves post-hoc analyses, where researchers examine the associations between dream content and semantic, episodic, or autobiographical memories (e.g., (Baylor & Cavallero, 2001; Blagrove, Fouquet, et al., 2011; M. J. Fosse et

al., 2003; Horton & Malinowski, 2015; Malinowski & Horton, 2014b, 2014a; Picard-Deland et al., 2022). This line of research has also extended towards exploring the presence of prospective memory and future-oriented thought within dreams (Wamsley, 2022). The second approach focuses on the experimental manipulation of pre-sleep conditions to assess how these factors influence subsequent dream content (e.g., (Cipolli et al., 2004; Corsi-Cabrera et al., 1986; De Koninck et al., 1996; De Koninck & Koulack, 1975; Foulkes & Rechtschaffen, 1964; Goodenough et al., 1975; Kusse et al., 2012; Picard-Deland et al., 2020; Schoch et al., 2019; Tauber et al., 1968; Wamsley, Tucker, et al., 2010; Wamsley & Stickgold, 2019; J. Zhang et al., 2024).

However, these methods face significant challenges. The variability in the timing between waking experiences and their appearance in dreams, as well as the potential for these experiences to be altered, distorted, or forgotten, complicates the accurate linking of real-life events to their dream representations. Moreover, there is still a lack of understanding of how various dream elements bind together to create virtual perceptually unified story-like subjective experiences (Corsi-Cabrera, 2003; Nielsen & Stenstrom, 2005; Revonsuo, 1999; Revonsuo & Tarkko, 2002). Another critical issue concerns the debate over the distinction between dream recall and dream generation (Fazekas et al., 2019; Nemeth, 2023; Ruby, 2020; Siclari et al., 2017). Consequently, several lines of research have shifted towards more direct and causal approaches to better understand the complex nature of dreams.

One promising avenue involves studying clinical conditions and parasomnias associated with overt behavioural representations of ongoing conscious experiences, such as sleepwalking, sleep-talking, confusional arousals, and dream enactments typical of REM behaviour disorder (Alfonsi et al., 2019; Baldini et al., 2019; Fasiello et al., 2022; Longe et al., 2022; Oudiette et al., 2011; Siclari, 2020; Uguccioni et al., 2013). The use of video-PSG in these clinical populations has demonstrated a correspondence between subjective reports and observed behaviours, with some sleep enactment sequences closely

resembling previously trained movements, providing evidence for the replay of recent memories during sleep (Mwenge et al., 2013; Oudiette et al., 2011; Rocha & Arnulf, 2020; Valli et al., 2012). Interestingly, recurrent dream enactment behaviour occurs even in patients who never recall subjective experiences from sleep, giving proof of a distinction between dream recall and dream generation (Herlin et al., 2015). Moreover, the degree of consciousness, awareness, and responsiveness to the environment varies greatly during parasomnia episodes, offering a unique window into sleep sensory disconnection mechanisms (Castelnovo et al., 2018; Cataldi et al., 2024; Perrault et al., 2014).

Another approach focuses on using non-invasive brain stimulation techniques to experimentally modify ongoing dream experiences (Nieminen et al., 2016; Noreika et al., 2010, 2020; Stumbrys et al., 2013; Voss et al., 2014). Studies using transcranial direct current stimulation (tDCS) to excite parietal cortical areas have demonstrated effects on dream imagery when applied during NREM 2 but not during SWS or REM sleep (Jakobson, Conduit, et al., 2012; Jakobson, Fitzgerald, et al., 2012b, 2012a). Instead, during REM sleep, tDCS application over the somatomotor cortex was shown to reduce dream movement, while targeting prefrontal regions increased dream lucidity (Noreika et al., 2020; Stumbrys et al., 2013). Dream awareness has also been linked to transcranial alternative current stimulation (tACS) in the gamma band over fronto-temporal regions (Voss et al., 2014), though this result has not been consistently replicated (Blanchette-Carrière et al., 2020). Furthermore, transcranial magnetic stimulation (TMS)-evoked activity over posterior regions during NREM sleep has shown to vary depending on the presence or absence of conscious experiences (Darracq et al., 2018; Nieminen et al., 2016). Nonetheless, evidence proving the efficacy of non-invasive brain stimulation techniques in modulating dream activity is still limited and their mechanism of action remain debated (Asamoah et al., 2019; Fertonani & Miniussi, 2017; Horvath et al., 2015; Noury et al., 2016).

Finally, sensory stimulation techniques emerge as optimal candidates for studying dreams in a simple and controlled manner, offering an easily adjustable and reproducible method for tweaking dream content. The impact of sensory perception on dreams has been documented for centuries. Early systematic analyses, such as those by Clavière (1897), Calkins (1893), and Hervey de Saint-Denys (1867), already highlighted the significant role of external stimuli in shaping oneiric activity (see Appendix I: Supplementary Text 1), as evidenced by the following observation: "*This fact, that in the sleeping man there is often an immediate correlation between the impressions which the body undergoes and the ideas which form the dream, is so universally recognised that I do not think I need to stop to demonstrate it.*" (Hervey de Saint Denys, 1867, p. 44).

The growing evidence that the brain remains responsive to its environment during sleep has sparked renewed interest in sensory stimulation within dream research. While the exact mechanisms linking this neural reactivity to conscious experiences are still not fully understood (Andrillon & Kouider, 2020; Andrillon & Oudiette, 2023), this area has gained momentum with the development of innovative 'dream engineering' techniques (Carr, Haar Horowitz, et al., 2020). These techniques combine controlled stimulation protocols with advanced technologies, leading to the creation of 'dream incubation' devices for both laboratory and personal use (Amores Fernandez et al., 2023; Amores & Maes, 2017; Haar Horowitz et al., 2018, 2020, 2023).

Over the years, various sensory stimulation methods have been proposed to influence sleep-dependent processes such as memory consolidation, emotional regulation, and creativity—functions that appear to be mirrored and potentially enhanced by concurrent changes in subjective experiences (Bloxham & Horton, 2024; Carbone & Diekelmann, 2024; Haar Horowitz et al., 2023; Picard-Deland et al., 2023; Schwartz et al., 2022). Sensory stimulation has also been used to induce lucid dreaming, a state particularly valuable for studying dream consciousness due to its ability to establish objective markers of dream

content and enable real-time communication with the dreamer (Konkoly et al., 2021; Oudiette et al., 2018).

However, despite the promising potential of sensory-based dream engineering techniques, much remains to be understood about their ability to alter dream content and the associated neural correlates. To advance this area, future research should employ cutting-edge neurophysiological and neuroimaging techniques, engage in collaborative efforts to allow for larger sample sizes, and work toward the systematic standardization and pre-registration of experimental protocols. By doing so, the field will enhance the replicability and reliability of findings, ultimately deepening our knowledge about how external stimuli can influence and shape dreaming.

## 1.4. Aims of the Dissertation

The overarching aim of this dissertation was to evaluate the role of sensory stimulation in dream research. This endeavour was pursued on several fronts. First, a theoretical analysis of the literature about sensory-dependent dream changes (SDDCs) was conducted through a systematic review, offering a comprehensive overview of the current state of knowledge in this field.

Following this, results from an experimental study involving multimodal sensory stimulation during REM sleep for dream lucidity induction are presented. This study relied on a sensory stimulation protocol based on the integration of portable EEG devices with open-source dream engineering software, providing an easily implementable and highly replicable dream engineering technique. The findings suggest that the stimulation procedure effectively modulated dream awareness and control, enabling the objective verification of sensory perception within the dream.

Finally, to explore potential markers of sleep subjective experiences, data from multimodal sensory stimulation applied during N2 sleep were analysed, focusing on aperiodic spectral features of the EEG signal. The results indicate that stimulus-induced changes in the

aperiodic slope may reflect within-stage fluctuations in consciousness and arousal levels during sleep, showing a significant association with the type of collected subjective reports.

Overall, the evidence presented here offers promising implications for advancing the understanding of sensory disconnection during sleep conscious experiences, providing deeper insights into the interplay between the external environment and the dreaming brain.

# Chapter 2.
# Influencing Dreams Through Sensory Stimulation: A Systematic Review

The content of this chapter and the corresponding appendices is adapted from the following open-access publication:

***Salvesen, L.**, Capriglia, E., Dresler, M., & Bernardi, G. (2024). Influencing dreams through sensory stimulation: A systematic review. Sleep Medicine Reviews, 101908. https://doi.org/10.1016/j.smrv.2024.101908*

## 2.1. Introduction

Dreams—those spontaneous, internally generated conscious experiences that emerge while we sleep—have sparked our curiosity since the dawn of humanity. However, despite being a prevalent component of our daily (or rather nightly) lives, dreams are still poorly understood. Contrary to the long-held belief that dreaming is exclusive to REM sleep, it is now clear that conscious subjective experiences ranging from simple abstract thoughts to complex movie-like narratives occupy a significant portion of our nights (Nir & Tononi, 2010; Siclari et al., 2017). Extensive sampling over multiple nights and different sleep stages revealed that the memory of having dreamt accompanies more than 70% of awakenings from sleep; nevertheless, individuals may be unable to recall any specific content in up to 40% of cases (Siclari et al., 2013). Therefore, if humans spend about one-third of their lives sleeping, they must also dream for at least one-fifth of their lives.

This estimate is already reason enough to drive scientific interest towards dream neurophysiology, yet it is hardly the only one. The occurrence and content of dreams are also intricately related to the dreamers' mental and physical health (Graveline & Wamsley, 2015;

Scarpelli, Alfonsi, et al., 2022). Changes in dream frequency or content are commonly reported symptoms of primary sleep disorders, including insomnia and parasomnias, and psychiatric and neurologic diseases such as post-traumatic stress disorder, anxiety disorder, narcolepsy, or Parkinson's disease (Siclari et al., 2020). However, studying dreams and their alterations objectively and reproducibly is difficult due to their highly subjective nature and large variability across and within individuals (Elce et al., 2021).

These considerations have piqued the scientific community's interest in approaches that may arbitrarily and systematically influence the features of dream experiences (Carr et al., 2020). Such 'dream engineering' approaches could significantly advance basic and translational research. For instance, they could allow for empirical investigation into the biological functions of dreaming via direct manipulations of oneiric features and even counteract dream alterations associated with pathological conditions (Vitali et al., 2022). Yet, while several dream engineering approaches have been scientifically tested, ranging from pre-sleep experience manipulation to sensory or brain stimulation procedures (Carr et al., 2020), their precise physiological and phenomenological effects remain largely unknown.

Among the available dream engineering techniques, sensory stimulation protocols seem particularly promising. In fact, while sleep is known to involve some degree of sensory disconnection from the external environment (Andrillon & Kouider, 2020), dream modifications caused by sensory perceptions have been documented and even sought after by philosophers, artists, and scientists alike for centuries (Solomonova & Carr, 2019; see Appendix I: Supplementary Text 1 for a brief narrative review of early research about this topic). Nonetheless, a consensus has yet to be reached regarding the underlying mechanisms and functional significance of stimulus-dependent dream changes (SDDCs), defined here as any change in dream features induced by an external stimulus. Crucially, advancing our understanding of how external stimuli affect dreams may provide new insights into the physiological mechanisms that ensure sleep

continuity in the presence of external disturbances and the functional underpinnings of perceptual awareness at different

Therefore, we aimed to summarise and evaluate the available evidence about the effects of experimental sensory stimulation during sleep on ongoing mental activity. We described previous findings about SDDCs and evaluated the feasibility and effectiveness of sensory stimulation approaches for dream engineering. All findings were assessed for potential methodological and statistical limitations. Finally, we addressed open issues and suggested a roadmap for future investigations.

## 2.2. Methods

### 2.2.1. Identification of Publications

This systematic review was conducted following the preferred reporting items for systematic reviews and meta-analyses (PRISMA) guidelines (Moher et al., 2009; Page et al., 2021). Four online databases (PsycNET, PubMed, ScienceDirect, and Scopus) were searched for publications investigating the effects of sensory stimuli administered during sleep on dream characteristics. The search query was "*dream* AND (stimul* OR sensory OR modulat*)*", with slight variations depending on specific search engine parameters. The literature search was first conducted on February 1, 2021, and then again on October 15, 2022. All resulting articles were screened based on the inclusion criteria outlined below. Additionally, the bibliographic references of all selected articles were recursively reviewed for potential inclusion; eligible ones are referred to as external references.

### 2.2.2. Inclusion Criteria

One author (LS) conducted a three-step evaluation process to select publications. First, off-topic publications were excluded based on their title. Then, the abstracts of all remaining articles were assessed to evaluate their potential compliance with a set of pre-selection criteria (see Appendix I: Supplementary Table 1). We pre-selected all published

or in-press research articles in English that included an experimental stimulation protocol during sleep targeting at least one of the following sensory modalities: visual, auditory, olfactory, gustatory, vestibular, or somatosensory, with the latter encompassing touch, thermal perception, nociception, and proprioception. We included any article that reported sensory stimulation effects on dreaming, even when this was not the study's primary goal. Instead, we excluded articles focusing only on neuromodulation or brain stimulation techniques, namely tDCS, tACS, and TMS. This type of stimulation aims to bypass canonical information processing pathways by modulating neuronal oscillatory activity directly and thus differs substantially from pure sensory stimulation techniques. Moreover, a sensory component may be involved (e.g., somatosensory perceptions due to electrical stimulation), which is indistinguishable from the direct neuromodulatory effects of the procedure. Articles that relied on drug administration were also excluded.

Subsequently, pre-selected articles were narrowed down based on finer exclusion criteria (see Appendix I: Supplementary Table 2). We discarded studies for which we could not retrieve the full manuscript. Publications that did not use a standard sleep monitoring technique (i.e., EEG or actigraphy) were excluded since participants' vigilance state might not have been adequately confirmed. We also excluded single-case studies and non-experimental publications, such as anecdotal reports and observational studies, as well as research involving hypnotic states or post-hypnotic conscious experiences. We further excluded papers that failed to provide any quantitative or qualitative information about the collected dream reports (i.e., studies that claimed to have gathered dream data without reporting it). Articles that lacked any methodological details about the stimulation procedure were also discarded. In the same vein, we excluded publications that reported multiple manipulations without properly separating the resulting data, as this prevented the identification of any specific effects of the different stimulation techniques.

Finally, we focused our review on non-lucid dream data since lucid dreaming is often regarded as a distinct state of sleep consciousness. In fact, lucid dreams are characterised by different patterns of brain activity relative to ordinary dreaming and present unique qualitative features, namely the recovery of metacognition (Baird, Mota-Rolim, et al., 2019). Nonetheless, we evaluated lucid-dreaming publications for prospective findings about SDDCs in non-lucid dreams. We thus excluded articles that solely reported on the effects of sensory stimulation on lucid dream induction or content, as well as those that pooled lucid and non-lucid dreaming data. A second reviewer (GB) approved of the final selection.

### 2.2.3. Data Extraction

A meta-analysis was not possible within this systematic review due to the broad differences concerning the metrics and methods adopted by the selected articles. Therefore, results were qualitatively synthesised by one author (LS) using textual descriptions and recapitulative tables. A second author (GB) verified the extracted data and discussed with the first author any disagreements, namely in cases of missing or unclear data.

### 2.2.4. Methodological Assessment

We assessed the empirical validity and bias risk of all selected publications using a partially modified version of the Downs and Black checklist (Downs & Black, 1998), which was originally developed for evaluating the methodological quality of randomised and non-randomised studies of health care interventions. The adapted checklist comprises 23 items and assesses several methodological aspects, including result reporting, external and internal validity, and statistical aspects, including power and effect size calculations (see Appendix I: Supplementary Text 2). The final scores range from 0 to 25.

Two authors (LS, GB) independently scored the studies using this checklist. A consensus was reached after discussing any grading differences. Of note, the checklist was applied to evaluate the reported

dream data and dream-related results specifically, even when these were not the focus of the study.

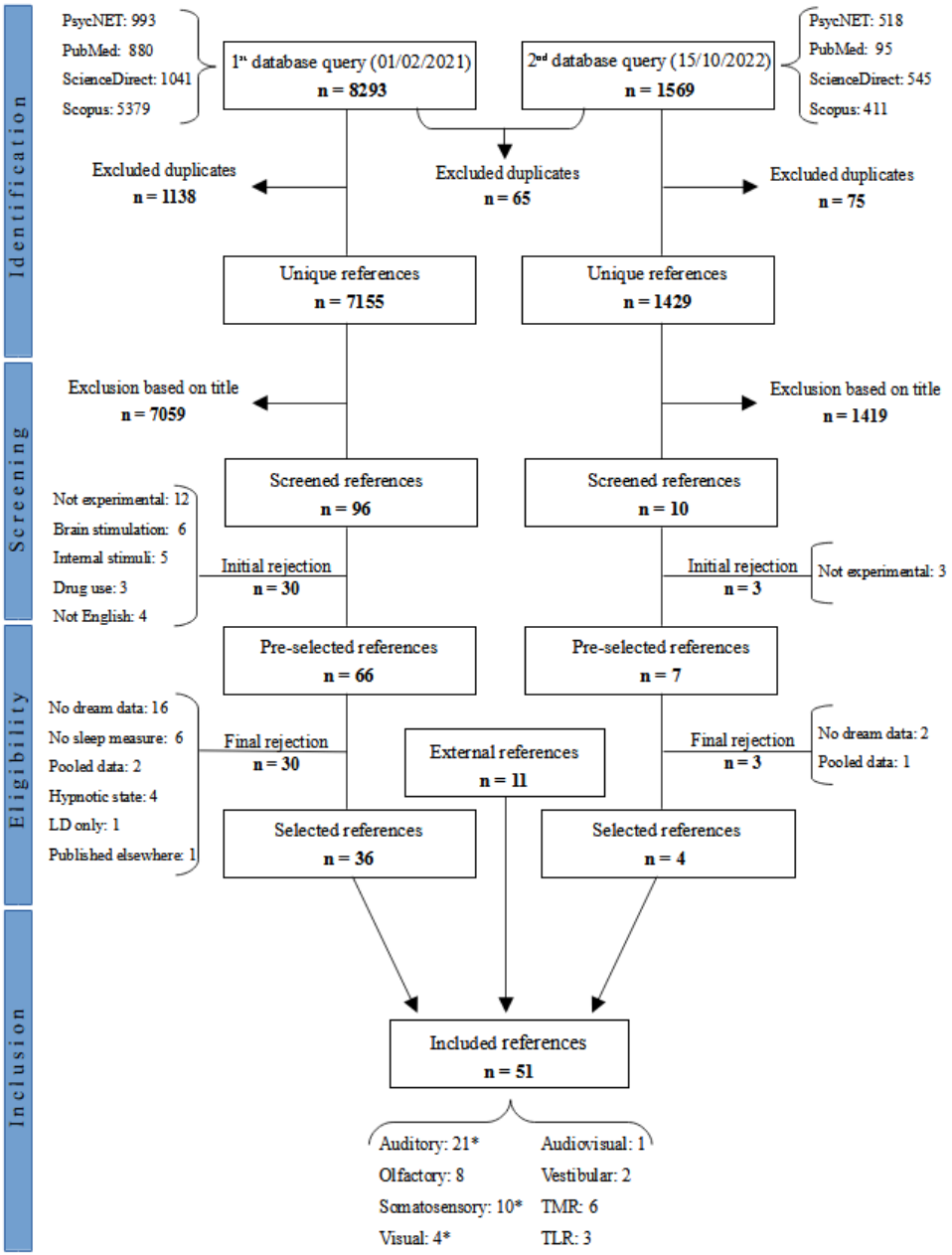
## 2.3. Results

### 2.3.1. Selected Publications

The literature search yielded 51 publications (Figure 1). Out of these, 21 reported data related to auditory stimulation, 10 to somatosensory stimulation, eight to olfactory stimulation, two to vestibular stimulation, four to visual stimulation, and one to multimodal (audio-visual) stimulation (Figure 2). Moreover, nine studies involved conditioned associative stimulation procedures: six used targeted memory reactivation (TMR) protocols, and three applied targeted lucidity reactivation (TLR) protocols.

**Figure 1. PRISMA-compliant article selection flowchart.**

* This modality was evaluated in a publication that studied more than one modality independently, justifying that the total count across all modalities is higher than the total number of references. TMR: targeted memory reactivation; TLR: targeted lucidity reactivation.


Identification
Screening
Eligibility
Inclusion
PsycNET: 993
PubMed: 880
ScienceDirect: 1041
Scopus: 5379
1st database query (01/02/2021)
n = 8293
2nd database query (15/10/2022)
n = 1569
PsycNET: 518
PubMed: 95
ScienceDirect: 545
Scopus: 411
Excluded duplicates
n = 1138
Excluded duplicates
n = 65
Excluded duplicates
n = 75
Unique references
n = 7155
Unique references
n = 1429
Exclusion based on title
n = 7059
Exclusion based on title
n = 1419
Screened references
n = 96
Screened references
n = 10
Not experimental: 12
Brain stimulation: 6
Internal stimuli: 5
Drug use: 3
Not English: 4
Initial rejection
n = 30
Initial rejection
n = 3
Not experimental: 3
Pre-selected references
n = 66
Pre-selected references
n = 7
No dream data: 16
No sleep measure: 6
Pooled data: 2
Hypnotic state: 4
LD only: 1
Published elsewhere: 1
Final rejection
n = 30
External references
n = 11
Final rejection
n = 3
No dream data: 2
Pooled data: 1
Selected references
n = 36
Selected references
n = 4
Included references
n = 51
Auditory: 21*
Olfactory: 8
Somatosensory: 10*
Visual: 4*
Audiovisual: 1
Vestibular: 2
TMR: 6
TLR: 3

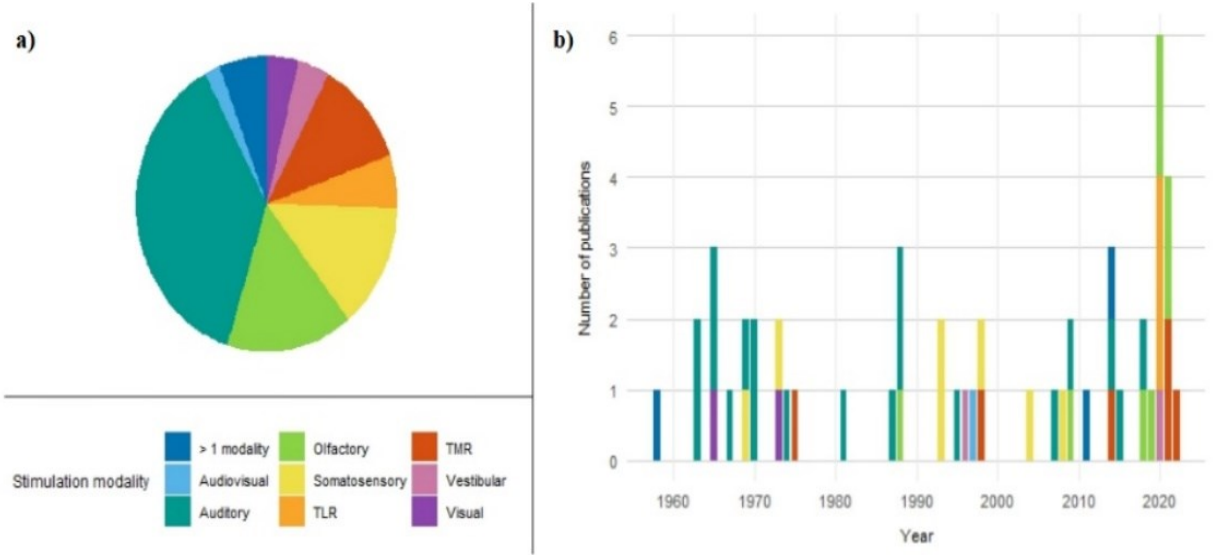



**Figure 2. Distribution of selected studies as a function of the targeted sensory modality (a) and year of publication (b).**

Note: Three articles (Bradley & Meddis, 1974; Dement & Wolpert, 1958; Paul et al., 2014) evaluated more than one modality independently. TMR: targeted memory reactivation; TLR: targeted lucidity reactivation.

In summary, the selected studies were characterised by high heterogeneity regarding experimental protocols and methodologies, both across and within sensory modalities. In particular, the timing of stimulation and the targeted sleep stage showed substantial variability. Out of the selected studies, 25 targeted only REM sleep, two focused solely on NREM sleep (N1–N2 and N3, respectively; (Haar Horowitz et al., 2018; Lewin et al., 1973), and the remaining 24 stimulated both during REM and NREM sleep (mainly N2). Six studies were performed during a daytime nap (Bloxham & Durrant, 2014; Conduit & Coleman, 1998; Haar Horowitz et al., 2018; Nozoe et al., 2020; Picard-Deland, Aumont, et al., 2021; Picard-Deland & Nielsen, 2022). Moreover, while most studies involved serial-awakening procedures, five articles used whole-night stimulation protocols, collecting data only once upon spontaneous morning awakening (Ackerley et al., 2020; Martinec Nováková, Kliková, et al., 2021; Martinec Nováková, Miletínová, et al., 2021; Schäfer et al., 2019; Ziegler, 1973). Finally, most studies monitored sleep using EEG, with only two relying on actigraphy measures (Ackerley et al., 2020; Schäfer et al., 2019).

### 2.3.2. Methodological Assessment

Overall, the included studies obtained a mean score of 13 (13.25 ± 4.48; range 1–22) out of a maximum possible score of 25, indicating the existence of significant methodological limitations. The item-by-item and total scores reflecting the methodological quality of each article based on our checklist are provided in Appendix I: Supplementary Table 3, while the score distribution for each checklist item is shown in Appendix I: Supplementary Figure 1.

Altogether, study results were typically based on a limited number of observations, with an average sample size of 17.43 ± 15.51 participants (range 3–65) and a small number of collected reports per participant. In this regard, it should be emphasised that both sample size and the number of observations play an essential role in determining statistical power (G. Chen et al., 2022). Additionally,

several publications merely reported descriptive findings, with around 30% of the assessed studies failing to provide statistical analyses.

Other significant issues are the implementation of protocols without any adequate control conditions and the absence of effective blinding measures. Some investigations, for example, made the conditions explicit to the participants or proceeded without randomising the stimulation schemes. Further, investigations relied on human raters to evaluate the occurrence of SDDCs, even though they were not always adequately blinded to the aims of the experiments. Crucially, most studies failed to provide clear definitions and guidelines for identifying SDDCs. Lastly, several studies include poor or misleading statistical reporting, such as across-sample data aggregation procedures. Indeed, rather than focusing on within-subject analyses, about 80% of the evaluated studies pooled data across participants, neglecting individual variance. Most analysed studies did not include power calculations, and many failed to report exact p-values and effect sizes.

The methodological quality of the publications shows a positive trend over time, as evidenced by a significant positive correlation between methodological scores and the year of publication ($r = 0.45$, $p = 0.001$; Figure 3), but there is still room for improvement, and future efforts should focus on addressing these limitations.

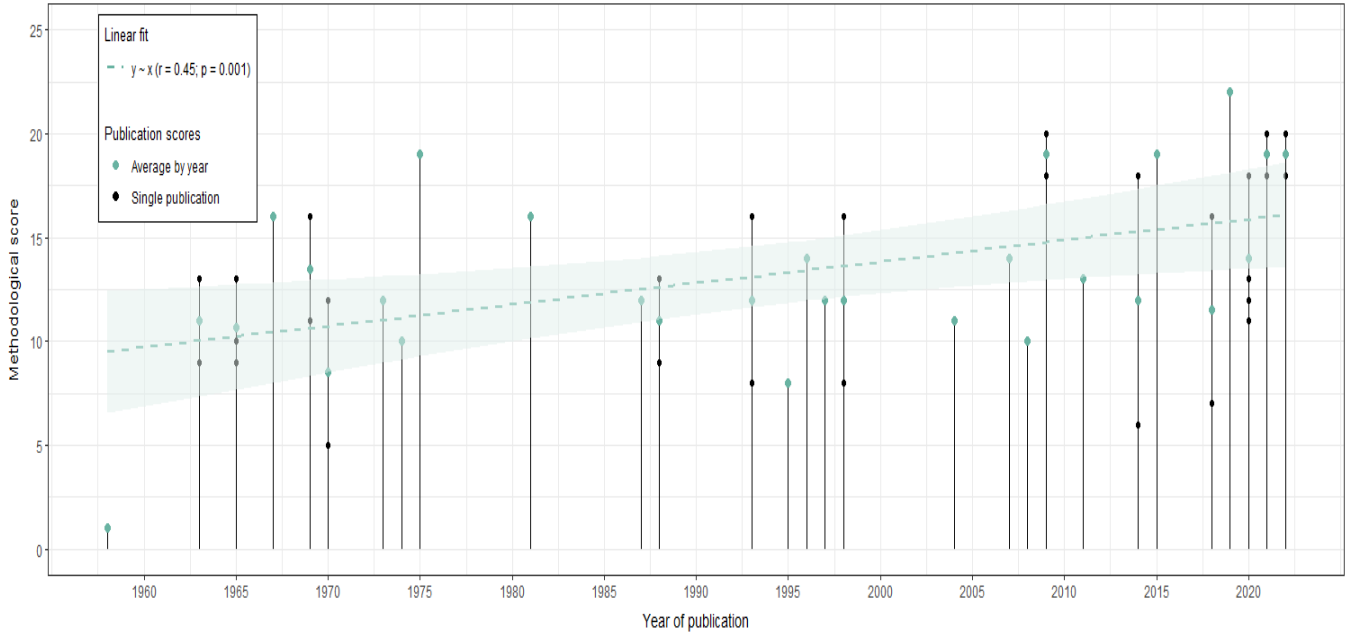



**Figure 3. Methodological score evolution across publication years for selected references.**

Note: The green dashed line is fitted to the average methodological score for each year; the light green shadow represents the standard error.

### 2.3.3. Evidence of SDDCs

Most reviewed studies focused on specific SDDC types, yet only a few described the adopted SDDC definitions and identification criteria. Based on these, we proceeded to classify SDDCs into two main categories: incorporation, which encompasses all instances in which the stimulus permeates the dream content as an identifiable element (i.e., the presence of a novel dream element that presents overlapping characteristics with the stimulus), and modulation, which includes all SDDCs that appear to be contingent on the stimulus's presence but cannot be explained by its intrinsic qualities (i.e., variations in general dream features, such as emotional valence or number of dream characters).

Whenever possible, depending on the availability of finer categorisation provided by the authors themselves or by the presence of detailed information about the dream content, incorporations were further distinguished as either being direct (whenever the stimulus is incorporated as is; e.g., a flashing light is incorporated as light in the dream) or indirect (whenever the stimulus is incorporated in a transformed way, namely through semantic or mnemonic associations; e.g., white noise may be incorporated as the sound of waves or as a visual representation of the ocean; see Figure 4). Otherwise, the terminology was kept as used by the authors in the corresponding publication.

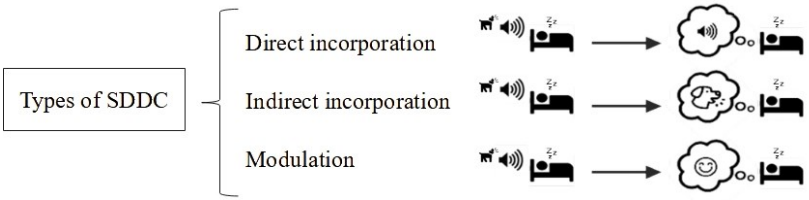



**Figure 4. Schematic representation of the main types of stimulus-dependent dream changes (SDDCs) identified in the present review.**

#### 2.3.3.1. Auditory Stimulation

Auditory stimulation was first implemented in the 1960s and remains the most targeted modality to this day. Indeed, over one-third of the articles selected for this review concerned auditory stimulation (N = 21; ~41%). Studies within this category may be classified into two types, which we summarised separately: those that employed sounds associated with semantic information, such as words or certain identifiable sounds (52%; Berger, 1963; Bloxham & Durrant, 2014; Bruck & Horasan, 1995; Castaldo & Holzman, 1969, 1969; Castaldo & Shevrin, 1970; Haar Horowitz et al., 2018; Hoelscher et al., 1981; Rahimi et al., 2015; Strauch, 1988; Tilley et al., 1987) and those that used non-semantic stimuli, such as pure tones or white noise (48%; (Bradley & Meddis, 1974; Burton et al., 1988; Dement & Wolpert, 1958; Fedyszyn & Conduit, 2007; Flo et al., 2011; Goodenough et al., 1965; Shapiro et al., 1963, 1965; Stuart & Conduit, 2009; Zimmerman, 1970).

Of note, one study (Flo et al., 2011) used both auditory and somatosensory stimulation independently and is described in the somatosensory stimulation section. Another study used multimodal stimulation (auditory and visual; Conduit et al., 1997) and is described within this section due to its close relatedness with a series of similar studies based on unimodal auditory stimulation.

##### *2.3.3.1.1. Semantic Stimuli*

These studies used verbal stimuli (i.e., spoken words or phrases), non-verbal vocalisations, or recognisable sounds (e.g., traffic noise) to influence ongoing sleep mentation. For instance, some authors explored the degree to which different simple verbal prompts could trigger the occurrence of semantically related elements within the dream. Tilley, Luke, and Boehle (1987) used sets of thematically connected words as stimuli and reported finding instances of 'representational relationship' in a third of the collected dream reports, with a higher incidence in REM (8/18) than in N2 reports (2/12). In another study, a specific word was presented immediately after sleep

onset during a daytime nap (Haar Horowitz et al., 2018). All six participants reported 'seeing' the prompted word while dreaming.

Other researchers focused on non-verbal auditory stimuli associated with semantic information. For example, Bruck and Horasan examined the effects of fire alarms on sleep arousal to evaluate the safety of these devices (Bruck & Horasan, 1995). Stimulus incorporation was detected in ~17% of the participant's dream reports. In another study, traffic sounds were played during REM sleep (Rahimi et al., 2015). There were more thematically related categories ('travel' and 'streets'; Hall & Van de Castle, 1966) after stimulation (~24%) than in non-stimulated dreams (~4%). Four direct incorporation instances were identified across the 26 dream reports collected during the stimulation night.

A series of studies explored whether variations in the saliency or emotional valence of the stimulus could impact the occurrence of SDDCs by using stimuli such as personally relevant names (R. J. Berger, 1963), concern-related words (Hoelscher et al., 1981), or human cries (Strauch, 1988). Hoelscher and collaborators showed that, in REM reports, the incorporation rate of concern-related stimuli was significantly higher than for non-concern-related stimuli. When comparing REM and N2, incorporation rates were higher in REM reports (Hoelscher et al., 1981). Similarly, Strauch observed higher incorporation rates in REM reports for the meaningful stimulus (the sound of a crying person) but not for the neutral stimulus (the sound of a jet plane), compared to the control condition (Strauch, 1988). Moreover, when comparing incorporation rates between stimulated waking and sleeping mentation, direct incorporation was more common than indirect incorporation during wakefulness, while the opposite was true for REM sleep.

Others tried to evaluate how linguistic aspects, such as voice ownership or language comprehension, were related to SDDCs. Castaldo and collaborators performed a series of studies in which they presented a set of words recorded either with the dreamer's own voice or a stranger's voice (Castaldo & Holzman, 1967, 1969; Castaldo &

Shevrin, 1970). Results showed that the main dream character was more active, assertive, and independent when participants heard their own voice, while the dreamer or main figure was more passive when a stranger's voice was played. Dream reports collected after stimulation also included more listening activities than non-stimulated dreams. The authors further evaluated both direct ('phonological') and indirect ('conceptual') incorporations of the stimuli: when comparing experimental to control awakenings, reports from N2 (but not from REM) showed a greater number of words conceptually related to the stimuli. Instead, Bloxham and Durrant investigated language comprehension by presenting phrases in either English or German to monolingual anglophones (Bloxham & Durrant, 2014). While all collected dream reports contained speech or conversational activities, those following German stimulation tended to be scored as stranger and more unfamiliar, showing a potential modulation effect. Only two reports were rated as possibly incorporating the stimulus.

*2.3.3.1.2. Non-Semantic Stimuli*

The employed stimuli included pure tones (800 Hz–1000 Hz), bell rings, and white noise. Interestingly, the only publication that compared different stimulation modalities found that pure tones had the lowest incorporation rate (9%) compared to visual (23%) and somatosensory (42%) stimuli (Dement & Wolpert, 1958).

Most studies in this category used sensory stimulation to investigate the relationship between induced arousal and ongoing conscious mentation. For instance, a series of works by Shapiro and colleagues investigated the effect of the mode of awakening (gradual or abrupt) on subsequently reported conscious experiences (Goodenough et al., 1965; Shapiro et al., 1963, 1965), showing that gradually increasing the stimulus volume until awakening led to more thought-like reports than abrupt awakenings. When groups of low and high dream recallers were compared, the difference between awakening modes in the tendency to yield thought-like reports was more pronounced for the former. An interaction between the time of night and the method of awakening was also found, with effects being more

significant in later REM periods for low recallers specifically. Consistent with this, the authors found an interaction between the sleep stage (NREM or REM) and the method of awakening, depending on the type of report. The authors mention the occurrence of incorporations in both dream-like and thought-like REM reports, although no distinction was made between stimulus-related and laboratory incorporations. Interestingly, the time between the last phasic REM period and awakening was longer for thought-like reports with incorporation than those without incorporation; conversely, for dream-like reports, incorporation instances were closer to the last phasic event.

Along similar lines, a few studies focused on the relationship between arousal thresholds and stimulus incorporation (Bradley & Meddis, 1974; Zimmerman, 1970). Zimmerman compared the effects of increasingly loud pure tones on light and deep sleepers by stimulating early REM and subsequent N3 stages (Zimmerman, 1970). He found no clear differences in incorporation rates between light and deep sleepers. Instead, Bradley and Meddis assessed variations of the arousal threshold at the individual level, showing that dream reports containing incorporations (43%) were associated with higher auditory arousal thresholds than those without (Bradley & Meddis, 1974).

Burton and colleagues used beeping tones to investigate changes in responsiveness to external stimuli during sleep (Burton et al., 1988). Specifically, participants were stimulated during REM and N2 sleep after being instructed to inhale deeply upon stimulus perception. Evidence of stimulus incorporation (e.g., direct, related to noise, or indirect, related to breathing) was found in 50.8% of REM and 37% of N2 reports, with no significant difference between stages. Behavioural responsiveness to the tones also appeared to be similar for REM and N2. However, it was significantly reduced for trials followed by a dream report, which held true even when only N2 trials were considered. Interestingly, the likelihood of responsiveness was lower in trials with incorporation (50%) than in trials without incorporation (79%), with no difference between sleep stages. In fact, the level of

responsiveness for trials where there was no evidence of incorporation was as high as when no dream report was collected.

In a series of three studies, Conduit and colleagues explored how arousal signs and eye movements relate to oneiric experiences (Conduit et al., 1997; Fedyszyn & Conduit, 2007; Stuart & Conduit, 2009). Two studies employed virtually identical experimental paradigms, although one used multimodal stimulation combining a pure tone with a red pulsing light (Conduit et al., 1997), while the other applied the pure tone alone (Fedyszyn & Conduit, 2007). The procedures involved repeatedly presenting the stimuli either in N2 or late REM, progressively increasing the intensity until ocular activity was observed. Stimulation in N2 sleep was associated with higher dream imagery scores and more alpha activity relative to the condition without stimulation. No differences were observed between stimulated and non-stimulated trials regarding the amount of visual imagery in REM dreams. Direct incorporation of the stimuli was observed in both studies: in the multimodal experiment, 33% of REM reports were deemed as have incorporated the stimuli, compared to only 12.5% of N2 reports; in the auditory experiment, incorporation was found in 50% of REM and 11% of N2 reports. A follow-up study focusing specifically on REM noted that stimulated trials were associated with a lower amount and amplitude of eye movements (Stuart & Conduit, 2009). Compared to control trials, dream reports from stimulated trials contained less visual imagery, presented fewer visualisable words, and received lower imagery scores than the no-stimulation condition.

#### 2.3.3.2. Somatosensory Stimulation

Ten (~20%) studies involved somatosensory stimulation: six focused on nociception (Bastuji et al., 2008; Dement & Wolpert, 1958; Flo et al., 2011; Koulack, 1969; Lavigne et al., 2004; Nielsen et al., 1993), one on thermoception (Ziegler, 1973), and the remaining three on mechanoreception (Nielsen, 1993; Paul et al., 2014; Sauvageau et al., 1998). Accordingly, stimulation methods differed substantially between investigations.

Only three studies by Nielsen and collaborators used comparable stimuli and approaches. In particular, they used inflatable blood pressure cuffs to stimulate the limbs during REM sleep (Nielsen, 1993; Nielsen et al., 1993; Sauvageau et al., 1998). Results from the first study showed that post-stimulation dreams contained more references to both pressure cuffs and leg sensations than unstimulated dreams, with over 80% of reports collected after stimulation containing instances of direct incorporation (Nielsen, 1993). In another study, pressure cuffs were inflated until they reached the pain threshold (Nielsen et al., 1993). The authors identified pain incorporation in almost a third of post-stimulation dream reports (13/42), of which 11 explicitly mentioned leg pain and two mentioned pain in a transformed way. Dreams presenting pain incorporation also included strong negative emotions. Of note, the dreamed pain was described as more intense than the actual pain experienced upon awakening, a characteristic that has been mentioned repeatedly for many centuries (Aristotle et al., 1908; Cubberley, 1923; see also Appendix I: Supplementary Text 1). The last study in this series compared the effect of pressure stimulation on dream activity in gymnasts and non-gymnasts (Sauvageau et al., 1998)]. Overall, post-stimulation reports included stimulus incorporation in nearly half of cases. However, non-gymnasts presented more such references in their dreams than gymnasts. Finally, stimulation was found to be associated with a smaller number of characters in the dream plot, with this modulation effect being mostly driven by the gymnast group.

Five other studies employed distinct types of somatosensory stimuli to induce painful sensations, thus evaluating the effect of nociceptive stimulation on sleep and dreams (Bastuji et al., 2008; Dement & Wolpert, 1958; Flo et al., 2011; Koulack, 1969; Lavigne et al., 2004). Dement and Wolpert sprayed cold water on different exposed body parts and found that subsequent dream reports incorporated the stimulus in up to 42% of cases (Dement & Wolpert, 1958). Koulack applied electrical impulses to the wrists of the participants while varying both the time of stimulation and awakening (Koulack, 1969).

Results showed that stimulating shortly after REM detection was more effective in modifying the dream experience than stimulating later in REM or during NREM sleep. Overall, stimulus incorporation was more frequent in stimulated than control trials. Furthermore, certain qualitative aspects of the dream content related to somatosensory perception ('body centrality' and 'body activity') were more frequently identified after stimulation in REM than in NREM or control trials. Interestingly, the author also compared trials containing alpha activity in the EEG signal with trials that did not and found that 'alpha dreams' presented higher incorporation rates than dreams without such arousal signs (Koulack, 1969).

The three studies described hereafter were mainly focused on exploring the physiological effects of nociceptive stimulation during sleep, assessing its possible effects on dreams only as a secondary aim. In the first one, hypertonic intramuscular infusions were applied to evaluate nociceptive thresholds across the wake-sleep cycle (Lavigne et al., 2004). Five out of nine participants reported perceiving pain in their sleep, and two reported pain incorporation in their oneiric experiences. In the second study, radiant heat laser pulses were applied overnight (Bastuji et al., 2008). In this case, only four out of ten participants could recall any conscious experience, none presenting any somatosensory or pain incorporation. The third study presented aversive stimuli, either unconditioned (mild electric shocks) or cued (by presenting a negatively conditioned neutral auditory stimulus), both in N2 and REM sleep (Flo et al., 2011). Self-reported dream emotionality showed a shift towards higher negative valence ratings after experimental nights compared to unstimulated baseline nights. Importantly, these three studies collected dream-related details only after morning awakening. This implies variable and potentially long temporal intervals relative to when the stimulation occurred, which could contribute to the lack of clear effects.

The only thermoception-based study included in our review investigated how room temperature influences the type and intensity of emotional content in dreams (Ziegler, 1973). Results showed that

emotional intensity was significantly lower at higher temperatures (and vice versa). Furthermore, unpleasant feelings tended to be scarcer at higher temperatures, with pleasant dreams appearing more frequently.

The last publication in this section focused on lucid dreaming, while also including data regarding non-lucid experiences (Paul et al., 2014). Paul and collaborators administered visual (see corresponding section) or vibrotactile stimuli during REM sleep. Self-rated incorporations were identified in 43% of cases following vibration applied to the index finger and in 48% of cases when stimulation was applied to the wrist or ankle.

#### 2.3.3.3. Olfactory Stimulation

Among the selected papers, eight (~16%) targeted olfaction (Ackerley et al., 2020; Martinec Nováková, Kliková, et al., 2021; Martinec Nováková, Miletínová, et al., 2021; Okabe et al., 2018, 2020; Schäfer et al., 2019; Schredl et al., 2009; Trotter et al., 1988). Odours have the particularity of being processed differently than other sensory stimuli since olfactory information bypasses the brainstem and thalamic hubs. As a result, pure or mildly trigeminal odorants do not cause arousal or increases in K-complexes during sleep; conversely, they even appear to promote slow-wave and spindle activity (Arzi et al., 2010; Perl et al., 2016). Furthermore, direct anatomical projections from the olfactory bulb to the primary olfactory cortex connect to the amygdala and hippocampi, which are known to be involved in emotional and memory processing (Klinzing et al., 2019; Yang & Wang, 2017). In line with this, most reviewed studies explored the potential effects of different odour attributes, such as odour pleasantness, on dream emotionality.

Trotter, Dallas, and Verdone presented a series of pleasant and unpleasant scents during REM sleep. They observed that the proportion of dream reports with a positive emotional tone was similar for all trials, indicating that dream emotional ratings were unaffected by odour pleasantness (Trotter et al., 1988). Stimulus incorporation was found in 27% of pleasant and 11% of unpleasant trials. Later, Schredl

and collaborators presented one pleasant and one unpleasant odour, again during REM sleep (Schredl et al., 2009). Results revealed that the emotional tone changed significantly based on pleasantness, with pleasant trials rated more negatively than unpleasant and control trials. No direct incorporation instances were identified.

Okabe and collaborators further investigated the impact of odour pleasantness using a group-level design accounting for individual differences concerning odour preferences (Okabe et al., 2018). Participants who liked the odour had more negative dreams after being stimulated than those who disliked it, indicating a significant interaction between the group and stimulation conditions. Again, no cases of direct incorporation were identified, but two post-stimulation reports included elements associated with olfactory perception. Since odour preference has been suggested to be associated with odour familiarity, another study compared groups of people who were either familiar or unfamiliar with the presented odour (Okabe et al., 2020). The high-familiarity group judged their dreams more negatively after stimulation than in the control condition, while no stimulus-induced changes were observed in the low-familiarity group. Yet, when only unstimulated trials were considered, the high-familiarity group rated their dreams more positively than the low-familiarity group.

More recently, Martinec Nováková and colleagues made their participants sleep one night with a pleasant or unpleasant odour and one without (Martinec Nováková, Kliková, et al., 2021; Martinec Nováková, Miletínová, et al., 2021). The authors found a significant effect of the stimulation condition on dream emotionality ratings, which seemed modulated by whether participants perceived the odour upon awakening. Specifically, perceiving an odour without stimulation was associated with lower dream pleasantness than accurate rejections. Nonetheless, neither stimulation nor odour appraisal upon awakening seemed to affect the frequency of chemosensory content in dreams. Instead, 'chemosensory dreams' were more commonly reported by participants with a greater propensity to detect and act upon smells in everyday life.

The last two studies in this category focused on the effects of olfactory stimulation on overall sleep quality. Both used actigraphy-based sleep monitoring to evaluate the influence of whole-night stimulation with a pleasant odour on clinical populations suffering from sleep disturbances (i.e., post-traumatic stress disorder (Schäfer et al., 2019) and mild to moderate chronic insomnia patients (Ackerley et al., 2020). The first found that emotional intensity ratings were significantly lower for dreams collected after stimulation nights compared to control nights, while no effect was observed regarding emotional tone (Schäfer et al., 2019). The second was home-based, with participants being asked to spray a fragrance on their pillow before bed. Although one of the two tested fragrances was associated with better sleep quality ratings, the results failed to show any effect of odour stimulation on dream content (Ackerley et al., 2020).

#### 2.3.3.4. Vestibular Stimulation

Two studies (~4%) targeted the vestibular system (Leslie & Ogilvie, 1996; Nozoe et al., 2020). One was originally aimed at inducing lucidity in dreams (Leslie & Ogilvie, 1996). To do so, participants slept in a hammock that started rocking either during early or late REM sleep. Dreams collected from early stimulated REM periods were rated as more self-reflective than unstimulated dreams. Stimulus incorporation was identified in 25% of stimulated dreams and 7% of unstimulated ones. Furthermore, there was a significant correlation between vestibular incorporation and dream bizarreness. The other study explored how different bed inclinations could affect conscious experiences during sleep (Nozoe et al., 2020). Participants reported hypnagogic imagery more frequently after control nap awakenings than after stimulation. However, the amount of vestibular or somatosensory content did not vary as a function of bed elevation.

#### 2.3.3.5. Visual Stimulation

Four articles (~8%) involved visual stimulation (Dement & Wolpert, 1958; Lewin et al., 1973; Paul et al., 2014; Rechtschaffen & Foulkes, 1965). In one study, participants slept with their eyes taped open while

physical objects were presented before them (Rechtschaffen & Foulkes, 1965). No obvious incorporation cases were identified among the 30 collected dream reports, and reports were matched to the corresponding object at the chance level. However, the authors stated that up to four reported experiences might have potentially incorporated the light used to illuminate the presented objects.

In the remaining studies, the stimuli consisted of simple flashing lights that could be perceived through closed eyelids. Using such an approach, Dement & Wolpert identified stimulus incorporation in seven of 30 dream reports (Dement & Wolpert, 1958). These included, for instance, the report of a sudden fire, lightning, shooting stars, or the experimenter shining a flashlight towards the eyes in the dream scene.

In another study, visual or tactile stimuli were administered during REM sleep to induce lucid dream episodes (Paul et al., 2014). Dream reports were collected in 18 out of 24 stimulation trials, of which the participants rated seven (38.9%) as having incorporated the stimulus. Visual stimulation was also used to change the frequency of oscillatory activity in visual areas during sleep. Specifically, photic stimulation flickering at the frequency of the participants' alpha peak (~10 Hz) was used to entrain neural oscillatory activity during N3, under the hypothesis that increasing alpha oscillations would lead to an increase in REM-like sleep mentation (Lewin et al., 1973). Oscillatory stimulation at 26 Hz was used as a control condition. The percentages of experiences judged as REM-like were 25% in unstimulated N3, 17% after stimulation at 26 Hz, and 93% after alpha stimulation.

#### 2.3.3.6. Conditioned Association

In nine selected studies (~18%), the presented stimuli had previously been paired with a task or other stimuli during wakefulness. Such procedures aim to associate a stimulus with some information that may be subsequently reactivated by using the stimulus as a cue. This technique can be used to induce the reactivation of specific memories,

as in TMR protocols (Oudiette & Paller, 2013), or to induce lucidity within the dream, as in TLR procedures (Carr, Konkoly, et al., 2020).

*2.3.3.6.1. TMR*

While most TMR studies focused on how memory reactivation relates to learning and behavioural performance, six assessed its effects on dream content. Of these, four used auditory cues (Borghese et al., 2022; De Koninck & Koulack, 1975; Picard-Deland, Aumont, et al., 2021; Picard-Deland & Nielsen, 2022), one used olfactory cues (Schredl et al., 2014), and one used visual cues (Conduit & Coleman, 1998). Overall, these studies showed inconsistent results regarding the immediate incorporation of the reactivated information.

De Koninck and Koulack asked a group of volunteers to watch a stressful film before sleep; the soundtrack was then played during REM sleep (De Koninck & Koulack, 1975). Film incorporation ratings were significantly higher for dreams collected after the soundtrack was presented, but only for participants who had previously watched the film. Direct incorporation of the audio stimulus reportedly occurred only once. Anxiety ratings of the collected dreams did not differ between stimulated and unstimulated conditions, and no correlation was found between dream anxiety and film incorporations.

In a more recent experiment, participants engaged in a virtual reality flying task before taking a nap, during which task-related audio cues were once again presented (Picard-Deland, Aumont, et al., 2021; Picard-Deland & Nielsen, 2022). Three of the 18 collected REM TMR dreams were rated as incorporating the auditory cue, whereas none of the 17 NREM TMR dream reports were. Yet, incorporation was not associated with any improvement in post-sleep task performance (Picard-Deland, Aumont, et al., 2021). On the other hand, the authors found a significant positive effect of REM TMR on post-sleep task performance, and spontaneous incorporation of kinaesthetic task elements into the content of REM dreams was predictive of greater performance improvement. Interestingly, while TMR cueing had no discernible immediate effects on task-element dream incorporation, an

increased incorporation of such elements was found in reports collected with a home dream diary two days after the REM TMR nap or five to six days after the NREM TMR nap (Picard-Deland & Nielsen, 2022).

The last auditory-based TMR study attempted to enhance social fear extinction in individuals suffering from social anxiety (Borghese et al., 2022). A group of patients participated in virtual-reality-based exposure therapy sessions, of which the positive feedback phase was either associated or not with an auditory cue. The following week, cueing was done during home-based REM sleep using a wearable EEG device. For participants in the experimental condition, the change in dream fear between the weeks before and after exposure was positively correlated with anxiety-related distress scores and spontaneous electrodermal activity, as measured at the end of the experimental procedure.

Schredl and colleagues (Schredl et al., 2014) paired images of either urban or rural landscapes with one of two distinct odours, which were then presented again during REM sleep. The presentation of the odour associated with rural pictures seemed to increase the frequency of rural-related dreams, but this effect was not observed for city topics. There was no evidence of stimulus-dependent modulation of the emotional tone of the dreams, and only two dream reports included some reference to smell, one of which was not preceded by any odour stimulation.

Finally, Conduit and Coleman implemented a protocol in which citrus juice, known to induce saliva production, was paired with the flashing of two red lights during wakefulness (Conduit & Coleman, 1998). The visual cue was then presented in REM sleep during a daytime nap. While salivary excretion rates measured upon awakening were significantly higher after cueing than after unstimulated REM awakenings, none of the 14 collected dreams included any content related to food, hunger, thirst, drinking, or citrus juice (i.e., indirect incorporation). Nonetheless, one-third of stimulated dreams showed signs of direct incorporation of the cue.

*2.3.3.6.2. TLR*

Erlacher and collaborators published three TLR studies that included non-lucid dreaming data (Erlacher, Schmid, Bischof, et al., 2020; Erlacher, Schmid, Schuler, et al., 2020; Schmid & Erlacher, 2020). The first evaluated the effectiveness of associating reality-testing techniques with an odour that would serve as a lucidity cue when presented during REM sleep (Erlacher, Schmid, Schuler, et al., 2020). Out of 16 participants, only one reported incorporating the stimulus, leading to lucidity.

The remaining studies were based on auditory cueing. Volunteers received specific training in performing reality tests for becoming lucid whenever they heard the cue—either a short phone ringtone (Erlacher, Schmid, Bischof, et al., 2020) or a music track (Schmid & Erlacher, 2020) —, which was then repeatedly presented during REM sleep. In the first study, 12 out of 40 TLR dream reports were judged as presenting some degree of direct incorporation of the ringtone; in two cases, this also led to lucid dream episodes. Three TLR reports showed potential indirect incorporation (i.e., the appearance of a phone within the dream), and the difference in incorporation rates between control and stimulation nights was significant (Erlacher, Schmid, Bischof, et al., 2020). In the second study, music as a theme was present in eight out of 38 late REM dreams without there being any differences between stimulated (4/24) and control (4/14) trials (Schmid & Erlacher, 2020). Direct incorporation of the stimulus within a dream unrelated to music led to a lucid dream episode, whereas lucidity was not reached when the stimulus was indirectly incorporated.

An interesting observation from all three studies is that the realisation of being within a dream seems to be more commonly triggered when the stimulus is directly incorporated as an out-of-context element relative to when the stimulus is transformed to fit into the ongoing dream narrative.

## 2.4. Discussion

In the following sections, we summarise the main observations reported in the literature regarding the effects of sensory stimuli on dreams and highlight key issues and open questions for future research.

### 2.4.1. Types of SDDCs

Most studies failed to provide any clear definition of what the authors considered SDDCs. However, cases of stimulus incorporation have been further classified by several authors as either direct or indirect incorporations (R. J. Berger, 1963; Castaldo & Holzman, 1969; Koulack, 1969), although often with different terms. Additionally, some studies have described SDDCs that do not fall into the above categories, which we collectively labelled as dream modulations.

Given the current state of the literature, a specific assessment regarding the comparative incidence and underlying mechanisms of the several types of SDDCs is currently lacking and impossible to achieve. Therefore, future research should consider at least two significant limitations encountered in prior studies. First, experimenters or blind raters can miss indirect incorporations and modulations. Indeed, forms of indirect incorporation based on idiosyncratic memories and beliefs may remain undetected unless the dreamer is directly involved in their identification (R. J. Berger, 1963). Moreover, dream modulations may take various forms, some of which may be difficult to anticipate. Therefore, the possibility of detecting such SDDCs depends on the specific study hypotheses and assumptions. Second, as discussed below, perceptual distortions of the stimuli may affect the ability of raters to identify instances of direct or indirect incorporation of the transformed stimuli.

### 2.4.2. Differences Between Sensory Modalities

Almost all included studies focused on one sensory modality, limiting the possibility of direct comparisons regarding the impact and efficacy of distinct sensory stimuli in inducing SDDCs. Only one investigation

(Dement & Wolpert, 1958) used different sensory stimuli (audio, visual, and somatosensory) within the same experimental protocol, sleep stage (REM), and participant sample. This work reported differences in the effectiveness of distinct sensory stimuli at inducing direct or indirect incorporations, with water spray being the most effective and a pure tone being the least effective. However, the reported data were pooled across participants, and the results remained at the descriptive level. Bearing this limitation in mind, studies on single modalities appear overall consistent with the reported findings. Indeed, somatosensory stimuli were typically reported as relatively effective at inducing SDDCs. In contrast, the success of auditory stimuli appeared to vary significantly depending on the stimulus characteristics, being lower for pure tones and higher for semantically charged stimuli.

It is interesting to note that olfactory stimuli are rarely associated with direct incorporations but tend to influence emotional aspects of oneiric experiences. Only one study (Trotter et al., 1988) reported incorporations for about one-fifth of the presented olfactory stimuli. However, as noted elsewhere (Schredl et al., 2009), the study lacked appropriate control for potential odour appraisal upon awakening and used potentially arousing trigeminal odours. The lack of an EEG arousal response for pure odours has been suggested to explain their low incorporation rate. In contrast, their impact on dreams' emotional tone could reflect the direct connection of the olfactory bulb to the amygdala (Schredl et al., 2009). Another interpretation is that specific functional mechanisms could prevent odours from appearing in dreams, in line with the meagre rate of spontaneous olfactory experiences observed in dream diaries (~1%) (Schredl, 2019). Studying congenitally blind individuals, who often present a substantial increase in the incidence of chemosensory content in dreams, could provide further insight into this matter (Meaidi et al., 2014).

Another interesting observation concerns the incorporation of visual stimuli. Indeed, the direct incorporation of flashing lights appeared to be relatively frequent, with light stimuli frequently being

incorporated as a flashing of the entire scene or of specific objects within the dream (Konkoly et al., 2021). On the other hand, visual stimuli rarely seemed to trigger indirect incorporations or direct incorporations of complex stimuli. Since almost all our dreams are predominantly visual (Meaidi et al., 2014), this might reflect a competition between ongoing visual experiences and bottom-up visual inputs.

### 2.4.3. Factors Influencing SDDCs

The reported probability for sensory stimuli to induce changes in dream content greatly varied across studies, ranging from ~0% (Rechtschaffen & Foulkes, 1965) to ~80% (Nielsen et al., 1993). Besides intrinsic differences between sensory modalities and possible experimental differences among studies, several factors have been suggested to contribute to this variability.

#### 2.4.3.1. Subjective Relevance of the Stimulus

The fact that stimulus relevance may modulate the probability of inducing an SDDC is especially evident for auditory stimuli. Indeed, semantic auditory stimuli bearing particular significance to the sleeper appear to be incorporated more frequently than less relevant sounds, such as pure tones. Similarly, it has been proposed that the higher incorporation rates for somatosensory stimuli compared to other sensory modalities could be attributed to their greater relevance for the sleeping organism, as physically close stimuli may indicate more imminent danger than distant ones (Schredl et al., 2009).

#### 2.4.3.2. Stimulus Intensity and Duration

The physical properties of a stimulus, such as its intensity or duration, have been suggested to affect its probability of inducing SDDCs (R. J. Berger, 1963; Castaldo & Holzman, 1967, 1969; Castaldo & Shevrin, 1970; Conduit et al., 1997; Fedyszyn & Conduit, 2007). Indeed, one study (Bradley & Meddis, 1974) observed a positive association between stimulus intensity and the probability of incorporation during REM sleep. However, since most studies applied a predefined

stimulation intensity, this observation requires further validation. The possible impact of stimulus duration or repetition is even less clear. Some authors specifically employed longer or repeated stimuli, suggesting that this could increase the incorporation probability. Nevertheless, stimulus repetition may reduce the relative saliency of the stimulus (Jasper & Sharpless, 1956) and thus its ability to induce an SDDC. Unfortunately, studies directly investigating the impact of repeated versus rare stimuli on SDDCs are still lacking.

#### 2.4.3.3. Coherence Between Stimulus and Oneiric Experience

Stimulus incorporation often occurs seamlessly within the ongoing dream narrative (R. J. Berger, 1963; Dement & Wolpert, 1958; Koulack, 1969). Considering this, several authors suggested that a stimulus might have a greater chance to be incorporated if it somewhat fits—or could be 'transformed' to fit—into the oneiric experience. Indeed, incorporating sensory stimuli as alien, out-of-context elements (e.g., a verbal stimulus directly incorporated as an 'external voiceover') seems less common. In these instances, dreamers may recognise the incoherence of the stimulus to the ongoing dream scenery and thus become aware that they are dreaming. This reasoning suggests two potential implications. On the one hand, identifying and using stimuli that are unlikely to fit into most dreams could increase the probability of inducing lucid dreams. On the other hand, knowing what a person is likely to dream about (e.g., typical or recurring dreams) may help select stimuli that are more likely to be incorporated.

#### 2.4.3.4. Sleep Stage and Time-Of-The-Night

About half of the reviewed articles investigated NREM (usually N2) and REM sleep, but only a few performed direct comparisons across stages. Of these, some reported a higher rate of SDDCs in REM relative to NREM sleep (Conduit & Coleman, 1998; Fedyszyn & Conduit, 2007; Tilley et al., 1987), some found more SDDCs in NREM than REM dreams (Castaldo & Shevrin, 1970), and others found similar SDDC rates for the two stages (Burton et al., 1988; Zimmerman, 1970). Therefore, no conclusions can be drawn regarding potential differences

across sleep stages. Moreover, although some studies tried to stimulate both early and late in the night, specific time-of-the-night effects on SDDCs and their relationship to different sleep stages remain to be systematically evaluated.

#### 2.4.3.5. Stimulation-To-Awakening Interval

The reviewed studies reported important methodological differences concerning the time interval between stimulation and dream report collection, which ranged from a few seconds to several hours. The impact of this variable is likely to be significant but has never been systematically addressed. Still, an increased SDDC probability has been shown for dreams collected during the second and fourth REM periods, even though only the second REM period had been stimulated (Rahimi et al., 2015). Moreover, increased rates of incorporation were observed two (for NREM) to six (for REM) days after a TMR experimental session (Picard-Deland & Nielsen, 2022). While preliminary, these findings suggest that SDDCs could occur with a delay spanning minutes, hours, or even days.

### 2.4.4. Sleep Sensory Disconnection and SDDCs

Dreams and SDDCs seem to have tight reciprocal links with the sensory disconnection mechanisms that preserve sleep continuity. Indeed, such mechanisms could filter out or attenuate some of the stimuli from the external environment. On the other hand, dreaming and SDDCs might be among the lines of defence adopted by the sleeping brain to tame potential sleep-disturbing stimuli.

#### 2.4.4.1. The Effects of Sensory Disconnection on SDDCs

Three main, non-mutually exclusive mechanisms have been suggested to sustain sensory disconnection during sleep (Andrillon & Kouider, 2020; Nir & Tononi, 2010). The so-called 'thalamic gating' hypothesis (McCormick & Bal, 1994) proposes that sensory information may be blocked or attenuated at the thalamus level before reaching the cortex. Related to this, the notion of ‘cortical gating’ refers to the fact that the information reaching sensory cortices may not propagate efficiently

towards other cortical areas. Lastly, an 'informational gating' mechanism has been hypothesised to be active during REM sleep and dreaming experiences, when the focus of cognitive resources on endogenous processes could prevent sleepers from processing incoming sensory stimuli (Foulkes, 1966).

Sensory disconnection mechanisms likely have a key role in determining whether a stimulus will affect an ongoing dream. However, they may also determine a partial distortion of external stimuli, which may ultimately increase the variability and, therefore, decrease the detectability of SDDCs. Indeed, incoming information may be partially altered or attenuated before or at the cortical level. Moreover, while the dreamer is immersed in the oneiric experience, the stimulus may be misperceived or even entirely missed, just as someone busy on a particular task may fail to perceive or misperceive something happening out of their attention focus. Following this, expectancy based on the dream context and internal logic may bias the perception of the stimulus towards something that fits the ongoing oneiric setting. Inevitably, such effects could add up to the stimulus's alterations or attenuations that may have taken place at any previous processing step.

2.4.4.2. The Role of SDDCs in Sensory Disconnection

A long-standing view, already proposed by Freud, is that dreams could represent the 'guardians of sleep' (Freud, 1990; see also Appendix I: Supplementary Text 1). In this view, when an external stimulus reaches the sleeping brain, "*either the mind does not concern itself at all with the causes of sensations' or 'if it is obliged to recognise the stimuli, […] the actual sensation is woven into the dream in order to deprive it of its reality*." In other words, when an external stimulus succeeds in reaching the dreamer's awareness, the brain might attempt to integrate it into the ongoing conscious stream, directly or through associations, to minimise potential effects on sleep continuity.

In line with this, two studies (Shapiro et al., 1963, 1965; see also pilot data in Schabus et al., 2012) suggested that arousal thresholds may be higher when stimuli are successfully incorporated into the dream

experience than when they are not incorporated or when no dreams are experienced. Hence, dreams may provide two-level protection: 1/ at a lower level, the stimulus may fail to reach awareness because the dreamer's attention is focused on the internally generated experience ('competition'); 2/ at a higher level, the stimulus may be integrated into the ongoing dream and is thus not recognised as an external and potentially arousing element ('integration').

Observations consistent with the sleep-protective role of SDDCs were also made in children aged 3 to 15 (Foulkes, 1982; Foulkes et al., 1969). In a series of experiments with different stimuli and age groups, Foulkes observed that stimulus incorporation rates in REM sleep were close to zero for the youngest groups and tended to increase with age, whereas the probability for stimulations to induce body movements, indicating arousal, decreased substantially with age.

However, not all evidence supports the described relationship between incorporation and arousal threshold. Indeed, no differences were found between individuals with high and low arousal thresholds regarding incorporation (Zimmerman, 1970). Although this discrepancy could be explained using between-participant designs instead of within-participant designs, additional research is required to clarify the role of stimulus incorporation in sleep sensory disconnection.

### 2.4.5. Open Questions and Future Directions

#### 2.4.5.1. The Neurophysiological Correlates of SDDCs

Although none of the studies reviewed in the present work directly investigated the neural correlates of SDDCs, we discuss the possible relationship between SDDCs and typical stimulus-evoked responses such as (micro)arousals or K-complexes, and we propose some hypotheses regarding the functional mechanisms that may underlie the different SDDC types.

*2.4.5.1.1. Microarousals*

The presentation of sensory stimuli during sleep is often accompanied by activations of the arousal system and the appearance of microarousals. Some authors hypothesised that the occurrence of states characterised by wake-like activity may be necessary for SDDCs—and specifically for stimulus incorporation—to occur (Koulack, 1969; Nielsen, 1993; Zimmerman, 1970). Following this viewpoint, several studies used 'cortical registration,' referring to microarousal-like responses in the EEG signal, as a trial-selection criterion indicating that the administered stimulus had reached the cortex (R. J. Berger, 1963; Castaldo & Holzman, 1967, 1969; Castaldo & Shevrin, 1970). However, only one study provided direct evidence in support of the arousal-dependency of SDCC, noting that stimulations followed by increases in alpha activity—typically accompanying microarousals—had a higher rate of incorporation relative to cases without alpha changes (Koulack, 1969).

The apparent positive correlation between stimulus relevance and the probability of arousal response and incorporation (Bonnet, 1989; Langford et al., 1974; Lavigne et al., 2000, 2004; Oswald et al., 1960; Rechtschaffen et al., 1966), and the common observation that non-arousing odour stimuli almost never lead to stimulus incorporation (Okabe et al., 2018, 2020; Schredl et al., 2009) provide additional indirect supporting evidence. However, some authors reported no discernible differences in SDDC occurrence for stimuli followed or not by changes in alpha activity (R. J. Berger, 1963; Hoelscher et al., 1981; Leslie & Ogilvie, 1996). Moreover, evidence of SDDCs has been reported in experimental studies that excluded microarousals from the analyses (Hoelscher et al., 1981; Koulack, 1969). These findings imply that, while visually detectable microarousals may be associated with SDDCs, they are unlikely to be a prerequisite for stimulus incorporation.

*2.4.5.1.2. K-Complexes*

Sensory stimuli presented during NREM sleep are known to evoke K-complexes (KCs; Halász, 2016; Schabus et al., 2012), but no studies have investigated the effects of these events on SDDCs. Since KCs reflect widely synchronised episodes of neuronal silence, they are commonly thought to have a sleep-protective function (Cash et al., 2009; Forget et al., 2011). In fact, they have been suggested to quench incoming sensory information to promote sleep continuity (Halász, 1993; Laurino et al., 2014). According to this view, a stimulus that evokes a KC should not be capable of influencing the ongoing dream experience. Instead, KCs may briefly disrupt the stream of consciousness through a widespread suppression of brain activity. However, the subsequent increase in high-frequency activity or full-fledged arousals often observed after KC suggests a temporary restoration of the brain's ability to integrate salient information (Halász, 1993; Legendre et al., 2019). This, in turn, could favour the processing and incorporation of stimuli administered after the KC. Altogether, it seems that both a suppressing and a promoting effect of KC on SDDCs may coexist on different timescales.

2.4.5.2. Functional Mechanisms Underlying SDDCs

The reviewed literature offered no hints as to which physiological mechanisms might underpin the distinct types of SDDCs. However, we may provide some hypotheses based on prior findings that showed a relationship between dream occurrence and local increases in wake-like activity, with the regional distribution of such activations corresponding to dream content (Perogamvros et al., 2017; Siclari et al., 2017, 2018). Considering this, direct incorporations could be explained by stimulus-dependent activations of brain areas involved in low-level sensory processing. Moreover, whether the stimulus is fully incorporated into the dream or remains as an alien element may depend functionally on its coherence with the ongoing experience and physically on the relative integration of the newly engaged areas within the previously activated brain network (e.g., Sasai et al., 2016; Figure 5).

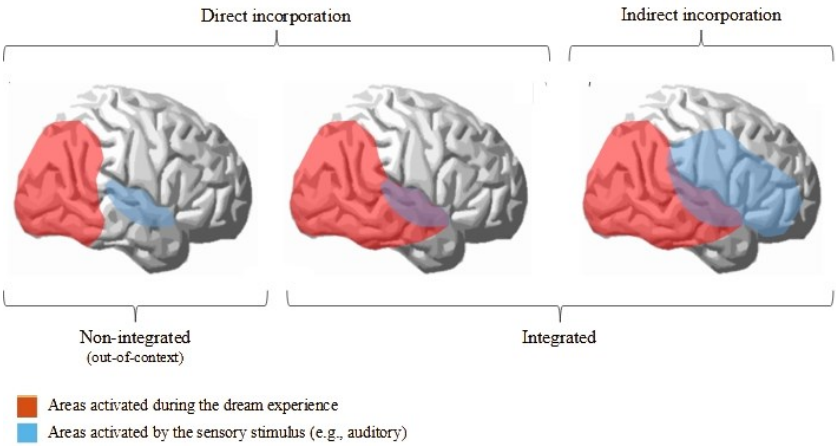



**Figure 5. Schematic representation of hypothetical neurophysiological mechanisms underlying the incorporation of sensory stimuli in dreams.**

Cases of indirect incorporation might instead reflect the reactivation of brain areas storing memories somehow linked to the stimulus (Favila et al., 2020), implying a higher-level processing of incoming information. Interestingly, one could hypothesise that a similar process may be involved in some forms of dream modulation. Alternatively, dream modulation could emerge in response to non-specific activations of ascending, arousal-related systems targeting multiple brain areas. Future studies on SDDCs should combine a rigorous definition of SDDC types and advanced neuroimaging techniques, such as high-density EEG or simultaneous EEG-fMRI, to test these hypotheses.

#### 2.4.5.3. Are We Truly 'Disconnected' During Sleep?

A common assumption in sleep research is that differences in stimulus processing between sleep and wakefulness should inform us of how sensory disconnection occurs during sleep. However, our review revealed several important flaws in this logic. Evidence indicates that many stimuli not only reach the cortex and influence brain activity

during sleep, but a significant portion of them may also be incorporated into the ongoing stream of consciousness. Still, understanding how and when this occurs is far from simple. Several factors, such as stimulus distortion or transformation, may prevent incorporations from being identified. In addition, dreamers may fail to report the perceived stimulus due to its potentially scarce relevance for the experience or an incomplete recall of the dream upon waking.

Real-time communication protocols with lucid dreamers overcome limitations related to dream retrieval and reporting (Konkoly et al., 2021; Türker et al., 2023), showing that dreamers might be able to consciously perceive -and even appropriately respond to-complex stimuli. Notably, one recent study provided evidence for transient windows of cognitive processing and behavioural responsivity to external stimuli during N1, N2, and REM sleep, suggesting that high-level stimulus processing may extend beyond the specific case of lucid dreaming (Türker et al., 2023). While further research is required to clarify the frequency and nature of observed 'sensory connection' windows, we suggest that the conscious processing of external sensory information during sleep may be considerably more prevalent than previously believed.

### 2.4.6. Conclusions

The ability to manipulate oneiric experiences holds the promise of substantial scientific breakthroughs, ranging from understanding the origin and function of dreams to developing new treatments for clinical conditions associated with dream alterations. Consequently, the recent surge in dream engineering is unsurprising (e.g., Carr, Haar, et al., 2020; Carr, Konkoly, et al., 2020; Haar Horowitz et al., 2018; Kamal et al., 2012). The utilisation of sensory stimuli is particularly relevant among the various dream engineering techniques due to its reliance on well-established physiological pathways and functions, ease of implementation, and extensive history of anecdotal and empirical observations. However, the present review revealed a substantial lack of understanding of the processes regulating external sensory stimuli's

effects on dreams. We highlighted several major concerns and open questions, hoping this work will advance the field by stimulating novel, rigorous, collaborative research efforts.

# Chapter 3.
# Lucid Dream Induction Using Cognitive-Sensory Training

The study presented here is part of a pre-registered (https://osf.io/zfs57/) multi-centric research project in collaboration with two partner institutions: the Donders Institute (the Netherlands) and University of Montréal (Canada). The results reported in this chapter exclusively concern the data collected at the SPACE sleep laboratory (IMT School for Advanced Studies Lucca, Italy). This chapter and the corresponding appendices are adapted from preliminary results published as a pre-print:

*Esfahani, M. J.*, **Salvesen, L.***, Picard-Deland, C.*, Matzek, T., Demsar, E., Buijtene, T. van, Libucha, V., Pedreschi, B., Bernardi, G., Zerr, P., Adelhöfer, N., Schoch, S., Carr, M., & Dresler, M. (2024). Highly effective verified lucid dream induction using combined cognitive-sensory training and wearable EEG: A multi-centre study (p. 2024.06.21.600133). bioRxiv.* *Co-first authors
https://doi.org/10.1101/2024.06.21.600133

## 3.1. Introduction

Lucid dreaming, the state in which one becomes consciously aware of dreaming, is a fascinating yet relatively rare phenomenon. Although approximately half of the population has experienced a spontaneous lucid dream (LD) at least once, such occurrences remain infrequent (Saunders et al., 2016). Lucid dreaming presents a unique opportunity to explore the neuroscience of dreams by allowing the use of measurable lucidity verification techniques, such as predefined eye movements, breathing patterns, or facial muscle contractions (Baird et al., 2022; Holzinger et al., 2006; Konkoly et al., 2021; LaBerge et al., 1981). This ability to verify lucidity enhances experimental control over dream content and duration, enables real-time external monitoring, and even allows for two-way communication with dreamers (Baird, Mota-

Rolim, et al., 2019; Dresler et al., 2012, 2015; Filevich et al., 2015; Konkoly et al., 2021).

Moreover, increasing the level of insight and control within dreams holds promise for various clinical applications, such as treating nightmare disorder (Aurora et al., 2010; de Macêdo et al., 2019; Morgenthaler et al., 2018; Sandell et al., 2024; Spoormaker & van den Bout, 2006), post-traumatic stress disorder (Holzinger et al., 2020; Yount et al., 2023), insomnia (Ellis et al., 2021b),, and narcolepsy (Rak et al., 2015), as well as for personal, recreational, and creative purposes (Gott et al., 2020; Zink & Pietrowksy, 2013). As such, a key challenge in current dream research lies in developing reliable methods for inducing lucid dreams in everyday settings, clinical environments, and laboratory conditions (Adventure-Heart, 2020; Mota-Rolim et al., 2019).

Previous attempts to induce LD have explored a wide array of approaches, including cognitive training (Adventure-Heart, 2020; Adventure-Heart et al., 2017; Appel et al., 2020; Baird, Riedner, et al., 2019; Dyck et al., 2017, 2018; Erlacher & Stumbrys, 2020; Saunders et al., 2017; Schredl et al., 2020; Taitz, 2011), external sensory stimulation during REM sleep (Erlacher, Schmid, Bischof, et al., 2020; Erlacher, Schmid, Schuler, et al., 2020; Kumar et al., 2018; Paul et al., 2014; Schmid & Erlacher, 2020), pharmacological interventions (Kern et al., 2017; LaBerge et al., 2018), brain stimulation (Blanchette-Carrière et al., 2020; Stumbrys et al., 2013; Voss et al., 2014), and combinations of different methods (Adventure-Heart, 2020; Carr, Konkoly, et al., 2020; Erlacher, Schmid, Bischof, et al., 2020; Erlacher, Schmid, Schuler, et al., 2020; Saunders et al., 2017; Schmid & Erlacher, 2020). Comprehensive reviews of these induction techniques are available elsewhere (Stumbrys et al., 2012; Tan & Fan, 2023). Despite extensive efforts, many of these approaches have demonstrated only limited to moderate success in reliably inducing objectively verified lucidity.

The most promising results in LD induction have been achieved through targeted lucidity reactivation (TLR) protocols, which currently hold the highest success rate in laboratory settings (Carr, Konkoly, et al., 2020). This method combines pre-sleep lucidity training

with sensory cues that are replayed during subsequent sleep. TLR based on visual and auditory REM cueing has been shown to successfully induce lucid dreams in 50% of participants (Carr et al., 2020). Furthermore, participants were able to objectively verify lucidity by signalling awareness within the dream through a predefined eye movement pattern (left-right-left-right, LRLR).

However, current research on lucid dream induction techniques faces several significant limitations, including small sample sizes, heavy reliance on self-reported questionnaires without physiological validation, and a focus on individuals with high baseline experience in lucid dreaming (≥ 1 episode per month; Snyder & Gackenbach, 1988). These factors restrict the generalisability of findings to the broader population. To address these issues, we designed a study to validate a novel combination of LD induction techniques in a large and diverse sample with varying levels of prior lucid dreaming experience. Our induction method combines a cognitive training based on the senses-initiated lucid dreaming technique (SSILD; Adventure-Heart, 2020) with multimodal (visual, auditory, and tactile) TLR during REM sleep, utilizing commercially available wearable devices. We compared the effects of SSILD training with and without REM cueing during morning naps in a laboratory setting, following a within-subject design. We hypothesized that REM cueing would significantly enhance dream awareness and control compared to no cueing.

## 3.2. Methods

This study is part of a multi-centre project involving data collection in three sleep laboratories located in the Netherlands (Donders Institute), Canada (Université de Montréal), and Italy (IMT School for Advanced Studies Lucca). The experimental protocol was pre-registered prior to data collection at any of the participating centres (Salvesen, Esfahani, Picard-Deland, et al., 2024). To achieve a pooled sample size of N = 60, each centre collected data from 20 participants, all of whom completed two nap sessions with at least one REM episode per session, following a within-subject design. We used minimal sensing systems, specifically

an EEG wearable headband (ZMax, Hypnodyne Corp., Sofia, Bulgaria) supplemented with three additional chin EMG electrodes, monitored through an open-source dream engineering toolbox, *Dreamento* (Esfahani, Daraie, et al., 2023). For the purposes of this report, we will focus exclusively on the data collected from the Italian centre.

### 3.2.1. Participants

Participants were recruited through various methods, including flyers, word of mouth, and online platforms such as blogs and social media. Compensation for each experimental nap session was set at 35 EUR, totalling 70 EUR for the entire study. The study was approved by the joint local ethical committee of Scuola Superiore Sant'Anna and Scuola Normale Superiore.

Interested individuals were initially screened based on general inclusion and exclusion criteria. The inclusion criteria required participants to be healthy, aged between 18 and 55, maintain a regular sleep-wake pattern, have experienced at least one prior lucid dream, and recall dreams frequently (> 3 times per week). Exclusion criteria included a history of neurological, psychiatric, or neurodegenerative disorders, previous brain surgery, an epilepsy diagnosis, pregnancy, and the use of sleep-altering medication. Participants also completed a series of questionnaires and underwent further screening for depression (Beck Depression Inventory (BDI-II), score ≥ 20), anxiety (Beck Anxiety Inventory, score > 15), prodromal symptoms (Prodromal Questionnaire 16-item version, score ≥ 9), sleep quality (Pittsburgh Sleep Quality Index, score > 7), and chronotype (Morningness-Eveningness Questionnaire, with sleep time before 23:00 or rise time before 07:00). Additionally, participants provided detailed information on their sleep, dreams, and waking cognition through the Mannheim Dream Questionnaire and the Vividness of Visual Imagery Questionnaire.

### 3.2.2. Study Procedure

Following an online screening process, eligible participants were invited to an intake session, where they received detailed information about the study and provided informed written consent. Participants then attended two morning nap sessions at the laboratory, scheduled approximately one and two weeks after the intake session. In preparation for the experimental sessions, participants were asked to maintain a home dream diary, beginning roughly one week before the first nap session and continuing until the second nap session, spanning a total of about two weeks (Figure 6).

Both nap sessions involved an SSILD cognitive training procedure paired with a set of sensory cues during wakefulness. In one session, these cues were also presented during subsequent REM sleep periods (REM cueing session), while the other session served as a control with no cueing during REM sleep (REM sham session), with the order of sessions counterbalanced across participants. During the sessions, participants were instructed to signal lucidity or cue perception in real-time during sleep using a predefined eye movement pattern (LRLR) and to report any subjective experiences upon awakening.

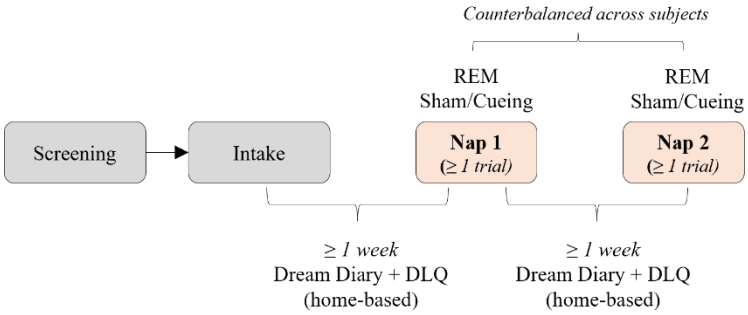



**Figure 6. General timeline of the study procedure.**
DLQ: Dream Lucidity Questionnaire

In this study, a nap 'trial' refers to each sleep opportunity within an experimental nap session. A trial was considered valid if the stimulation procedure—whether cued or sham—was correctly applied during REM sleep according to the session's condition. A participant qualified as valid if they completed at least one valid nap trial in both experimental sessions; otherwise, a replacement participant was recruited to maintain the target sample size of N = 20. To ensure blinding to the experimental condition, participants were informed that cueing might or might not occur during each nap trial, regardless of the session. All analyses presented here are based exclusively on data from valid participants.

#### 3.2.2.1. Sleep and Dream Diaries

Participants were required to document their sleep-wake schedule and provide subjective assessments of sleep quality throughout the entire study. Additionally, they completed daily dream reports and Dream Lucidity Questionnaires (DLQ; Stumbrys et al., 2013) to practice the reporting procedure and enhance dream recall. These home diaries were accessed and stored online through CastorEDC, an electronic survey data management platform.

### 3.2.3. Experimental Nap Protocol

Participants arrived at the laboratory between 05:00 and 08:00 a.m., depending on their usual sleep-wake schedule and laboratory availability. They were asked to refrain from consuming any alcoholic or caffeinated beverages on the evening before and the morning of the nap sessions. The experimental protocol for the nap sessions (Figure 7) was based on a modified version of the SSILD procedure, adhering to the preregistered study protocol (https://osf.io/rh286). Both sessions followed an identical structure during the wakefulness period preceding sleep, consisting of 30 minutes of cognitive training combined with multimodal sensory stimulation. After the cognitive training, participants were permitted to sleep for up to 2.5 hours.

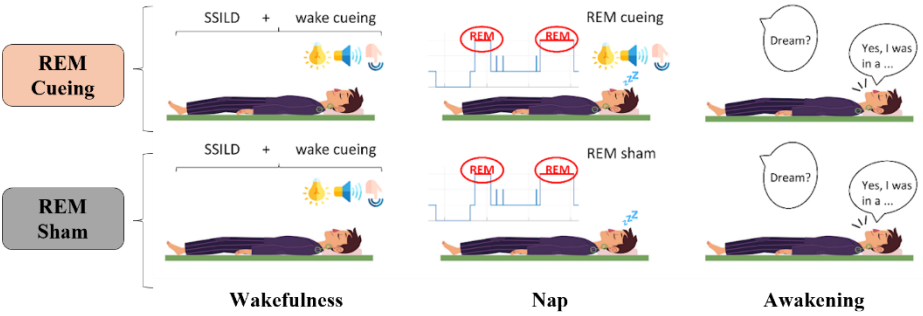



**Figure 7. Schematic representation of the protocol during the experimental nap sessions.**

3.2.3.1. Cognitive training

The cognitive training was delivered through a 30-minute vocal recording, organized into distinct blocks (see Appendix II: Supplementary Text 1 for the commented transcript of the training recording). Before starting the training, participants' baseline intensity thresholds for visual (minimum subjective light intensity) and auditory stimuli (minimum subjective audio volume), as well as the continuous background noise level, were individually calibrated based on their subjective assessment. Once these thresholds were set, the recording commenced.

Following a brief introduction, participants were guided through a series of SSILD cycles. They were instructed to lie with their eyes closed and focus their attention on each sensory modality (i.e., vision, hearing, bodily sensations). The cycles began with rapid shifts between modalities (2-3 seconds per modality), then moved to medium-length shifts (20 seconds), and finally to slower cycles (60 seconds). During the slow cycles, each sensory step was accompanied by the corresponding cue (i.e., light, sound, vibration), signalling the transition from one sensory focus to the next. In the first half of the slow cycles, a vocal prompt encouraged participants to maintain a lucid

mindset in sync with the sensory cues. In the latter half, the cues were presented without vocal prompts, allowing participants to implicitly consolidate the learned association and naturally drift into sleep.

#### 3.2.3.2. REM Cueing Protocol

Cueing during sleep began approximately 20 seconds after detecting the first rapid eye movement in the context of low EMG activity, which indicated the onset of phasic REM sleep. The sensory cues were presented in the same cyclic order as during the cognitive training cycles in wakefulness (i.e., visual, auditory, and tactile), with each cue delivered approximately every 20 seconds. The experimenter initiated the cue presentation at the previously determined lowest subjective perceptual thresholds. The intensity of each cue was gradually increased as long as REM sleep persisted without any signs of arousal. Specifically, audio and visual cues were increased by 5 dBA and 5% in each cycle, respectively, while vibration cues were escalated from a single repetition to up to three repetitions in subsequent cycles.

If the participant responded to a cue with the intentional predefined eye signalling (LRLR), the intensity levels of the cues were maintained unchanged until awakening. If signs of microarousal were detected—such as a relative increase in EMG activity or alpha wave activity—stimulation was temporarily halted and only resumed after these signs had fully dissipated. When cueing was resumed, the intensity levels were reduced to the settings used in the cycle preceding the arousal (i.e., decreasing light intensity by 5%, reducing audio volume by 5 dBA, and adjusting the tactile cue accordingly). Gradual intensity increments were then reapplied as described previously. At the end of each nap trial, the intensity levels for all cues were reset to their baseline levels.

#### 3.2.3.3. Dream Interview

Participants were awakened at the end of each REM period and asked to report any subjective experiences they could recall from the moments immediately preceding waking, including any sensations, feelings, thoughts, or emotions (see Appendix II: Supplementary Figure

1 for a representation of the dialogic flow of the semi-structured interview). They were also asked whether they had felt asleep during this period and if they were aware of their conscious state. Whenever possible, participants were encouraged to provide additional details about their experience, such as the estimated duration, specific content, perception of cues, and whether they performed the eye signalling.

After completing the semi-structured interview, participants were asked to fill out the DLQ based on their reported experience, except in cases where no conscious experience or where a conscious experience without recall was reported. Following this, an additional nap trial was initiated until the 2.5-hour session was complete. To maximize the likelihood of participants falling asleep multiple times within the allocated time window, the experimenter kept the interviews after intermediate nap trial awakenings brief, especially when no significant experience was reported.

Dream reports were also collected after spontaneous LRLR signal detection or in the event of experimental interruptions. Upon final awakening, after the 2.5 hours had elapsed, participants provided a final report and completed the LuCiD scale questionnaire (Voss et al., 2013) for each subjective experience reported during the session. If multiple trials were conducted during a single nap session, the measures from associated questionnaires (i.e., DLQ, LuCiD) were averaged across the session. These averaged values were then used for subsequent statistical comparisons between conditions.

#### 3.2.3.4. Lucidity Instructions

Participants were instructed to perform a predefined LRLR eye movement sequence in the following scenarios: 1/ upon becoming aware that they were dreaming, to provide an objective marker for the initiation of the lucid episode; 2/ each time a sensory cue was perceived during sleep, offering a physiological marker for potential incorporation of the stimuli into the dream; and 3/ approximately every 30 seconds if no sensory cue was perceived, to help estimate the duration of the lucid dream. This approach aimed to provide more

objective measures of both the initiation and duration of each lucid dreaming episode.

Participants were also informed about the high likelihood of dreaming about the sleep laboratory and experiencing false awakenings. They were instructed to perform a reality check—such as attempting to breathe through a pinched nose or counting their fingers—whenever they felt uncertain about whether they were awake or dreaming. Additionally, if participants entered a state of dream lucidity, they were encouraged to explore or observe the dream scene and to avoid engaging in highly stimulating activities, such as flying or free-falling, during the first few seconds of lucidity. This strategy was intended to increase the chances of maintaining lucidity for a longer duration.

### 3.2.4. Physiological Data Collection

Physiological data measurements were collected using *ZMax* EEG headbands (Hypnodyne Corp., Sofia, Bulgaria), a validated sleep wearable device (Esfahani, Weber, et al., 2023) equipped with various sensors, including two frontal EEG channels (F7-Fpz, F8-Fpz), an accelerometer, a photoplethysmography sensor, ambient light and sound sensors, and a thermometer. In parallel, three EMG channels recorded muscular activity from the chin area using a g.USBamp Research system (g.tec medical engineering GmbH, Graz, Austria). Data acquisition was managed through system-specific software (g.Recorder for g.tec Suite).

We used the open-source dream engineering toolbox, Dreamento (Esfahani, Daraie, et al., 2023), for real-time EEG signal monitoring, recording, sensory stimulation, and offline data analysis. For redundancy, ZMax signals were also recorded using the manufacturer's proprietary software, as recommended (Esfahani, Daraie, et al., 2023).

The session began with determining individual stimulation thresholds, followed by a one-minute calibration period of closed-eye

resting wakefulness to establish baseline physiological measures. Participants were then instructed to clench their teeth three times to synchronize the EMG recordings with the headband data at the beginning and end of the session. This synchronization was repeated after each awakening or experimental interruption. The EEG and EMG signals were later synchronized offline using specific functions in Dreamento. Participants also performed the predefined LRLR lucidity signal with their eyes closed, which served as a reference for identifying their unique eye movement patterns during sleep. After the calibration period, the cognitive training session began.

### 3.2.5. Sleep Scoring

The data collected from each site underwent sleep scoring by researchers from the other two participating laboratories to ensure objectivity. Manual scoring was conducted using *Offline Dreamento* and included the evaluation of sleep stages, arousals, and predefined eye signals. The raters were blinded to both the experimental condition and the real-time annotations from the experimenter, and had no access to the participants' subjective data, such as dream reports or questionnaires.

Inter-rater agreement for scoring each nap session was assessed using Cohen's kappa statistic. Due to the occasional difficulty in differentiating between wake and N1 stages—particularly when frontal alpha activity was not clearly visible and in the absence of occipital EEG channels—we opted to merge both stages when calculating inter-rater agreements. If the agreement scores for a nap session fell below the 80% threshold, the scorers would reevaluate the conflicting epochs until a consensus was reached. Sleep assessment metrics were further analysed using a dedicated Python toolbox (*YASA*; Vallat & Walker, 2021).

### 3.2.6. Lucid Dream Classification

In this study, a signal-verified lucid dream (SVLD) was confirmed when both objective and subjective indicators of lucidity were present:

specifically, when a predefined eye movement was detected, and the participant reported becoming lucid and intentionally performing that signal. A lucid dream was classified as non-signal verified (non-SV LD) if the participant reported becoming lucid or indicated being at least moderately aware of dreaming (scoring at least 2 out of 4 on the first question of the DLQ, "*I was aware that I was dreaming*"), but no corresponding predefined eye signal was reported or detected. Lucid episodes included both SVLD and non-SV LD episodes.

Additionally, dreams that were associated with a detected predefined eye signal but lacked awareness were classified as signalled non-LDs. Finally, dreams were categorized as non-LDs when participants neither reported any awareness of dreaming nor exhibited any predefined eye signals.

Predefined eye movements were assessed by the three main experimenters from the participating centres (LS, MJE, and CPD). A signal was considered valid only if it was confirmed by at least two of the three scorers. If a participant performed a lucidity signal that differed from the predefined LRLR sequence—such as a partial sequence like LRL or a slower version of the LRLR movement used during wakefulness—it was accepted as valid only if the participant reported an attempt to perform the predefined sequence. The duration of SVLDs was measured in two ways: 1/ the total SVLD duration, which spanned from the first to the last predefined eye signal within the same REM period, and 2/ the continuous SVLD duration, which considered only the time between consecutive eye signals occurring within one minute of each other. The one-minute threshold was chosen because, in cases where participants perceived only a single type of cue, that cue was presented every minute, based on the predefined 20-second inter-stimulus interval.

Average scores from the DLQ and LuCiD questionnaires were also used to assess various aspects of lucidity, including insight, control, thought, realism, memory, dissociation, negative emotion, and positive emotion (Voss et al., 2013).

### 3.2.7. Statistical and Methodological Evaluation

Statistical analyses were conducted using Python (version 3.10) and R (version 4.4.0; R Core Team) within the RStudio integrated development environment (version 2023.06.0; RStudio Team). Visualizations were created using Python's *matplotlib* library (Hunter, 2007) and R packages *ggplot2* (Wickham, 2016) and *raincloudplot* (Allen et al., 2021).

Descriptive statistics were reported to summarise the data, specifically the mean and standard deviation (m ± std). For hypothesis testing, paired t-tests were used to analyse continuous data that met normality assumptions, as confirmed by the Shapiro–Wilk and D'Agostino-Pearson tests. When normality assumptions were violated, Wilcoxon signed-rank tests were applied. McNemar's test was used to compare paired nominal data, such as the presence or absence of (SV)LD across experimental conditions. Eye signal response times across the three cue modalities were compared using Friedman's test. In line with our a priori hypothesis, statistical tests comparing lucidity-related measures between REM cueing and REM sham sessions were one-tailed, predicting higher values in the cueing condition. Conversely, comparisons of sleep assessment metrics between conditions were two-tailed, given the absence of directional hypotheses.

The methodological quality of this study was independently evaluated using an adapted version of the Downs & Black (1998) methodological quality checklist (see Chapter 2; Appendix I: Supplementary Text 1). This 23-item checklist assesses various aspects of internal and external validity, as well as the thoroughness in reporting methods and outcomes, resulting in a score ranging from 0 to 25. This standardized evaluation tool provides an objective measure of scientific rigor, specifically validated for use in sleep and lucid dreaming research (Stumbrys et al., 2012; Tan & Fan, 2023). The adapted version has been tailored to assess the quality of studies in the field of sleep and dream engineering (Salvesen et al., 2024).

## 3.3. Results

The methodological assessment for this study reached a score of 20 out of 25 (see Appendix II: Supplementary Table 1 for a detailed account of all checklist item scores). This score is a compound of the assessment of several aspects of the present manuscript: reporting (10/10), external validity (2/4), internal validity - comprising bias (6/7) and confounding (2/2) -, and power calculations (0/2).

### 3.3.1. Participants

A total of 57 participants were initially recruited for the study. Of these, 14 were excluded following the intake session due to exceeding threshold scores on baseline questionnaires. Additionally, 4 participants voluntarily withdrew after the intake session. Among the remaining participants, 13 failed to enter REM sleep during at least one of the experimental nap sessions, with 1 participant withdrawing voluntarily after the first session. Technical difficulties, including signal loss or high noise levels, occurred in 6 sessions, rendering those data unscorable and leading to the exclusion of those participants. The final sample comprised 20 valid participants (mean age: 30.75 ± 6.84 years; 9 females), on whom all subsequent analyses are based (Figure 8).

### 3.3.2. Sleep Measures

Following an initial round of independent sleep scoring by main experimenters from the other two study sites, Cohen's Kappa scores indicated nearly perfect inter-rater agreement levels when combining wake and N1 stages (Kappa = 0.83 ± 0.11). Nap sessions that did not meet the 80% agreement threshold (13/40 sessions) were re-evaluated the data until consensus was achieved.

Standard sleep metrics indicated that the REM cueing procedure did not significantly alter the global sleep architecture or efficiency (see Appendix II: Supplementary Table 2). However, two specific metrics differed significantly between REM cueing and REM sham naps. Sleep period time was longer during REM cueing sessions (164.03 ± 16.13 min) compared to REM sham sessions (151.65 ± 16.20

min; Wilcoxon signed-rank test, $W = 32$, $p = 0.005$). Additionally, the percentage of NREM 2 sleep relative to total sleep time was lower during REM cueing sessions (46.49 ± 11.78%) compared to REM sham sessions (54.95 ± 14.51%; paired t-test, $t = 2.48$, $p = 0.02$).

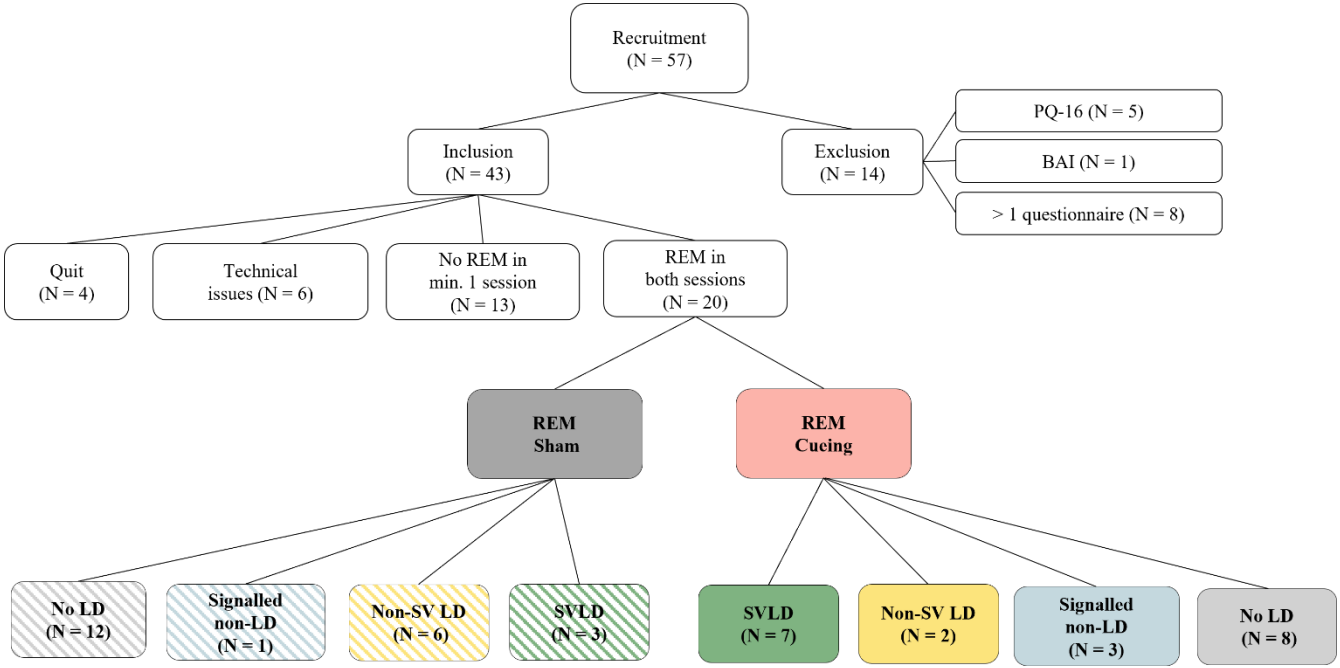



**Figure 8. Diagram of the participant selection process and lucidity-related outcomes for valid participants.**

LD: Lucid Dream; Non-SV LD: Non-Signal-Verified Lucid Dream; SVLD: Signal-Verified Lucid Dream; PQ-16: Prodromal Questionnaire; BAI: Beck Anxiety Inventory

### 3.3.3. Dream Measures

Among the 20 valid participants, 12 (60%) experienced at least one episode of lucidity in the laboratory, with 9 of them (45%) achieving signal verification (SVLD). When comparing lucidity rates across experimental conditions, we observed that 9 participants (45%) achieved lucidity during the REM cueing sessions, of which 7 (35%) included SVLDs. During the REM sham sessions, 9 participants (45%) attained lucidity, but only 3 of them (15%) presented SVLDs (Figure 8). Statistical analysis revealed that the occurrence of SVLDs was significantly higher in REM cueing sessions compared to REM sham sessions (McNemar test, $\chi^2(1) = 3.0$, $p = 0.021$).

To account for potential habituation effects between sessions, we assessed differences in the incidence of lucid episodes between the first and second experimental naps. The analysis revealed no significant difference in the occurrence of lucid episodes between the two sessions (Session 1: n = 11 (55%); Session 2: n = 7 (35%); McNemar test, $\chi^2(1) = 11.0$, $p = 0.84$). However, a trend-level difference was observed in for SVLD episodes (Session 1: n = 7 (35%); Session 2: n = 3 (15%); McNemar test, $\chi^2(1) = 7.0$, $p = 0.064$).

Notably, both signalled and non-signalled lucidity were successfully induced in participants who did not identify as highly experienced lucid dreamers (Figure 9). The following SVLD induction rates were observed: 20% (1/5) for those with less than yearly LD experiences, 0% (0/3) for those with approximately yearly LD experiences, 80% (4/5) for those with 2-4 times yearly LD experiences, 66.67% (2/3) for those with monthly LD experiences, 100% (2/2) for those with weekly LD experiences, and 0% (0/2) for those with more than once-a-week LD experiences.

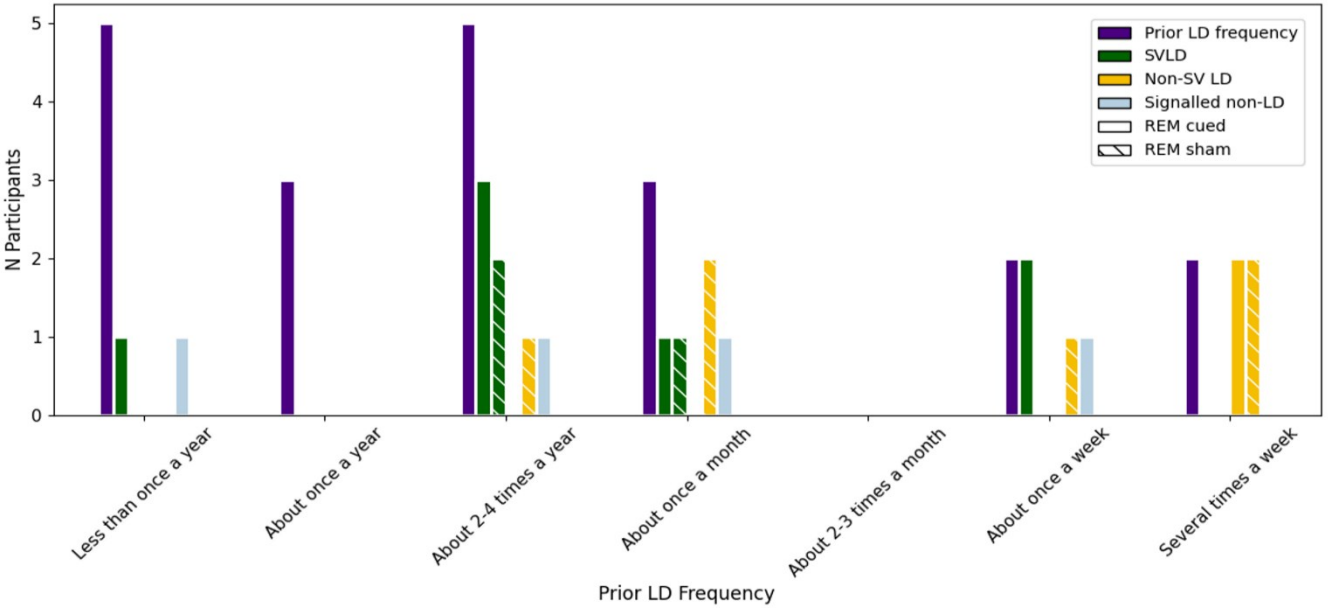



**Figure 9. Distribution of dream categories by experimental condition and prior lucid experience.**

SVLD: Signal-Verified Lucid Dream; Non-SV LD: Non-Signal Verified Lucid Dreams; Signalled non-LD: Signalled Non-Lucid Dreams

#### 3.3.3.1. Lucid Dream Classification

In total, 68 valid REM trials were collected: 33 from sham sessions and 35 from cued REM sessions (paired t-test, $t = -0.44$, $p = 0.67$). Of these, 9 trials (27.27%) from sham sessions and 12 trials (34.29%) from cued sessions included lucid experiences. Specifically, 3 (33.33%) of the lucid trials in the sham condition and 8 (75%) in the cued condition were SVLD, with the remainder classified as non-SV LD.

While the total number of trials resulting in a lucid experience (both SVLD and non-SV LD) did not significantly differ between the two conditions, SVLD trials tended to be more frequent in cued sessions ($0.40 \pm 0.60$) compared to sham sessions ($0.15 \pm 0.37$), approaching statistical significance (Wilcoxon signed-rank test, $W = 32.0$, $p = 0.07$). It is noteworthy that in three trials, participants reported signalling lucidity without any detected predefined eye movements (one in a sham session and two consecutive trials in a single cued session), which were therefore classified as non-SV LD episodes.

Additionally, four REM trials (three cued and one sham) exhibited predefined eye movements detected by the scorers without participants reporting lucidity, leading to their classification as signalled non-LD. In two of these cued REM trials, participants provided non-lucid dream reports but acknowledged perceiving sensory cues and responding with the predefined eye movement: in one case, the participant reported not feeling asleep, while in the other, the signalling occurred in response to the final sensory cue immediately before awakening. In the third cued REM trial, the participant confirmed perceiving and responding to multiple sensory cues but was unable to recall any dream content upon awakening, instead describing a state of confusion and not feeling fully asleep. The fourth case involved a sham REM trial, which resulted in a non-lucid dream report without any mention of signalling intention by the participant, potentially representing a false identification of the eye movement signal by the scorers.

#### 3.3.3.2. Predefined Eye Movement Signalling

A total of 58 predefined eye movements were detected during the study: 12 were spontaneous (10 observed during REM sham sessions and 2 during REM cueing sessions), while 46 were in response to sensory cues (including seven instances of repeated responses to cues that had already been signalled). A trend was observed suggesting a higher frequency of eye movements during cued REM trials (2.4 ± 6.56) compared to sham REM trials (0.5 ± 1.40), although this difference did not reach statistical significance (Wilcoxon signed-rank test, $W = 44.0$, $p = 0.09$).

When examining the impact of different cue modalities within REM cueing sessions, considering only the first eye signal following each cue, we found that 13 eye movements were in response to visual cues, 13 to auditory cues, and 13 to tactile cues. The average response time for predefined eye signalling following a sensory cue was 6.26 ± 7.86 seconds, with no significant difference between cue modalities (visual: 5.77 ± 8.96 s; auditory: 6.62 ± 6.42 s; tactile: 6.38 ± 8.58 s; Friedman test, $\chi^2$ (2) = 0.86, p = 0.65).

Among all SVLD trials, 8 included at least two predefined eye movements, allowing for a more accurate estimation of the episode's duration. These comprised 6 cued trials and 2 sham trials. The average total duration of SVLD episodes was 516.38 ± 612.81 seconds (REM cued: 506.33 ± 643.73 s; REM sham: 546.5 ± 744.58 s), with substantial variability, ranging from 12 to 1783 seconds (see light red highlights in Figure 10). Focusing on continuous SVLD episodes, defined as those with a maximum of 1 minute between consecutive signals, we identified 9 distinct bouts of continuous SVLD, averaging 83.22 ± 70.40 seconds. Of these, 8 occurred during cued REM sessions (91.13 ± 70.87 s), involving 31 ocular responses to sensory cues, and 1 during a sham REM session (20 s), involving 2 spontaneous eye signals (see dark red highlights in Figure 10). Unfortunately, due to the limited and uneven number of observations, statistical comparison was not feasible.


**Figure 10. Visualization of signal-verified lucid dream episodes and their estimated duration.**

The initial verified eye signal in each trial was aligned to t=0 and subsequent eye signals were plotted sequentially. Continuous (dark red; t: continuously verified lucid duration) and total (light red; T: total verified lucid duration) SVLD episode durations are indicated in seconds. Black markers correspond to spontaneous eye signals, red to visual cue responses, blue to auditory cue responses, and green to tactile cue responses. SVLD: Signal-Verified Lucid Dream

3.3.3.3. Lucidity Scores

DLQ scores were analysed to assess dream awareness (DLQ item #1) and control (DLQ item #4), as well as the total summed score for all DLQ items (Figure 11). Scores were averaged within each session. Awareness ratings showed a trend toward being higher in REM cueing sessions (1.74 ± 1.55) compared to REM sham sessions (1.3 ± 1.46), although this difference did not reach statistical significance (Wilcoxon signed-rank test, W = 55, p = 0.07). In contrast, DLQ control ratings were significantly higher in the REM cueing condition (1.19 ± 1.34) than in the REM sham condition (0.56 ± 0.90), indicating greater dream control during REM cueing (Wilcoxon signed-rank test, W = 40.0, p = 0.047). However, total DLQ scores did not differ significantly between the two conditions (REM sham: 9.24 ± 9.33; REM cueing: 10.73 ± 9.96; Wilcoxon signed-rank test, W = 78, p = 0.17).

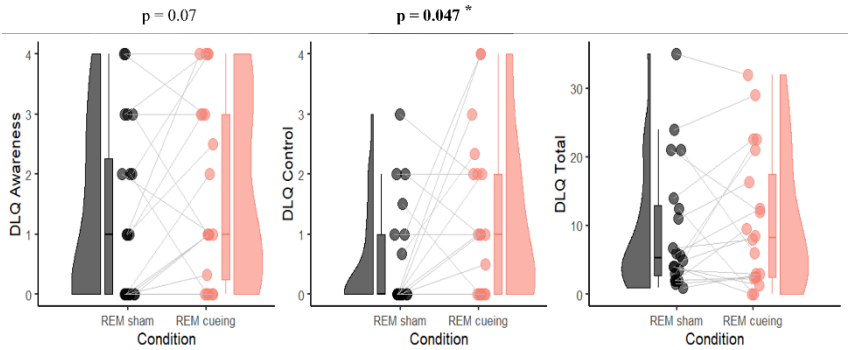



**Figure 11. DLQ score distribution for dream awareness (left), dream control (centre), and total score (right), averaged per session, as a function of experimental condition.**
DLQ: Dream Lucidity Questionnaire; * p < 0.05

We examined potential differences in LuCiD scale factors, averaged within sessions (Figure 12). Among participants who completed at least one LuCiD questionnaire for each session (N = 18

out of 20), the 'memory' factor was significantly higher in REM cueing sessions (7.38 ± 4.70) compared to REM sham sessions (4.93 ± 4.51; paired t-test, t = -2.26, p = 0.04). Additionally, there was a trend toward higher 'control' scores in REM cueing sessions (4.36 ± 5.98) compared to REM sham sessions (2.49 ± 3.72), though this difference did not reach statistical significance (Wilcoxon signed-rank test, W = 48, p = 0.09). Differences in the remaining LuCiD scale factors were not statistically significant: 'insight' (paired t-test, t = -0.74, p = 0.24), 'thought' (paired t-test, t = -0.69, p = 0.25), 'realism' (paired t-test, t = -0.93, p = 0.18), 'dissociation' (Wilcoxon signed-rank test, W = 58, p = 0.14), 'negative emotion' (Wilcoxon signed-rank test, W = 93.5, p = 0.65), and 'positive emotion' (paired t-test, t = 0.37, p = 0.64).

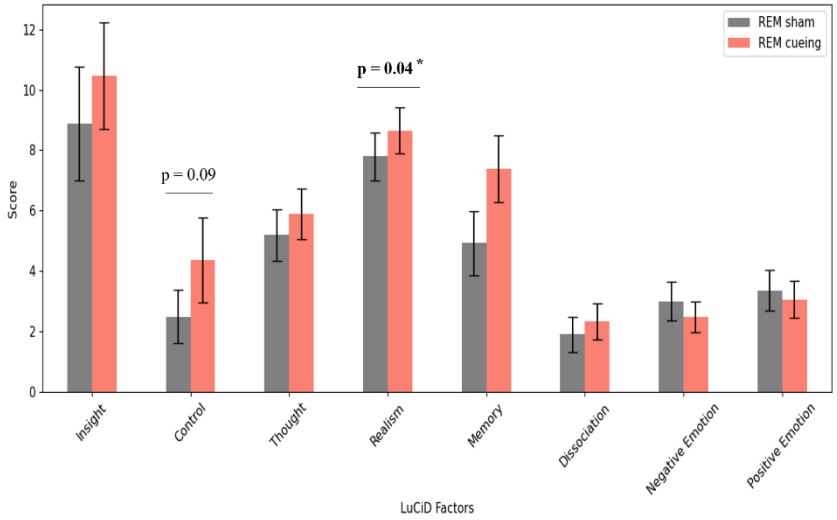



**Figure 12. LuCiD factor scores as a function of the experimental condition.**
LuCiD factor scores are averaged within sessions. Bars indicate the standard error.
* $p < 0.05$

## 3.4. Discussion

This study aimed to evaluate a novel LD induction technique that integrates SSILD with TLR, using wearable EEG devices and an open-source dream engineering toolbox. The method, involving multimodal sensory cueing during REM sleep, significantly enhanced both objective lucidity and dream control, successfully triggering predefined eye-movement signals even in participants with limited prior LD experience. This approach addresses critical limitations in existing LD research by incorporating physiological measurements, allowing for objective assessments of lucidity, and enhancing the generalizability of findings through the inclusion of a larger, more diverse sample.

### 3.4.1. Lucid Dream Induction Effectiveness

Overall, nearly half of participants achieved lucidity when considering both SVLD and non-SV LD episodes, with no significant differences between conditions. Notably, SVLD incidence was significantly higher for REM cueing than REM sham sessions. Moreover, we observed a significant enhancement in dream control ratings for REM cueing sessions compared to sham, as well as higher scores for the 'memory' factor of the LuCiD scale in cued relative to sham REM sessions.

These results align with previous studies suggesting that SSILD and TLR are promising methods for LD induction. SSILD has shown moderate success based on home-based subjective reports (Adventure-Heart, 2020; Tan & Fan, 2023), requiring further validation within controlled experimental settings. On the other hand, studies involving sensory stimulation and TLR have led to inconsistent outcomes. Paul et al. (2014) found visual and tactile stimulation to be ineffective, whereas Erlacher and collaborators (Erlacher, Schmid, Bischof, et al., 2020; Schmid & Erlacher, 2020) reported that auditory stimulation enhanced subjective LD experiences but had limited impact on objective measures. In contrast, Carr et al. (2020) achieved the highest SVLD induction rates using a combination of visual and auditory cues, underscoring the potential effectiveness of multimodal TLR approaches.

Our findings build on this research by demonstrating that the combination of SSILD and TLR is effective in inducing objective lucidity. This technique was associated with higher SVLD frequency, enhanced dream control ratings, and improved memory scores in cued compared to sham sessions. These effects may reflect cue-dependent reminiscence and execution of lucid instructions, particularly regarding predefined eye signalling. However, our SVLD success rate of 35% is somewhat lower than the 50% reported by Carr et al. and the 40% reported by Appel et al. (2020), indicating that further optimization of the induction protocol is warranted.

Our study also provided objective measurements of the duration of induced verified lucid episodes, although the limited number of observations precluded statistical comparisons. Notably, the collected SVLD episodes were relatively lengthy, with the longest episode lasting nearly 30 minutes, corresponding to a cued session. This suggests that cueing may help sustain lucidity, as indicated by the higher number of predefined eye signals in response to sensory cues compared to spontaneous signals (46 vs. 12). Thus, this induction method could be a valuable tool for researchers conducting specific tasks within lucid dreams, especially when prolonged dream control is necessary.

Importantly, our approach was effective independently from baseline LD frequencies, successfully inducing SVLD episodes even in participants with limited prior experience in dream awareness and control. This suggests that the method may be broadly applicable for modulating conscious experiences during sleep in the general population, opening new avenues for dream engineering and enhancing our understanding of stimulus-dependent dream changes (SDDCs) and sensory awareness during sleep.

### 3.4.2. Sensory Cueing Efficacy

All three evaluated sensory modalities—visual, auditory, and tactile—appeared to be similarly effective in eliciting behavioural responses during REM sleep. The rates of predefined eye signalling in response to

these cues showed no modality-specific differences, nor did the response times between cue presentation and the subsequent eye movement. This suggests that lucid REM sleep is equally receptive to all tested sensory modalities, with cues being integrated and recognized as external elements requiring a predefined signalling response, all while preserving sleep continuity.

Future research should conduct more detailed analyses of the reported conscious content to determine whether different types of SDDCs are distinctly related to the occurrence of each evaluated category (i.e., SVLD, non-SV LD, signalled non-LD, and non-LD) namely by relying on computational linguistic methods. Additionally, it would be interesting to explore potential inter-individual differences in the effectiveness of various sensory modalities, as well as to examine how different levels of stimulus saliency influence the induction of dream lucidity and the corresponding SDDCs.

In our study, some subjective reports described the sensory stimulation procedure as more detrimental than beneficial to the lucid experience. Paradoxically, one of the clearest examples of this coincided with the longest recorded SVLD episode of the entire study: *"I decided to fly a lot. [...] I perceived all [the stimuli], in a very vivid way. [...] They were almost annoying, in the sense that every time a stimulus arrived, it seemed as if I had to learn to fly again. As if they were bringing me back to reality*". Instead, others explicitly noted the positive impact of cueing on initiating and maintaining lucidity: *"As long as [the stimuli] were there, they helped me maintaining the thought of telling myself 'It's a dream'. Then I lost them [the stimuli], so I started thinking 'Wait, then it has to be real [the experience] ...*". These examples underscore the considerable variability in LD phenomenology, SDDCs, and awareness of external stimuli during dreaming.

Despite this variability, sensory cues have demonstrated clear potential to initiate and sustain objective lucidity, independent of subjective appraisal. We propose that the extent to which conscious subjective experiences are influenced by sensory stimulation may depend on the stability of sleep, suggesting that cueing is most effective

as a lucidity reminder when sleep is properly consolidated. Conversely, if sleep stability is compromised, cue perception may lead to arousal rather than lucidity. Comparing factors such as the presence of microarousals, arousal thresholds, the proportion of phasic and tonic REM, and subjective sleep depth ratings in relation to different SVLD content and durations could offer valuable insight into the factors that contribute to successful sensory cueing.

Interestingly, our cueing protocol has also shown promise for the objective assessment of sensory perception and conscious processing during sleep outside of lucidity. The present findings demonstrated the possibility to trigger stimulus-induced behavioural responses in both lucid and non-lucid REM sleep, thereby opening new avenues for the field of dream engineering, which currently lacks reliable methods for tracking SDDCs. In this context, cueing techniques emerge as valuable tools for the objective investigation of the determinants of stimulus permeability during sleep and dreaming, beyond the confines of lucidity.

### 3.4.3. Limitations and Future Prospects

This study demonstrated the effectiveness of a novel lucidity induction technique using a recently developed open-source dream engineering toolbox with minimal sensing systems. Our goal was to present a comprehensive, ready-to-use lucid dream induction 'package'—comprising an easily implementable induction protocol, minimal technical equipment, and the necessary software environment—to illustrate the feasibility of achieving objective lucidity without the need for complex setups or cumbersome experimental methods. However, this approach was not without limitations.

The current design did not allow for a clear assessment of the individual contributions of SSILD training and sensory cueing on lucid dream induction. To address this, future studies should include a control condition without pre-sleep SSILD training or REM cueing to determine whether the high induction rates observed in the sham condition were due to the combined sensory-cognitive training during

wakefulness, or if other factors inherent to the protocol (e.g., the sleep laboratory environment, participation in a lucid dream study, early-morning napping, etc.) contributed to our findings. The trend-level higher incidence of SVLD during the first nap session compared to the second may suggest an effect of the novelty of the experimental setting or the influence of the first-night effect (Tamaki & Sasaki, 2019) on the ability to attain dream control and maintain environmental awareness, although these interpretations remain speculative. Moreover, it would be interesting to investigate the effects of laboratory incorporations on the incidence of lucidity, as these have been related to 'meta-dreaming' and sensory incorporation (Picard-Deland, Nielsen, et al., 2021), potentially facilitating the occurrence of dream awareness.

Furthermore, the use of EEG wearables for sleep recordings brings several challenges, particularly in terms of the resolution of physiological measurements. The *ZMax* device, for instance, lacks occipital EEG channels, which can hinder the detection of alpha band fluctuations, complicating the distinction between N1 sleep and wakefulness and potentially affecting accurate arousal detection. Moreover, the limited number of frontal channels, which are also used to detect ocular activity, restricts the ability to conduct in-depth spectral analyses.

Despite these limitations, general EEG-based sleep metrics were reliably extracted from the data. These metrics indicated a longer total sleep period time –defined as the duration from the first to the last period of sleep –and a lower proportion of N2 relative to total sleep time in REM cued sessions compared to sham sessions. This discrepancy may be attributed to longer intermediate nap interruptions due to more extensive dream interviews when SVLDs were reported, which occurred more frequently during cued sessions. Even so, since no differences in REM sleep metrics were observed between conditions, these effects are unlikely to have significant implications for the validity of our findings.

Remarkably, the minimalistic design of the employed system enables the possibility of home-based study replications, offering a

more natural sleep environment and thereby enhancing external validity. However, conducting a study outside the laboratory would necessitate further automation improvements. These would require the development of reliable automatic arousal detection algorithms capable of adjusting stimulus intensity based on real-time brain activity and individual arousal thresholds. Additionally, more accurate real-time autoscoring models would be needed to reliably identify REM sleep. Lastly, while most existing studies on sensory stimulation for LD induction have used open-loop techniques (Antony et al., 2022; Esfahani, Farboud, et al., 2023), future research could benefit from adopting closed-loop stimulation approaches that take into consideration the temporal dynamics of the EEG signal to enhance the effectiveness of the sensory cueing (Harrington et al., 2021).

In terms of methodological quality, our study was evaluated as moderate (20/25), aligning with much of the existing literature, which generally ranges from poor to moderate quality (Stumbrys et al., 2012; Tan & Fan, 2022). This underscores the imperative for heightened scientific rigor to advance the field—an issue we aim to address by aggregating data from the three laboratories involved in this multi-centre research project. This strategy will substantially increase the sample size to 60 participants, positioning it as the most extensive laboratory-based LD study conducted to date, thereby enhancing both the statistical robustness and generalisability of our findings.

Finally, concerns have been raised regarding the potential adverse effects of lucid dreaming. Frequent LD may, in some cases, disrupt sleep hygiene, blur the boundaries between wakefulness and sleep, and lead to restlessness or sleep paralysis (Ableidinger & Holzinger, 2023; Soffer-Dudek, 2020). Yet, recent evidence suggests that lucidity itself does not negatively impact sleep quality (Ribeiro et al., 2020; Schadow et al., 2018; Schredl et al., 2020; Stocks et al., 2020; Stumbrys, 2021). Instead, the risks seem to be associated with unsuccessful LD induction attempts. This highlights the critical need for developing effective LD induction techniques that minimize potential risks while maximizing benefits. Our study contributes to this

effort by advancing the development of more reliable, adaptable, and practical methods for LD induction that can be applied across various settings, from everyday life to research and clinical practice.

# Chapter 4.
# Stimulus-Dependent Variations in Aperiodic EEG Activity and Their Relation to Subjective Experiences During Sleep

## 4.1. Introduction

Sleep has long been considered a state of disconnection from the environment due to the concurrent lack of behavioural responsiveness to external stimuli (Andrillon & Kouider, 2020; Carskadon & Dement, 1989). However, this unawareness does not imply the absence of consciousness, since reports of subjective experiences that we refer to as dreams are observed throughout all stages of sleep (Nir & Tononi, 2010; Siclari et al., 2017). While the content of such conscious experiences is mainly spontaneously internally originated, often paralleled to hallucinatory activity (Waters et al., 2016), it has been shown that dreams may also be influenced by external information (see Chapter 2). Therefore, our brain seems able to monitor and process environmental cues even while remaining deep asleep.

At the neural level, stimulus-dependent activation patterns can be observed in the EEG during sleep, typically manifesting as evoked oscillatory activity or event-related potentials in response to external stimulation (Bastuji et al., 1995; Blume et al., 2017, 2017, 2018, 2018; Halász, 2005; Hayat et al., 2022; Kouider et al., 2014; Legendre et al., 2019, 2022; Nir et al., 2013; Perrin et al., 1999; Portas et al., 2000; Strauss & Dehaene, 2019; Wislowska et al., 2022). NREM sleep hallmarks have also repeatedly been shown to track external sensory stimuli. For instance, spindle activity increases shortly after auditory, visual, or somatosensory stimulation in modality-specific cortical regions (Cote et al., 2000; Sato et al., 2007); oscillating white noise can entrain slow and

fast spindles in frontal and parietal regions, respectively (Antony & Paller, 2016); and power in several frequency bands including delta, theta, alpha and sigma seem to be modulated in a saliency-dependent manner (Ameen et al., 2022; Blume et al., 2017, 2018; C. Chen et al., 2016; Legendre et al., 2019).

However, the most prominent response to sensory stimuli during sleep remains the evoked K-complex (eKC), a slow wave shortly following an initial positive response over modality-dependent primary sensory areas, characterised by a very large global cortical negative-to-positive deflection with maximal amplitudes in frontocentral regions (Bastuji & García-Larrea, 1999; Colrain, 2005; Halász, 2005, 2016; Laurino et al., 2014, 2019; Riedner et al., 2011). Importantly, eKCs seem to be a key element in the selective processing of relevant information during NREM sleep, being associated with other sensory-dependent EEG changes such as micro-arousals, spindles, or variation in low- or high-frequency activity (Ameen et al., 2022; Forget et al., 2011; Latreille et al., 2020).

The role of K-complexes (KCs) in sleep is still debated, with evidence pointing on one side to a sleep-protective, sensory-quenching role (Bastien et al., 2000; Blume et al., 2017, 2018; Campbell et al., 2005; Cash et al., 2009; Forget et al., 2011; Laurino et al., 2014), and on the other, to an arousal-promoting, sensory processing function (Ameen et al., 2022; Koroma et al., 2022; Legendre et al., 2019; Perrin et al., 1999). This long-standing interpretative ambivalence is consistent with the understanding of the sleeping brain's responsiveness to external stimuli as a state of 'standing sentinel,' allowing to monitor potential danger while gating irrelevant information that could disrupt rest (Andrillon & Kouider, 2020).

Most previously reported evidence is based on the evaluation of stimulation-dependent oscillatory changes in the EEG signal, typically computed within canonical fixed-frequency bands (Capilla et al., 2022; Cole & Voytek, 2017). However, neural oscillations exhibit significant variation in peak frequencies both within and between individuals and brain regions (Klimesch, 1999; Lansbergen et al., 2011;

Saad et al., 2018; Watrous & Buchanan, 2020). Consequently, commonly used frequency range boundaries remain arbitrary and potentially sub-optimal, hindering comparability and complicating interpretation (Donoghue, Dominguez, et al., 2020).

Importantly, the EEG signal reflects complex neural interactions beyond rhythmic oscillatory patterns. Its spectrum is characterised by a 1/f-like power-law decay, indicating a continuous decline in power from low to high frequencies (Donoghue, Haller, et al., 2020; He, 2014; He et al., 2010). The exponent of this power-law distribution expresses the steepness of the slope of the power spectrum when plotted on a log-log scale. This fitted line is referred to as the aperiodic slope, representing the spectral power decay rate across frequencies and corresponding to non-oscillatory background activity (Ahmad et al., 2022; Podvalny et al., 2015). However, typical frequency band analyses sometimes fail to isolate oscillatory activity from this background, conflating the two and potentially leading to misinterpretation of the data (Cellier et al., 2021; Donoghue, Dominguez, et al., 2020; Donoghue, Haller, et al., 2020; Donoghue & Watrous, 2023; Finley et al., 2022; Ouyang et al., 2020; Schneider et al., 2022; Thuwal et al., 2021; Tröndle et al., 2022).

The functional relevance of the background aperiodic component of the EEG has long been overlooked, often attributed to random noise. However, seminal computational work proposed that aperiodic spectral slopes reflect the balance of excitatory and inhibitory activity (E/I ratio), with high-frequency aperiodic slopes becoming steeper with increased inhibition and flatter with more excitation (R. Gao et al., 2017). Recognizing the biological significance of neuronal background activity has brought great ferment to the field, leading to substantial interest in aperiodic EEG activity in recent years (e.g., (Helfrich et al., 2021; Lendner et al., 2020; Lombardi et al., 2017; Medel et al., 2023; Voytek & Knight, 2015; Waschke et al., 2021). Studies have shown that the aperiodic EEG component varies with age and development (Favaro et al., 2023; Hill et al., 2022; Schaworonkow & Voytek, 2021; Voytek et al., 2015), gender (Kozhemiako et al., 2022), and

cognitive and behavioural performance (Bueren et al., 2023; Euler et al., 2024; He et al., 2010; Höhn et al., 2024; Immink et al., 2021; Ouyang et al., 2020; Pathania et al., 2021; Pi et al., 2024; Podvalny et al., 2015; Virtue-Griffiths et al., 2022), while demonstrating high within-subject reliability (Demuru & Fraschini, 2020; Kozhemiako et al., 2022).

Aperiodic slopes have shown promise in distinguishing clinical populations from healthy controls and even differentiating between distinct medication regimes within the same diagnosis in conditions such as schizophrenia (Peterson et al., 2023), attention-deficit/hyperactivity disorder (Arnett et al., 2022; Karalunas et al., 2022; Ostlund et al., 2021; Pertermann et al., 2019; Robertson et al., 2019), autism (Manyukhina et al., 2022), Alzheimer's disease (Martínez-Cañada et al., 2023), and multiple sclerosis (Akbarian et al., 2023). Remarkably, some of these studies suggest that aperiodic-based methods may even outperform traditional narrow-band frequency analyses in characterising individual traits (Demuru & Fraschini, 2020; Peterson et al., 2023).

Aperiodic activity also appears to vary significantly across different states of consciousness and arousal, as evidenced by its modulation during anaesthesia (Colombo et al., 2019; Lendner et al., 2020; Waschke et al., 2021; Y. Zhang et al., 2023) and disorders of consciousness (Alnes et al., 2021; Colombo et al., 2023; Maschke et al., 2023). Notably, aperiodic slopes exhibit spontaneous fluctuations across the sleep-wake cycle (Ameen et al., 2024; Bódizs et al., 2021; Favaro et al., 2023; Höhn et al., 2024; Horváth et al., 2022; Lendner et al., 2020; Miskovic et al., 2018; Rosenblum et al., 2022, 2024; Schneider et al., 2022). During wakefulness, the aperiodic slope is generally flat, reflecting a more complex and dynamic neural landscape. In contrast, the slope steepens during NREM stages, reflecting increasingly synchronised neural activity (Lendner et al., 2020; Schneider et al., 2022), often accompanied by scarcer and rather simple conscious experiences (Siclari et al., 2013).

During REM sleep—a state characterised by vivid perceptual conscious experiences (Siclari et al., 2013) and high subjective sleep

depth (Stephan et al., 2021)—the aperiodic slope tends to flatten toward wakefulness levels when considering low (upper boundary ≤ 30 Hz; Alnes et al., 2024; Rosenblum et al., 2024) and broadband frequency ranges (Ameen et al., 2024; Höhn et al., 2024; Miskovic et al., 2018; Schneider et al., 2022) but becomes even steeper for higher frequencies (30-45 Hz in Höhn et al., 2024; Kozhemiako et al., 2022; Lendner et al., 2020; 20-40 Hz in Alnes et al., 2024). Interestingly, this progressive steepening of the high-frequency slope from wakefulness to NREM and REM sleep is accompanied by parallel changes from low to high subjective sleep depth (Stephan et al., 2021).

Moreover, aperiodic slopes have been shown to differ significantly between individuals with chronic insomnia—including sleep state misperceptors, who report abnormally low subjective sleep depth (Stephan et al., 2021)—and healthy sleepers, with the former presenting flatter slopes during NREM compared to controls (Andrillon et al., 2020). These findings collectively suggest a possible link between the aperiodic slope and subjective sleep measures, such as sleep depth or sleepiness (Chatburn et al., 2024), both between and within sleep stages. However, these associations still require confirmation through empirical evidence.

Given these state-dependent variations, the potential of the aperiodic slope as an indicator of different levels of arousal and consciousness during sleep is particularly compelling. However, aperiodic slopes have predominantly been used to measure spontaneous brain activity. Their capacity to reflect changes in brain activity in response to external stimulation—and how these changes relate to subjective experience—remains largely unexplored.

This knowledge gap provides a strong rationale for the present study, which aimed to probe the effects of external stimulation on NREM sleep by measuring stimulus-dependent variations in the aperiodic slope and how these could, in turn, predict subsequent subjective reports. To do so, we first examined the effects of auditory, tactile, and visual stimulation events on the aperiodic slope in different frequency ranges (low: 0.5-30, high: 30-45, broadband: 0.5-45 Hz) and

scalp locations (Fz, Cz, Pz, Oz). Then, we evaluated how such event-related aperiodic slope variations (ΔS) related to subjective experiences, namely the recall and content of conscious experiences (i.e., dreams), and subjective ratings of sleep depth and sleepiness upon awakening. In a more exploratory way, we assessed the characteristics of the eKC to probe any potential mediating effect they could have on the relationship between ΔS and the reported subjective experiences.

## 4.2. Methods

### 4.2.1. Experimental Protocol

#### 4.2.1.1. Participants

We collected data from 25 healthy adults aged 18 to 40 (m = 27.7 ± 4.53 years; 12 females). The following inclusion criteria were applied: right-handedness, Italian as native speaking language, regular sleep-wake patterns, intermediate chronotype, 6 to 9 hours of nightly sleep, no diagnosed sleep-related or other pathological conditions affecting brain function or behaviour. We excluded individuals with neurological, psychiatric, or neurodegenerative diseases, sleep disorders, a history of substance abuse, contraindications to MRI, recent COVID-19 symptoms or exposure, and pregnancy or breastfeeding. All participants provided informed consent and were requested to abstain from alcohol and limit caffeinated beverage consumption before noon on experimental days to minimise potential confounding effects on sleep quality. The study was approved by the joint local ethical committee of Scuola Superiore Sant'Anna and Scuola Normale Superiore.

#### 4.2.1.2. Study Design

Participants completed four non-consecutive overnight sleep sessions at the laboratory following a serial awakening paradigm. We measured high-density EEG (256 channels) with additional bodily sensors to record comprehensive PSG data, including EOG, EMG, ECG, and respiratory activity. Sleep-wake patterns during the study were controlled by continuous actigraphy measurement (*MotionWatch 8*,

MotionWare, Camntech, UK), starting 7 days before the first session and continuing until the last experimental session.

Each overnight session consisted of a waking resting-state period with closed eyes, followed by a sleep period during which auditory, vibrotactile, or visual stimuli were presented at pseudo-random intervals during NREM sleep. Stimulation was followed by an awakening whenever a KC was evoked. In particular, the alarm sound was played 4 to 6 seconds after the sensory stimulus if a potential eKC was visually identified by the experimenter. Sham trials involved awakening without prior stimulation. Each night included 6 to 12 awakenings following a pseudo-randomized order concerning the stimulated modality. Upon awakening, participants were asked to report their last subjective experience (if any) and were probed using a standardised pre-recorded questionnaire assessing several aspects of the recalled experience.

4.2.1.3. Sensory Stimulation Procedure

Sensory stimulation was performed after at least 10 minutes of stable NREM sleep. The order of stimulation modalities was pseudo-randomized within each night, and attempts were made to balance the number of stimulations for each modality across nights. For cases where the stimulation was not followed by a visually detected KC, the same modality was stimulated after a waiting period of at least 2 minutes. If no eKC was detected the second time, a different modality was stimulated after a waiting period of at least 2 minutes.

All stimuli had a fixed duration of 50 ms with a single repetition. Auditory stimuli were 1000 Hz pure tones (50 ms duration, including a 5 ms ramp-up and 5 ms ramp-down) delivered binaurally through stereo in-ear headphones (Maxrock, Guangdong, China) at a stable intensity level of 40 dB. Tactile stimuli were 80 Hz mechanical vibrations applied to the right index fingertip via an electromagnetic solenoid-type vibrotactile stimulator (*Tactor*, Dancer Design, Ingleton, UK) connected to a four-channel amplifier (*Tactamp*, Dancer Design, Ingleton, UK). Visual stimuli consisted of a 50 ms red light flash

delivered through two LED lights (*FL1P-8QW-2-R12V*, Mallory Sonalert Products Inc., IN, US). These LEDs were integrated into a custom-made sleep mask, positioned bilaterally in 8 mm cutouts centred above the eyes, emitting light with a wavelength of 622 nm at an intensity level of 1500 millicandela and a 35° viewing angle.

#### 4.2.1.4. Subjective Reports Upon Awakening

Upon experimental awakening, participants were prompted by a pre-recorded vocal message to orally report any conscious experiences (i.e., dreams) they could recall from the time immediately preceding the alarm. Participants first indicated whether they could recall an experience and, if so, were asked to provide a detailed description of it (contentful dream, CD). If an experience was recalled, participants were then asked to rate the type of conscious content (thought-like vs. perceptual) on a 5-point Likert scale. Several other dream dimensions were evaluated as part of the protocol, including vividness, bizarreness, awareness of the dream state (i.e., lucidity), emotional valence and intensity, and completeness and accuracy of the recall, but were not considered in the present study. If participants did not recall any experience, they were asked to report whether they had the impression of having had an experience without being able to recall it (white dream, WD) or not having had any experience at all (no dream, ND).

Regardless of the presence and type of conscious content report, participants were asked to rate their sleep depth level immediately before awakening using a 5-point Likert scale from 1 (feeling fully awake) to 5 (feeling deeply asleep), as well as their sleepiness levels upon awakening, using a 5-point Likert scale from 1 (very low) to 5 (very high).

### 4.2.2. EEG Data

#### 4.2.2.1. PSG Recordings

Overnight high-density EEG was recorded using the actively shielded *eego*™ *mylab* system (ANT Neuro, The Netherlands) with 256-

electrodes *waveguard™ original* caps (ANT Neuro, The Netherlands). Electrode impedances were maintained below 20 kΩ. Data were collected using the *eego™ mylab* software package (ANT Neuro, The Netherlands), with a 500 Hz sampling rate. The EEG recording was extended with electrooculogram, electromyogram, electrocardiogram, and respiratory belt recordings. Sleep stages were scored according to the American Academy of Sleep Medicine criteria (Berry et al., 2017) by expert sleep scorers.

#### 4.2.2.2. Data Pre-processing

Recordings were segmented into 6-minute epochs preceding each awakening, and only NREM-scored epochs were kept for further analysis. Data segments were pre-processed using a custom, semi-automated pipeline developed in MATLAB (The Matworks) and based on the *EEGLAB* toolbox (version 2021.0; Delorme & Makeig, 2004). Line noise was removed using *ZapLine* toolbox (de Cheveigné, 2020), while noisy channels were identified and excluded using the PREP pipeline's *findNoisyChannels* wrapper function (Bigdely-Shamlo et al., 2015). Artifacts were reduced via independent component analysis (ICA; *runica* function): a duplicate of the raw data was filtered between 0.5 and 45 Hz (*pop_eegfiltnew* function), and a principal component analysis for dimensionality reduction was performed on it, keeping only the first 150 components. The *ICLabel* plugin (Pion-Tonachini et al., 2019) was then applied to the extracted independent components (IC). Those classified as 'brain' with a probability above 25%, or with a brain-to-noise ratio (based on the first non-brain IC) above 0.80 were kept. Selected ICs were confirmed or modified after visual inspection by expert scorers. Finally, ICA weights and IC indices were applied to the original, unfiltered recording, and bad channels were interpolated using spherical splines (*pop_interp* function).

#### 4.2.2.3. Slow Wave Detection

For each trial, slow waves were automatically detected following methods similar to those described by Avvenuti et al. (2020). First, the EEG recordings were filtered between 0.5 and 40 Hz and re-referenced

to the average of the two mastoid electrodes. Then, a negative-going signal envelope was calculated by computing, for each time-point, the average of the three most negative samples (across electrodes) after exclusion of the most negative value. This computation was restricted to a subset of 191 electrodes, excluding those covering the neck and cheeks, to minimise the inclusion of residual artefactual high-amplitude signal changes. Finally, the signal envelope was filtered between 0.5 and 4 Hz) before applying a slow-wave detection procedure based on half-wave zero-crossings (Siclari et al., 2014; Vyazovskiy et al., 2007). We selected negative half-waves with a duration between 0.25 and 1.25 seconds.

While the negative-going signal envelope allows the detection of potential slow waves regardless of their amplitude and scalp location, the signal may become very different from the one recorded at the level of individual electrodes. For this reason, slow waves were detected also at the level of individual channels and, for each slow wave detected on the envelope signal, we identified the channel in which the largest corresponding temporally overlapping slow wave was found. For this 'representative wave', we extracted the overall negative amplitude (in microvolts, μV) and the lag relative to the stimulation event (in seconds).

4.2.2.4. Trial Selection

Our trials consisted of data segments that included the 4 seconds immediately preceding and the 4 seconds immediately following the stimulation (or sham) events. For this study, only trials where the N2 sleep stage was confirmed by sleep scoring were included in the analysis. Additionally, only trials with more than 4 seconds between the event and the alarm sound were retained.

For stimulation trials to be considered valid, the detected slow wave parameters needed to meet specific criteria: there had to be a lag between the stimulus onset and the maximum negative peak of 0.25 to 1.75 seconds, and a negative amplitude of at least 20 μV. These

thresholds were applied to avoid including spurious or non-evoked brain activity as stimulus responses.

#### 4.2.2.5. Aperiodic Slope Extraction

The spectral features of our pre-processed EEG data were extracted following the methods from Rosenblum et al. (2020). Specifically, the signal was decomposed into its aperiodic and oscillatory components using the irregularly resampled auto-spectral analysis (*IRASA*; Wen & Liu, 2016)toolbox implemented in *FieldTrip* (revision 20230118; Ostenveld et al., 2011). We applied the *ft_freqanalysis* function with *cfg.method = 'irasa'* to the data segments, with *cfg.output = 'fractal'* to extract the aperiodic component. The aperiodic component was then transformed to log-log coordinates using standard least-squares regression, where the slope of the line was calculated as the power-law exponent estimation. Aperiodic slopes were computed for all measured EEG channels in three distinct frequency ranges: low (0.5-30 Hz), high (30-45 Hz), and broadband (0.5-45 Hz).

Slope variations (ΔS) relative to the stimulation event were calculated by subtracting the absolute value of the aperiodic slope in the 4 seconds following the stimulation event from the absolute value of the aperiodic slope in the 4 seconds preceding the stimulation event.

$$\Delta S = |\text{Aperiodic slope pre-event}| - |\text{Aperiodic slope post-event}|$$

We computed ΔS for all channels in all frequency bands. To ensure coherence in further interpretation, instances for which the slope was positive either in the pre-event or post-event period were omitted, i.e., 16 out of 11,064 (922 trials * 3 frequency bands * 4 channels) = 0.15% excluded values. Therefore, positive ΔS indicated a post-event steepening of the slope, whereas negative ΔS indicated a flattening.

### 4.2.3. Statistical Analyses

We investigated the effect of sensory stimulation on ΔS by pooling across stimulation trials (stimulation vs. sham) and by examining potential ΔS differences between various modalities (auditory, visual, tactile, and sham). Statistical analyses focused on ΔS within three selected frequency ranges (low, high, and broadband) using data from four midline electrodes representative of the frontal (Fz, channel Z4Z), central (Cz, channel Z9Z), parietal (Pz, channel Z13Z), and occipital (Oz, channel Z18Z) regions. To control for multiple comparisons, we applied the Bonferroni correction, setting the significance threshold at p = 0.0042 (0.05 / [3 frequency bands * 4 channels]).

Depending on the results of the Shapiro-Wilk test for normality, we employed either paired t-tests or Wilcoxon signed-rank tests to compare ΔS in stimulation trials (pooled or for each modality) against the sham condition, and between different stimulation modalities, averaged per subject. Raincloud plots were generated with the *dplyr* (version 1.1.4; Wickham et al., 2023), *ggplot2* (Wickham, 2016), *ggpubr* (version 0.6.0; Kassambara, 2023), and *ggpp* (version 0.5.7; Aphalo, 2024) packages in R (version 4.4.0; R Core Team) within the RStudio integrated development environment (version 2023.06.0; RStudio Team).

We investigated the relationship between conscious experiences and ΔS using generalised linear mixed models (GLMMs) in MATLAB (R2022b, version 9.13). These models included ΔS and time of the night as predictors, while controlling for night order and subject as random effects. Conscious experience categories (CD, WD, ND) were evaluated through pairwise comparisons (CD vs. ND, CD vs. WD, WD vs. ND), modelled as dichotomous outcomes with a binomial distribution (*Content recall ~ ΔS + Time of night + 1|Night + 1|Subject*).

The relationship between subjective reports (type of conscious content, sleep depth, sleepiness) and ΔS was assessed using cumulative link mixed models (CLMMs) with the *ordinal* package (version 2023.12-4; Christensen, 2023) in R. This method allowed us to model ordinal

outcomes, such as subjective ratings on 5-point Likert scales, including fixed effects (ΔS and time of the night) and random effects (night order and subject), akin to the GLMMs (*Subjective rating ~ ΔS + Time of night + 1|Night + 1|Subject*). Before fitting the CLMMs, fixed effect variables were standardised (m = 0, std = 1) to optimise model convergence and improve the comparability of estimated coefficients.

To assess potential modality-dependent differences in eKCs and determine the degree to which slope variations represent a non-redundant informative marker of the subjective experiences reported upon awakening, we set out to exclude the possibility that these variations were mediated by the presence of the eKC. Therefore, whenever ΔS showed significant effects on subjective reports, we included the negative amplitude of the eKC as an additional predictor. This allowed us to compare outcomes from models with and without factoring in the eKC, enabling us to detect potential mediation effects.

## 4.3. Results

Of the 922 collected trials, 852 were scored as N2 sleep stage (70 trials excluded; 7.59%). Of these, 777 trials included at least 4 seconds between the stimulation event and the alarm sound (75 trials excluded; 8.8%). When applying slow-wave detection thresholds to the remaining 548 stimulation trials, 491 showed the maximum negative peak between 0.25 and 1.75 seconds after the stimulation event (57 trials excluded; 10.4%). Of these, 482 trials exhibited a maximum negative peak of at least 20 μV (9 trials excluded; 1.83%). Overall, 711 trials were retained for further analysis: 214 trials (23.35%) involved auditory stimulation events, 166 trials (23.35%) involved tactile stimulation

events, 102 trials (14.35%) involved visual stimulation events, and 229 trials (32.21%) involved sham events (Figure 13).

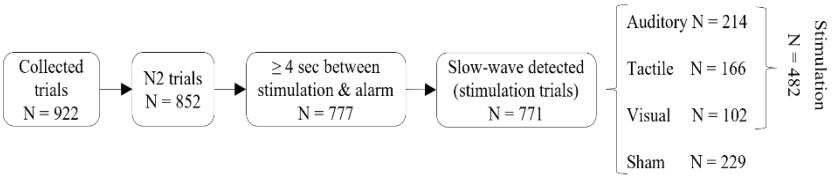



**Figure 13. Trial selection procedure.**

### 4.3.1. Stimulus-Dependent Aperiodic Slope Variations

We plotted the topographical distribution of ΔS for all evaluated modalities (Figure 14) and performed pairwise statistical comparisons for selected channels to assess potential differences across stimulation modalities. To enhance readability, detailed results are provided in forms of tables reporting descriptive and inferential statistics.

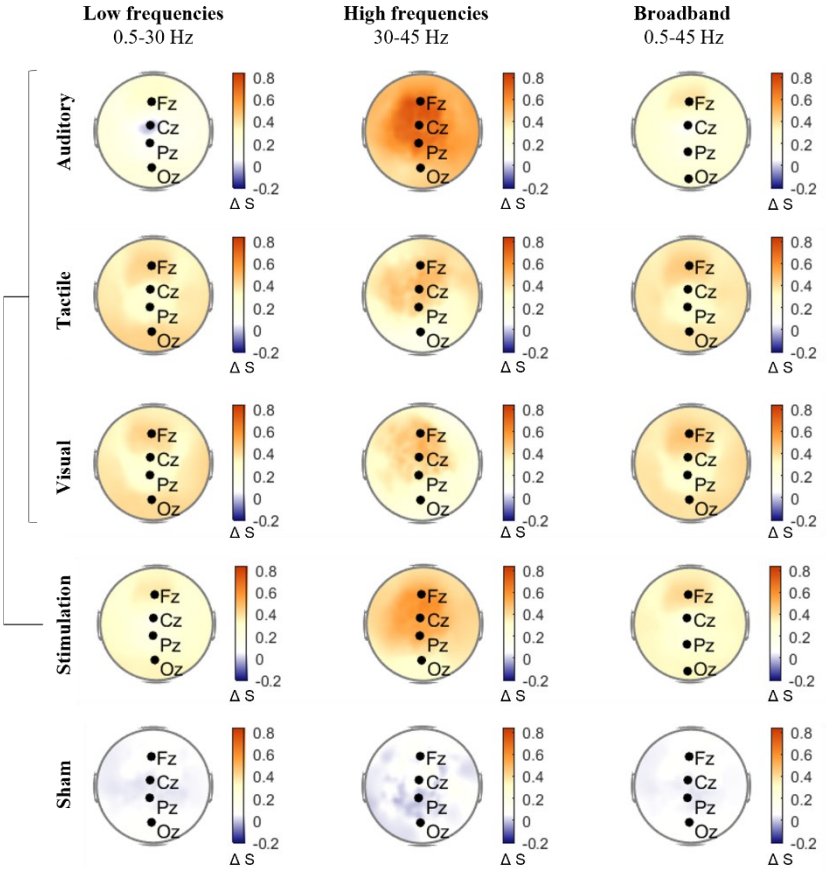



**Figure 14. Topographical distribution of the slope variation relative to the stimulation event (ΔS) for different stimulation modalities.**

Stimulation values were computed by averaging across auditory, visual, and tactile trials. Positive differences denote a post-event steepening of the slope following a red gradient, while negative differences indicate a flattening following a blue gradient. Black dots indicate electrodes of interest.

#### 4.3.1.1. Comparison Between Stimulation and Sham Conditions

When pooling across stimulation trials, we found a significant increase in ΔS compared to the sham condition in the high-frequency band for all evaluated channels. When considering the low and broadband frequency ranges, a significant increase in ΔS was observed at all channels but Cz (Table 1).

| Frequency range | EEG Channel | ΔS Stimulation | ΔS Sham | Statistics | P-value |
|---|---|---|---|---|---|
| Low | Fz | 0.35 ± 0.21 | 0.07 ± 0.11 | t(24) = 6.73 | 5.78E-07 * |
| Low | Cz | 0.14 ± 0.21 | 0.03 ± 0.12 | t(24) = 2.15 | 4.16E-02 |
| Low | Pz | 0.19 ± 0.23 | 0.03 ± 0.12 | t(24) = 3.29 | 3.08E-03 * |
| Low | Oz | 0.31 ± 0.21 | 0.07 ± 0.08 | t(24) = 5.72 | 6.89E-06 * |
| High | Fz | 0.58 ± 0.25 | 0.05 ± 0.22 | t(21) = 9.64 | 3.70E-09 * |
| High | Cz | 0.56 ± 0.23 | 0.08 ± 0.19 | t(22) = 8.45 | 2.35E-08 * |
| High | Pz | 0.55 ± 0.23 | -0.03 ± 0.23 | t(22) = 9.41 | 3.60E-09 * |
| High | Oz | 0.31 ± 0.25 | 0.06 ± 0.18 | t(21) = 5.00 | 5.94E-05 * |
| Broadband | Fz | 0.42 ± 0.21 | 0.07 ± 0.10 | t(24) = 7.88 | 4.08E-08 * |
| Broadband | Cz | 0.19 ± 0.19 | 0.04 ± 0.13 | z = 2.54 | 1.10E-02 |
| Broadband | Pz | 0.24 ± 0.22 | 0.03 ± 0.10 | t(24) = 4.82 | 6.64E-05 * |
| Broadband | Oz | 0.31 ± 0.20 | 0.07 ± 0.08 | t(24) = 5.90 | 4.39E-06 * |

**Table 1. Stimulus-dependent aperiodic slope variation comparison (ΔS) between stimulation (pooled) and sham trials for all evaluated frequency ranges and channels.**

Low frequency: 0.5-30 Hz; High frequency: 30-45 Hz; Broadband: 0.5-45 Hz. ΔS values correspond to m ± std. * statistical significance at Bonferroni-corrected threshold ($p < 0.042$)

Then, we compared ΔS in trials from each specific sensory modality to sham trials (Figure 15). Auditory stimulation resulted in a significant increase in ΔS in the high-frequency band for all evaluated channels. When considering the broadband frequency range, a significant increase in ΔS was observed only in Fz. In the low-frequency band, no significant differences were observed in any of the evaluated regions (Table 2).

| Frequency range | EEG Channel | ΔS Auditory | ΔS Sham | Statistics | P-value |
|---|---|---|---|---|---|
| Low | Fz | 0.27 ± 0.42 | 0.07 ± 0.11 | t(24) = 2.43 | 2.30E-02 |
| Low | Cz | -0.03 ± 0.34 | 0.03 ± 0.12 | t(24) = -0.85 | 4.02E-01 |
| Low | Pz | 0.09 ± 0.41 | 0.03 ± 0.12 | t(24) = 0.79 | 4.36E-01 |
| Low | Oz | 0.20 ± 0.40 | 0.07 ± 0.08 | z = 1.55 | 1.22E-01 |
| High | Fz | 0.75 ± 0.36 | 0.05 ± 0.22 | t(21) = 9.57 | 4.20E-09 * |
| High | Cz | 0.69 ± 0.28 | 0.08 ± 0.19 | t(23) = 9.95 | 8.33E-10 * |
| High | Pz | 0.74 ± 0.32 | -0.03 ± 0.23 | t(22) = 9.50 | 3.03E-09 * |
| High | Oz | 0.47 ± 0.33 | 0.06 ± 0.18 | t(21) = 6.28 | 3.17E-06 * |
| Broadband | Fz | 0.37 ± 0.42 | 0.07 ± 0.10 | t(24) = 3.59 | 1.48E-03 * |
| Broadband | Cz | 0.05 ± 0.35 | 0.04 ± 0.13 | t(24) = 0.23 | 8.17E-01 |
| Broadband | Pz | 0.18 ± 0.40 | 0.03 ± 0.10 | t(24) = 1.90 | 6.92E-02 |
| Broadband | Oz | 0.24 ± 0.38 | 0.07 ± 0.08 | z = 2.25 | 2.47E-02 |

**Table 2. Stimulus-dependent aperiodic slope variation comparison (ΔS) between auditory and sham trials for all evaluated frequency ranges and channels.**

Low frequency: 0.5-30 Hz; High frequency: 30-45 Hz; Broadband: 0.5-45 Hz. ΔS values correspond to m ± std. * statistical significance at Bonferroni-corrected threshold ($p < 0.042$)

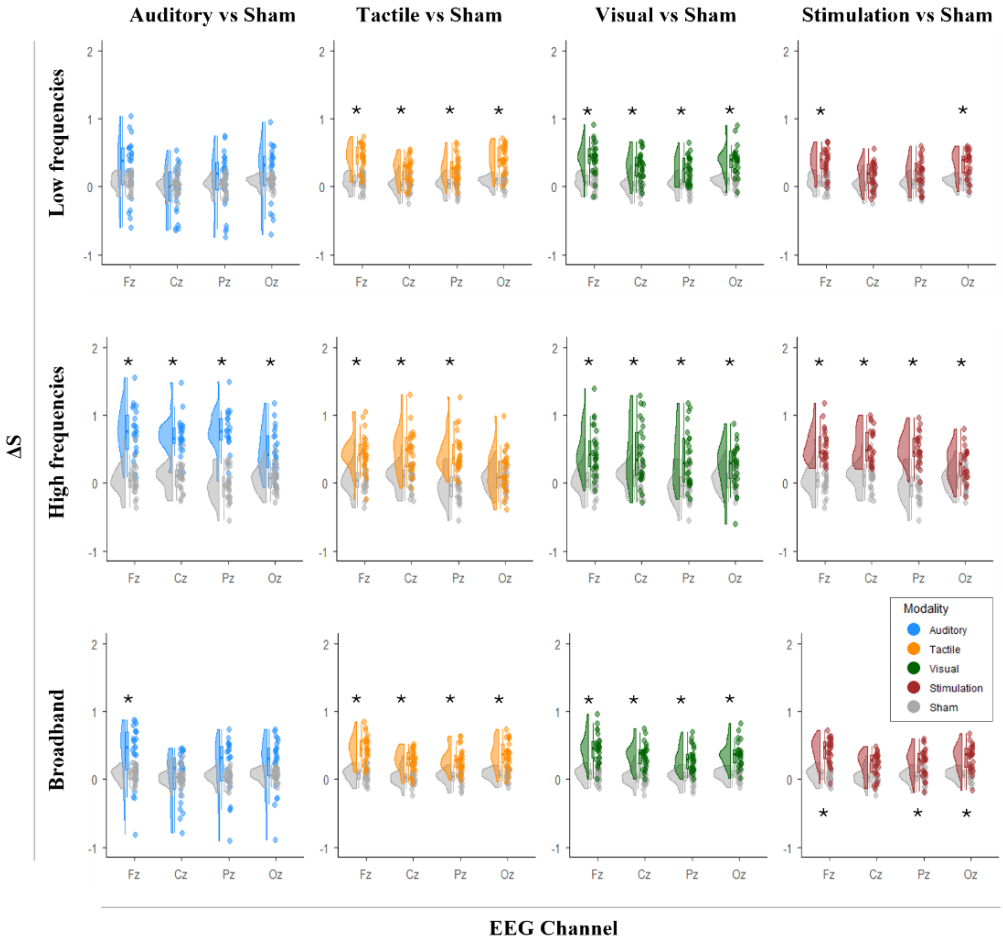



**Figure 15. Distribution of stimulus-dependent aperiodic slope variation (ΔS) across all evaluated channels and frequency bands for different stimulation modalities in comparison to sham.**

Low frequency: 0.5-30 Hz; High frequency: 30-45 Hz; Broadband: 0.5-45 Hz.
* statistical significance at Bonferroni-corrected threshold ($p < 0.042$)

Tactile stimulation was associated with a significant ΔS increase relative to sham for all evaluated frequencies and regions. Significant differences were observed in all channels of interest for the low and the broadband frequency ranges, and for all but Oz in the high frequency range (Table 3).

| Frequency range | EEG Channel | ΔS Tactile | ΔS Sham | Statistics | P-value |
|---|---|---|---|---|---|
| Low | Fz | 0.43 ± 0.19 | 0.07 ± 0.11 | t(24) = 8.87 | 4.90E-09 * |
| Low | Cz | 0.25 ± 0.19 | 0.03 ± 0.12 | t(24) = 4.87 | 5.72E-05 * |
| Low | Pz | 0.27 ± 0.19 | 0.03 ± 0.12 | t(24) = 5.30 | 1.93E-05 * |
| Low | Oz | 0.42 ± 0.20 | 0.07 ± 0.08 | t(24) = 8.29 | 1.68E-08 * |
| High | Fz | 0.44 ± 0.27 | 0.05 ± 0.22 | t(23) = 5.54 | 1.24E-05 * |
| High | Cz | 0.47 ± 0.31 | 0.08 ± 0.19 | z = 4.00 | 6.33E-05 * |
| High | Pz | 0.45 ± 0.28 | -0.03 ± 0.23 | t(24) = 6.71 | 6.18E-07 * |
| High | Oz | 0.16 ± 0.30 | 0.06 ± 0.18 | t(24) = 1.59 | 1.25E-01 |
| Broadband | Fz | 0.45 ± 0.19 | 0.07 ± 0.10 | t(24) = 8.39 | 1.34E-08 * |
| Broadband | Cz | 0.28 ± 0.16 | 0.04 ± 0.13 | t(24) = 6.14 | 2.43E-06 * |
| Broadband | Pz | 0.29 ± 0.17 | 0.03 ± 0.10 | t(24) = 6.73 | 5.85E-07 * |
| Broadband | Oz | 0.37 ± 0.20 | 0.07 ± 0.08 | t(24) = 7.05 | 2.76E-07 * |

**Table 3. Stimulus-dependent aperiodic slope variation comparison (ΔS) between tactile and sham trials for all evaluated frequency ranges and channels.**

Low frequency: 0.5-30 Hz; High frequency: 30-45 Hz; Broadband: 0.5-45 Hz. ΔS values correspond to m ± std. * statistical significance at Bonferroni-corrected threshold ($p < 0.042$)

Significant increases in ΔS were also observed in visual stimulation trials relative to sham for all evaluated cases. Significant differences were observed for all selected channels and frequency ranges (Table 4).

| Frequency range | EEG Channel | ΔS Visual | ΔS Sham | Statistics | P-value |
|---|---|---|---|---|---|
| Low | Fz | 0.43 ± 0.23 | 0.07 ± 0.11 | t(24) = 6.83 | 4.58E-07 * |
| Low | Cz | 0.30 ± 0.20 | 0.03 ± 0.12 | t(24) = 5.37 | 1.64E-05 * |
| Low | Pz | 0.25 ± 0.19 | 0.03 ± 0.12 | t(24) = 4.62 | 1.10E-04 * |
| Low | Oz | 0.39 ± 0.21 | 0.07 ± 0.08 | t(24) = 6.63 | 7.36E-07 * |
| High | Fz | 0.48 ± 0.35 | 0.05 ± 0.22 | t(23) = 4.92 | 5.71E-05 * |
| High | Cz | 0.43 ± 0.44 | 0.08 ± 0.19 | t(24) = 3.53 | 1.72E-03 * |
| High | Pz | 0.37 ± 0.41 | -0.03 ± 0.23 | t(24) = 4.19 | 3.28E-04 * |
| High | Oz | 0.26 ± 0.33 | 0.06 ± 0.18 | t(24) = 3.43 | 2.16E-03 * |
| Broadband | Fz | 0.46 ± 0.22 | 0.07 ± 0.10 | t(24) = 7.56 | 8.44E-08 * |
| Broadband | Cz | 0.35 ± 0.18 | 0.04 ± 0.13 | t(24) = 6.54 | 9.16E-07 * |
| Broadband | Pz | 0.29 ± 0.18 | 0.03 ± 0.10 | t(24) = 5.78 | 5.86E-06 * |
| Broadband | Oz | 0.37 ± 0.19 | 0.07 ± 0.08 | t(24) = 7.22 | 1.86E-07 * |

**Table 4. Stimulus-dependent aperiodic slope variation comparison (ΔS) between visual and sham trials for all evaluated frequency ranges and channels.**

Low frequency: 0.5-30 Hz; High frequency: 30-45 Hz; Broadband: 0.5-45 Hz. ΔS values correspond to m ± std. * statistical significance at Bonferroni-corrected threshold ($p < 0.042$)

#### 4.3.1.2. Inter-Modality Comparisons for Stimulation Conditions

When comparing the different sensory modalities (Figure 16), auditory trials showed larger ΔS compared to tactile and visual trials in several conditions. Instead, no differences were observed between tactile and visual trials. Significant outcomes are reported in Table 5 (see Appendix III: Supplementary Table 1 for a comprehensive summary of the outcomes for all evaluated comparisons).

| Frequency range | EEG Channel | ΔS A | ΔS T | ΔS V | Test | Statistics | P-value |
|---|---|---|---|---|---|---|---|
| Low | Cz | 0.03 ± 0.34 | 0.25 ± 0.19 | 0.30 ± 0.20 | A-T | t(24) = -5.54 | 1.08E-05 * |
| | | | | | A-V | t(24) = -4.69 | 9.17E-05 * |
| Low | Oz | 0.20 ± 0.40 | 0.42 ± 0.20 | 0.39 ± 0.21 | A-T | t(24) = -3.21 | 3.76E-03 * |
| High | Fz | 0.75 ± 0.36 | 0.44 ± 0.27 | 0.48 ± 0.35 | A-T | t(22) = 4.20 | 3.71E-04 * |
| | | | | | A-V | t(22) = 3.27 | 3.47E-03 * |
| High | Pz | 0.74 ± 0.32 | 0.45 ± 0.28 | 0.37 ± 0.41 | A-T | t(22) = 4.57 | 1.50E-04 * |
| | | | | | A-V | t(22) = 3.99 | 6.23E-04 * |
| High | Oz | 0.47 ± 0.33 | 0.16 ± 0.30 | 0.26 ± 0.33 | A-T | z = 3.62 | 2.95E-04 * |
| Broad band | Cz | 0.05 ± 0.35 | 0.28 ± 0.16 | 0.35 ± 0.18 | A-T | t(24) = -4.16 | 3.50E-04 * |
| | | | | | A-V | t(24) = -3.78 | 9.18E-04 * |

**Table 5. Significant comparisons of stimulus-dependent aperiodic slope variation (ΔS) across sensory modalities.**

Low frequency: 0.5-30 Hz; High frequency: 30-45 Hz; Broadband: 0.5-45 Hz. A: Auditory; T: Tactile; V: Visual. ΔS values correspond to m ± std. * statistical significance at Bonferroni-corrected threshold ($p < 0.042$)

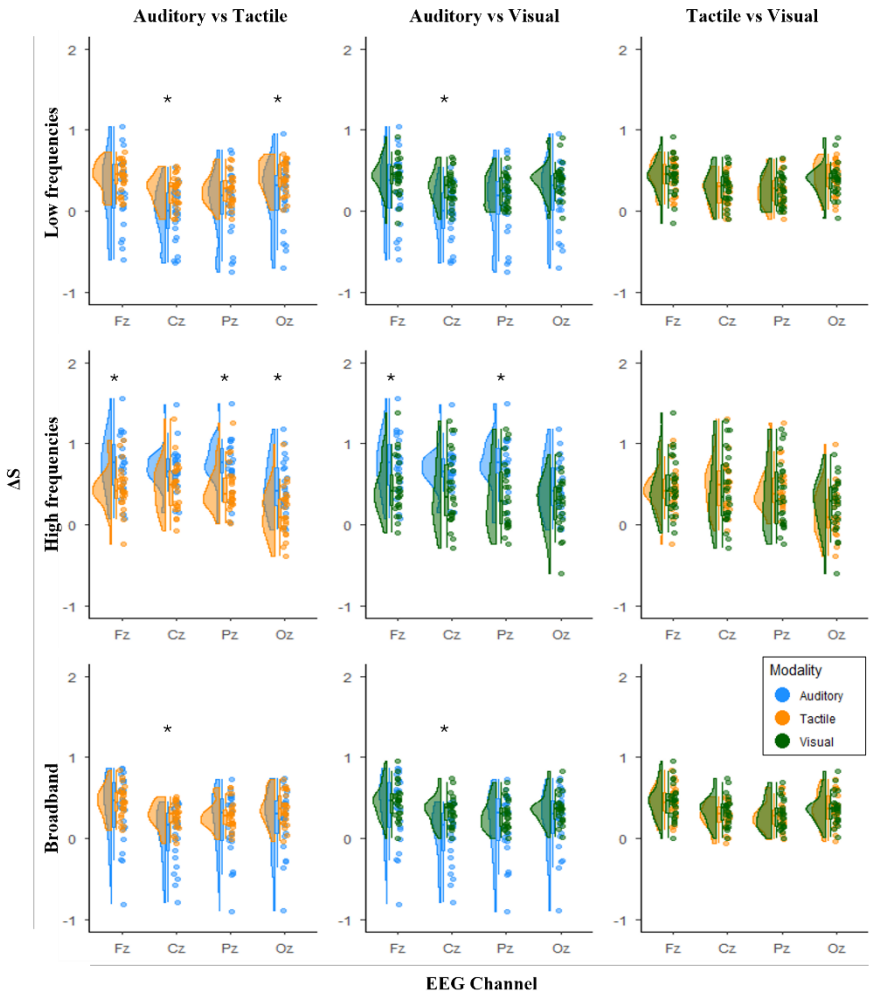



**Figure 16. Distribution of stimulus-dependent aperiodic slope variation (ΔS) across all evaluated channels and frequency bands for each stimulation modality.**

Low frequency: 0.5-30 Hz; High frequency: 30-45 Hz; Broadband: 0.5-45 Hz.
* statistical significance at Bonferroni-corrected threshold ($p < 0.042$)

#### 4.3.1.3. K-Complex Amplitude Variations Between Conditions

We explored potential modality-specific variations regarding KC amplitudes. Significant differences in the KC negative amplitude were observed across and between various stimulation modalities. However, it is important to note that stimulation trials were selected based on the presence and amplitude of the detected evoked slow wave (see Section 4.2.2.3). Moreover, many sham trials did not include spontaneous slow waves, with only 13 subjects presenting at least one unthresholded detected slow wave among their sham trials.

When comparing trials from all sensory modalities against sham, stimulation trials exhibited significantly higher KC negative amplitudes. Similarly, when examined modality-wise, each stimulation modality resulted in significantly higher KC negative amplitudes compared to sham (Table 6).

| Sham KC amplitude | Modality | eKC amplitude | Statistics | P-value |
|---|---|---|---|---|
| 54.72 ± 16.37 | Stimulation | 116.80 ± 27.77 | t(12) = 8.62 | 1.73E-06 * |
| | Auditory | 129.12 ± 34.51 | t(12) = 9.48 | 6.32E-07 * |
| | Tactile | 111.12 ± 35.49 | w = 91 | 2.44E-04 * |
| | Visual | 102.05 ± 33.18 | t(12) = 5.27 | 1.99E-04 * |

**Table 6. Comparison of slow-wave negative amplitudes across sensory modalities and sham trials.**

Slow wave negative amplitudes (KC and eKCs) values correspond to m ± std (in μV). (e)KC: (evoked) K-Complex. * statistical significance at Bonferroni-corrected threshold ($p < 0.042$)

Comparing between stimulation modalities, auditory stimulation resulted in significantly higher eKC negative amplitudes relative to tactile and visual stimulation. Instead, no differences were found between tactile and visual stimulation eKCs.

| Test | Statistics | P-value | |
|---|---|---|---|
| A-T | t(24) = 4.25 | 2.83E−04 | * |
| A-V | t(24) = 3.34 | 2.72E-03 | * |
| T-V | t(24) = 0.95 | 3.50E-01 | |

**Table 7. Statistical comparison of evoked K-complex (eKC) negative amplitudes across different sensory modalities.**

A: Auditory; T: Tactile; V: Visual. * statistical significance at Bonferroni-corrected threshold ($p < 0.042$)

### 4.3.2. Subjective Experience as a Function of Stimulus-Dependent Aperiodic Slope Variations

To understand the impact of ΔS on subjective experiences reported upon awakening, we analysed the data using mixed-effects models, including binomial GLMMs and CLMMs. In the case of CLMMs, the coefficient estimates for each tested predictor correspond to normalised fixed effect variables (see Section 4.2.3). Furthermore, we aimed to assess the extent to which ΔS serves as a non-redundant and informative marker for variations in subjective experiences upon awakening. Therefore, whenever ΔS demonstrated significant effects on subjective reports, we included the negative amplitude of the eKC as an additional predictor to identify any potential mediation effects. To enhance readability, we report only the outcomes related to the fixed effects (i.e., ΔS and time of night), with detailed results provided only when the effect of ΔS was significant.

#### 4.3.2.1. Conscious Experience Reports

##### *4.3.2.1.1. Type of Conscious Reports*

We investigated the relationship between variations in the type of reported conscious experience upon awakening (i.e., contentful dream, CD; white dream, WD; no dream, ND; see Table 8), ΔS, and the time of night using binomial GLMMs. Conscious report categories were modelled pairwise, with each computed model contrasting only two categories at a time.

| Conscious Category | Auditory | Tactile | Visual | Sham | Stimulation | TOTAL |
|---|---|---|---|---|---|---|
| **CD** | 100 | 83 | 48 | 98 | 231 | 329 |
| **WD** | 59 | 55 | 21 | 75 | 135 | 210 |
| **ND** | 55 | 28 | 33 | 56 | 116 | 172 |
| **TOTAL** | 214 | 166 | 102 | 229 | 482 | 711 |

**Table 8. Contingency table of trials by conscious report category across stimulation modalities.**

CD: Contentful Dream; WD: White Dream; ND: No Dream

In the comparison of CD and ND trials, the GLM identified a significant effect of ΔS in the auditory modality for the high-frequency band at electrode Cz ($\Delta S_{CD}$: 0.44 ± 0.74; $\Delta S_{ND}$: 0.99 ± 0.87; p = 4.10E-04), but not between WD ($\Delta S_{WD}$: 0.68 ± 0.56) and ND, nor CD and WD trials. To better understand the direction of this effect, we plotted the values of the pre- and post-event aperiodic slopes (Figure 17). The graphical interpretation of the aperiodic slope variation indicates that the effect is due to a greater steepening of the slope in ND relative to CD trials.

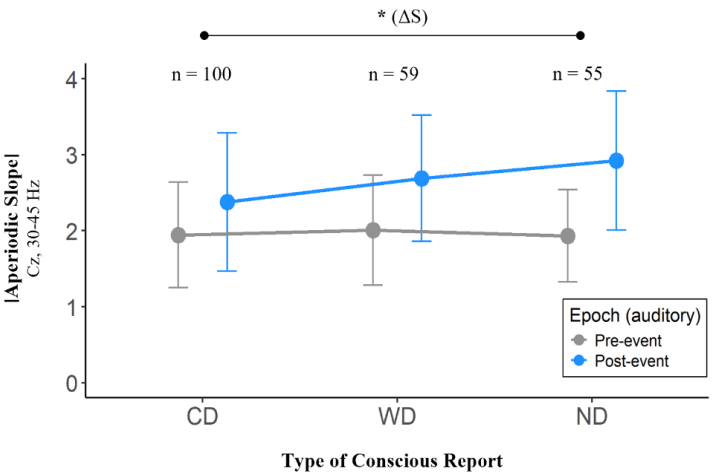



**Figure 17. Aperiodic slopes before and after auditory stimulation events at Cz in the high-frequency range (30-45 Hz) for different types of conscious reports.**

Aperiodic slope values are presented as absolute values. Error bars represent the standard deviation. The number of ratings for each conscious category is shown. CD: Contentful Dream; WD: White Dream; ND: No Dream; ΔS: stimulus-dependent aperiodic slope variation. * statistical significance at Bonferroni-corrected threshold ($p < 0.042$).

We explored the potential role of eKC in the observed effects (*Recall CD vs ND ~ ΔS + Time of night + Negative amplitude of eKC + 1|Night + 1|Sub*). The effect of ΔS in this new model remained consistent with the original model (p = 4.43E-04).

No other effects of ΔS were found for the auditory modality in any other frequency band or region. Moreover, no significant effects of the fixed predictors (ΔS and time of the night) were found when evaluating all stimulation trials, nor for the other stimulation modalities when tested individually (tactile, visual, or sham).

*4.3.2.1.2. Type of Conscious Content*

We evaluated whether variations in the type of reported conscious content, rated on a 5-point scale ranging from purely thought-like (1) to purely perceptual (5), were related to ΔS and the time of the night using CLMMs. A significant effect of ΔS was identified for the auditory

modality in the low-frequency band at Fz (normalised ΔS estimate = 0.64, std = 0.21, z = 3.03, p = 2.49E-03; Figure 18). No other effects of ΔS were found for the auditory modality in any other frequency band or region.

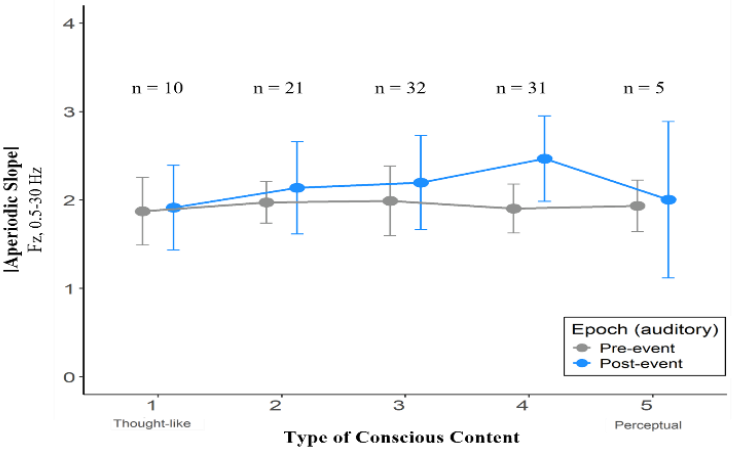



**Figure 18. Aperiodic slopes before and after auditory stimulation events at Fz in the low-frequency range (0.5-30 Hz) for different types of conscious content.**

Aperiodic slope values are presented as absolute values. Error bars indicate the standard deviation. The number of ratings for each content level is shown. Note: One auditory trial was missing its corresponding conscious content rating.

We explored the potential role of the eKC in the observed effect (*Type of content ~ ΔS + Time of night + Negative amplitude of KC + 1|Night + 1|Sub*). When including the KC amplitude, the previously significant effect of ΔS in the low frequencies on the type of content disappeared.

To verify whether the KC amplitude alone could predict the type of content, we modelled it without ΔS (*Type of content ~ Time of night + Negative amplitude of KC + 1|Night + 1|Sub*). No significant effects were observed with this model. No significant effects of the fixed predictors (ΔS and time of the night) were found when evaluating

all stimulation trials, nor for any of the other stimulation modalities when tested individually.

#### 4.3.2.2. Subjective Sleep Ratings

##### *4.3.2.2.1. Sleep Depth*

We investigated the relationship between sleep depth ratings, ΔS, and the time of night. In sham trials, sleep depth was significantly positively correlated with the time of night, showing increased ratings as the night progressed across all regions of interest and frequency bands (normalized time of night estimates: 0.94-1.05, all $p < 9.58E-05$). No effect of ΔS was identified for sham trials.

In stimulation trials, sleep depth was positively associated with ΔS in the broadband frequency range at Fz (normalised ΔS estimate = 0.47, std = 0.15, z = 3.16, p = 1.58E-03), Pz (normalised ΔS estimate = 0.51, std = 0.17, z = 3.09, p = 1.98E-03), and Oz (normalised ΔS estimate = 0.47, std = 0.15, z = 3.15, p = 1.63E-03), but not at Cz. This suggests that higher ΔS is associated with increased sleep depth ratings (Figure 19). We also evaluated modality-specific effects within these significant outcomes by examining auditory, tactile, and visual trials separately; however, no significant results were found.

When analysing low and high-frequency bands, ΔS did not significantly affect sleep depth in any region of interest. Nonetheless, a positive association between time of night and sleep depth was consistently observed across all regions and frequencies (time of night estimates: 0.41-0.48, all $p \leq 3.13E-03$).

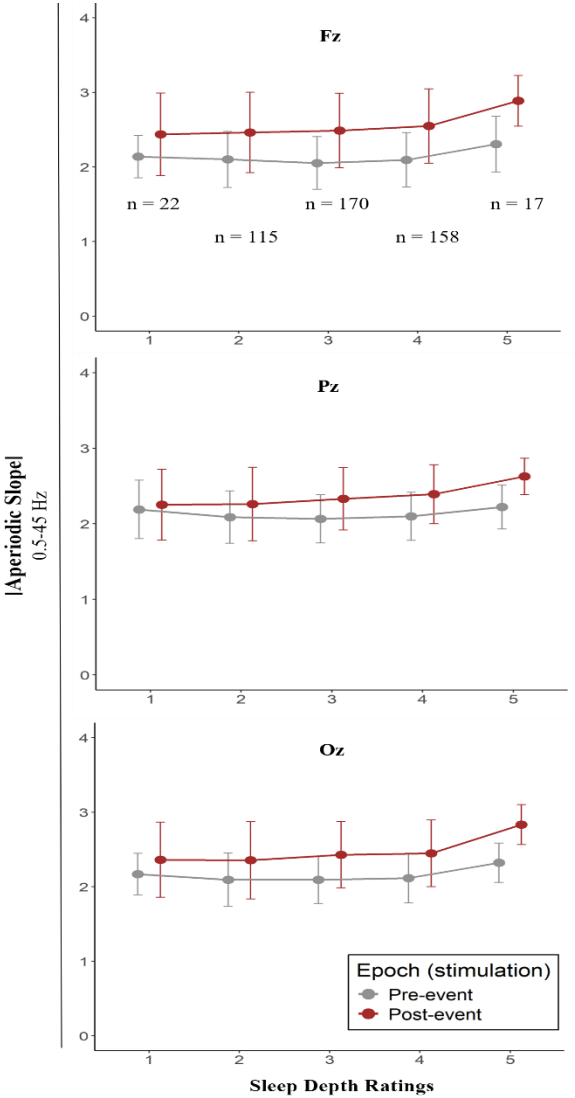



**Figure 19. Aperiodic slopes before and after stimulation events at Fz (top), Pz (centre), and Oz (bottom) in the broadband frequency range (0.5-45 Hz) across different sleep depth ratings.**

Aperiodic slope values are presented as absolute values. Error bars indicate the standard deviation. The number of ratings for each sleep depth level is shown in the top subfigure.

We explored the potential impact of eKC on the significant effects observed at Fz, Pz, and Oz in the broadband frequency range (*Sleep depth ~ ΔS + Time of night + Negative amplitude of eKC + 1|Night + 1|Sub*). The results remained similar to the previously described findings (Fz: normalised ΔS estimate = 0.48, std = 0.16, z = 3.05, p = 2.30E-03; Pz: normalised ΔS estimate = 0.50, std = 0.17, z = 2.99, p = 2.76E-03; Oz: normalised ΔS estimate = 0.47, std = 0.15, z = 3.03, p = 2.42E-03).

*4.3.2.2.2. Sleepiness*

We evaluated the relationship between sleepiness ratings, ΔS, and time of night, analysing sham and stimulation trials separately. While no significant relationships were found in sham trials, stimulation trials revealed a significant variation in sleepiness ratings as a function of ΔS in the low-frequency band at Fz (normalised ΔS estimate = 0.46, std = 0.16, z = 2.87, p = 4.08E-03; Figure 20). No modality-specific effects were identified when auditory, tactile, and visual trials were evaluated separately, and no additional ΔS effects were observed in other frequency bands or locations.

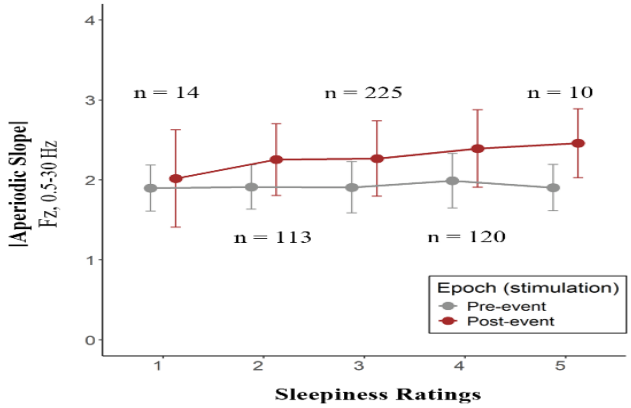



**Figure 20. Aperiodic slopes before and after stimulation events at Fz in the low frequency range (0.5-30 Hz) across different sleepiness ratings.**

Aperiodic slope values are presented as absolute values. Error bars indicate the standard deviation. The number of ratings for each sleepiness level is shown.

To assess the potential impact of eKC on our results, we added the negative amplitude of eKC to the model (*Sleepiness ~ ΔS + Time of night + Negative amplitude of eKC + 1|Night + 1|Sub*). Including the eKC amplitude led to the disappearance of the previously significant effect of ΔS on sleepiness ratings at Fz in the low frequencies. To explore whether the eKC amplitude alone could predict sleepiness, we removed ΔS from the model (*Sleepiness ~ Time of night + Negative amplitude of eKC + 1|Night + 1|Sub)* but found no significant effects.

Finally, in stimulation trials, sleepiness showed a significant positive association with the time of night, with sleepiness ratings increasing significantly as the night progressed (normalised time of the night estimates range: 0.44-0.48, all p-values < 2.88E-03).

## 4.4. Discussion

This study aimed at investigating the effects of multimodal sensory stimulation on EEG aperiodic activity, exploring whether stimulus-dependent aperiodic slope variations (ΔS) relate to subjective experiences during sleep. Our results show that auditory, tactile, and visual stimulation applied during N2 sleep induce significant variations in the aperiodic slope relative to no stimulation, with specific local and modality-dependent differences. Moreover, we found that ΔS in response to auditory stimulation varied as a function of the presence and type of conscious experience reported upon awakening. Finally, ΔS in response to stimulation events were associated with subjective measures of sleep depth and sleepiness.

### 4.4.1. Stimulus-Dependent Aperiodic Slope Variations

The aperiodic slope steepened from pre- to post-stimulation for all evaluated modalities compared to sham events (i.e., no stimulation). When pooling data across modalities, ΔS differed significantly from sham trials for all evaluated channels in the high-frequency range (30-45 Hz). In the low (0.5-30 Hz) and broadband (0.5-45 Hz) frequency ranges, the difference was significant at all evaluated channels but Cz.

The auditory modality induced the largest ΔS in the higher frequencies, with significant effects observed across all channels within this range. However, in the broadband range, significant differences were noted only at Fz, and no effects were observed in the lower frequencies. In contrast, both tactile and visual modalities, when compared to the sham condition, exhibited significant differences in ΔS across all channels and frequency ranges. Overall, we observed a consistent steepening of the slope from pre- to post-stimulation, particularly in the higher frequencies. Interestingly, steeper aperiodic slopes have been linked to a decrease in the excitation/inhibition (E/I) ratio in previous studies (R. Gao et al., 2017; Medel et al., 2023), suggesting the possibility of a post-stimulation reduction in this ratio.

Inter-modality comparisons revealed that auditory ΔS differed significantly from tactile and visual ΔS in several instances, while no significant differences were observed between tactile and visual ΔS. These findings may reflect distinct modality-specific sensory processing mechanisms during sleep, as indicated by the steeper slopes—and the potentially lower E/I ratio—following auditory stimulation. However, further investigation is needed to confirm this. Alternatively, the observed differences between modalities could be due to the fixed stimulation intensities used in our protocol, which were not adjusted for individual sensory thresholds, perhaps making auditory stimuli more arousing than tactile and visual stimuli.

Interestingly, comparisons of eKCs across modalities paralleled results obtained for ΔS. Indeed, significantly larger negative amplitudes were observed for the auditory modality compared to the visual and tactile modalities, which, in turn, did not present any differences. This finding aligns with previous research indicating that auditory eKCs tend to exhibit higher amplitudes than those elicited by other sensory modalities (Bellesi et al., 2014; Laurino et al., 2014). Since eKCs are a type of slow wave that contributes to lower frequency activity, the modality-specific effects on high-frequency ΔS and eKCs may reflect two distinct functional mechanisms that could conceivably interact.

Given that our stimulation trials systematically involved an eKC, the results may also be interpreted as evidence of an inhibitory drive associated with the eKC. The steeper post-stimulation slopes in the high-frequency band could indicate a decrease in the E/I ratio, supporting the notion that eKCs may play a sensory quenching role by triggering an inhibitory response in higher-order cortical areas. This interpretation aligns with the concept of a cortical gating mechanism (Andrillon & Kouider, 2020; Halász, 2005; Halász et al., 2004). The most pronounced and consistent ΔS effects were observed in fronto-central regions, where KCs are most prominent, further reinforcing this interpretation. However, further studies should investigate this hypothesis, particularly by including trials that do not involve eKCs.

A recent study by Ameen et al. (2024) examining ΔS in response to sensory stimulation during NREM sleep found that slopes became steeper following auditory stimulation, with a notable effect of saliency: higher ΔS values were observed in response to unfamiliar voices compared to familiar ones. This study demonstrated that ΔS is not solely dependent on the presence of eKCs or clear event-related potentials, although ΔS values were indeed higher in trials containing an eKC (Ameen et al., 2024). In another study, Alnes et al. (2024) investigated ΔS using pure tones during both wakefulness and sleep. Contrary to Ameen et al. (2024) and our own findings, significant ΔS changes were observed only during wakefulness, not during sleep. This discrepancy could be attributed to differences in the epoch lengths used: Alnes et al. (2024) analysed 500 ms before and after the auditory tone, whereas Ameen's study (2024) assessed 10-second epochs centred around stimulus onset, more closely aligning with the two 4-second segments used in our study. Overall, the evidence suggests that ΔS is a valuable proxy for brain dynamics associated with sensory processing, offering insights beyond those provided by eKCs and event-related potentials.

### 4.4.2. Conscious Experience as a Function of ΔS

#### 4.4.2.1. Type of Conscious Report

Our results indicate that auditory ΔS in the high-frequency band (30-45 Hz) measured at Cz predicts whether a subject will report a dream upon awakening. Specifically, smaller ΔS values were observed when a dream was reported compared to when not. In other words, the aperiodic slope became steeper following an auditory stimulation event when subjects reported no dreams (ND) as opposed to contentful dreams (CD). Importantly, this effect was independent of the amplitude of the evoked K-complex.

One possible interpretation of this finding is that neural responses to external perturbation, as reflected by ΔS, may be influenced by the ongoing brain state. During conscious experiences, the brain may be more resilient to sensory stimulation, while in the absence of consciousness, the brain reacts more readily, resulting in a larger ΔS. This is consistent with previous evidence showing that TMS-evoked EEG responses are larger during NREM 2 sleep when no dreams are reported compared to when a dream is recalled upon awakening (Nieminen et al., 2016). Furthermore, this aligns with the idea that during dreaming, the brain's attentional resources are primarily internally oriented, potentially competing with external sensory inputs. In contrast, in the absence of conscious experience, attention may be more easily directed towards external stimuli (Ameen et al., 2024; Gyurkovics et al., 2022).

Although not statistically explored, it is noteworthy that pre-stimulus slopes appear similar across different report types, with differences emerging primarily in the post-stimulus period. This observation suggests that sensory stimulation may directly influence the occurrence or encoding of dream experiences by altering the brain's functional states. Prior research has shown that dreaming—whether involving CD or WD—is associated with decreased low-frequency and increased high-frequency power within a 'posterior hot zone' relative to ND (Siclari et al., 2017). Moreover, CD is related to an increase in

high-frequency activity in centro-frontal areas relative to WD. Our findings reveal that high-frequency ΔS is greater for ND compared to CD at Cz, which might indicate a higher level of post-stimulation high-frequency activity in central regions of the scalp during CD trials, consistent with previous studies. This suggests that stimulation events producing stronger high frequency ΔS may suppress dreaming activity or disrupt the encoding of dream content, while smaller ΔS might preserve these processes.

Interestingly, the ΔS for WD falls between the values observed for CD and ND at Cz, showing greater slope steepening than when recalling a dream but less than when reporting no experience, although these differences did not reach statistical significance. Notably, some researchers have proposed that the WD category could encompass a range of report types, including forgotten content, the absence of experience with a positive response bias, and withheld recalled experiences (Fazekas et al., 2019). This variability could explain why WD is positioned between CD and ND in our findings.

4.4.2.2. Type of Conscious Content

Auditory ΔS demonstrated a predictive relationship with the type of reported content when measured in the low-frequency band (0.5-30 Hz) at Fz. Specifically, ΔS was significantly associated with variations in the perceptual versus thought-like dimension of the conscious experience, with greater ΔS corresponding to more perceptual ratings. However, it's important to acknowledge that the most extreme perceptual ratings exhibited a high degree of variability, which could complicate interpretation. This variability may stem from a response bias or the limited number of instances in the ‘purely perceptual content' category, consistent with the more thought-like nature typically associated with NREM 2 reports (Siclari et al., 2013).

Previous research has demonstrated that differences in dream content, particularly along the perceptual versus thought-like dimension, follow an anterior–posterior gradient. Thought-like reports have been associated with increased high-frequency power in frontal

regions, whereas perceptual reports have been linked to heightened high-frequency activity in posterior regions (Siclari et al., 2017). Our findings align with this pattern, as we observed increased frontal low-frequency slope steepening with more perceptual ratings. This suggests that thought-like reports are characterized by a reduced frontal low- to high-frequency activity ratio, in line with prior research (Siclari et al., 2017), while perceptual reports are associated with greater frontal low-frequency activity. These results provide further evidence of a relationship between local activation patterns and the nature of reported content. Additionally, since aperiodic slope values did not differ between conditions prior to the stimulus, it is possible that the characteristics of the reported dream content were influenced by the stimulation event. However, this interpretation remains speculative and warrants further investigation.

Notably, the predictive power of low frequency ΔS at Fz on the type of reported conscious content was no longer significant when the amplitude of the eKC was accounted for, suggesting a potential correlation between these two measures. This aligns with the understanding that eKCs are low-frequency (<2 Hz) oscillations with the largest amplitudes in fronto-central regions (Laurino et al., 2014; Wennberg, 2010), indicating possible partial redundancy between eKCs and low-frequency ΔS, especially when measured in overlapping scalp areas.

### 4.4.3. Subjective Sleep Ratings as a Function of ΔS

Our study revealed a positive association between subjective ratings of sleep depth and sleepiness with ΔS in stimulation trials, irrespective of the sensory modality. Specifically, greater subjective sleep depth was linked to increased stimulus-dependent broadband slope steepening (0.5-45 Hz) at Fz, Cz, and Pz. On the other hand, higher sleepiness ratings were associated with increased low-frequency slope steepening (0.5-30 Hz) at Fz. Remarkably, while the effect of ΔS on subjective sleep depth remained independent of the eKC, its relationship with

sleepiness disappeared when the negative amplitude of the eKC was taken into account.

Traditionally, sleep depth has been defined as the resilience of sleep to external stimulation and is typically associated with SWA in NREM sleep, an indicator of homeostatic sleep pressure that correlates with subjective sleepiness in wakefulness (Blake & Gerard, 1937; Bódizs et al., 2024; Bonnet et al., 1978; De Gennaro et al., 2007; Finelli et al., 2000, 2001; Snipes et al., 2023). Recent studies have proposed spectral slopes as markers of homeostatic sleep pressure, potentially bridging the gap between sleep depth and aperiodic activity (Bódizs et al., 2024; C. G. Horváth et al., 2022). Moreover, evidence shows that broadband aperiodic slopes become steeper with deeper sleep stages, paralleling increased neural synchrony and decreased complexity across these stages (Alnes et al., 2024; Ameen et al., 2024; Höhn et al., 2024; Miskovic et al., 2018). Additionally, the age-related flattening of broadband NREM fractal slopes mirrors the progressive lightening of sleep over the lifespan, further highlighting the association between aperiodic slopes and objective sleep depth (Bódizs et al., 2021; Carrier et al., 2001).

However, clinical observations in individuals with insomnia and sleep-state misperception indicate that the relationship between objective and subjective sleep depth may not be as straightforward (Andrillon et al., 2020; Stephan et al., 2021; Zhao et al., 2021). These conditions are characterized by fragile sleep and increased subjective awareness during sleep, with patients often mistakenly feeling awake, especially in early NREM sleep (Stephan et al., 2021). Affected individuals show decreased low-frequency activity, increased high-frequency activity, lower delta/beta ratio, and flatter NREM slopes relative to controls (Andrillon et al., 2020; Fasiello et al., 2024; Stephan et al., 2021; Zhao et al., 2021). This association between wake-like activation patterns and poor subjective sleep perception is also observed in good sleepers and seems to be independent from SWA variations typically associated with objective sleep depth (Stephan et al., 2021). These patterns indicate that lower subjective sleep depth

correlates with more wake-like patterns during sleep, in agreement with the observed association between larger broadband ΔS—reflecting larger low to high frequency ratio—and higher subjective sleep depth ratings in our data.

On the other hand, high sleep inertia upon awakening—characterized by decreased alpha and increased delta activity over fronto-central areas—correlates with increased subjective sleepiness (De Gennaro et al., 2010; Finelli et al., 2001; Marzano et al., 2010, 2011; Trotti, 2017). This suggests that the feeling of sleepiness relates to local increases in low frequency activity, consistent with our finding of larger low frequency ΔS at Fz for higher sleepiness ratings.

Notably, this study is the first, to our knowledge, to examine the relationship between aperiodic slope variations and subjective sleep ratings. Previous research has primarily focused on between-stage spontaneous slope variations, making direct comparisons with our within-stage event-related approach challenging. Furthermore, since we did not assess whether stimuli were perceived or compute changes in spectral power, we cannot directly comment on the relationship between subjective ratings and objective sleep depth or sleepiness markers. Nevertheless, our findings suggest that ΔS may be a valuable indicator of within-stage fluctuations in subjective sleep ratings.

In addition to ΔS variations, a significant positive correlation was identified between the time of night and subjective sleep ratings, with both sleep depth and sleepiness increasing as the night progressed. Fluctuations in subjective sleep depth throughout the night have already been documented, with lighter sleep ratings in the early and late parts of the night, and the deepest ratings occurring in the middle (Stephan et al., 2021). However, that study did not differentiate between N2 and N3 sleep, instead grouping them together under a general NREM category. In contrast, our findings focused exclusively on N2 data, which may account for the discrepancy with the previously reported U-shaped pattern.

### 4.4.4. Limitations of the Study

Our study has several limitations that should be considered when interpreting the findings. Firstly, the generalizability of our results regarding conscious experiences is limited by the fact that ΔS effects were observed only in the auditory modality. Since we used fixed stimulation intensities that were not individually thresholded, it is possible that auditory stimuli were generally more arousing than the selected tactile and visual stimuli. Alternatively, the modality-dependent differences in ΔS might reflect specific processing mechanisms that are more responsive to auditory information. Indeed, we found that auditory eKCs had larger amplitudes compared to visual and tactile ones, consistent with previous research (Bellesi et al., 2014; Laurino et al., 2014). Given that eKCs are known to include an initial modality-specific positive component (Laurino et al., 2014, 2019; Riedner et al., 2011), this activation might contribute differently to the aperiodic slope across sensory modalities. However, our results also showed greater overall ΔS variability following auditory stimulation compared to other modalities, highlighting the importance of controlling for individual arousal thresholds and post-stimulation signs of arousal, such as increases in high-frequency EEG activity or EMG activity.

Our study was limited to N2 sleep, which enabled us to explore within-stage fluctuations but restricted our ability to make between-stage comparisons that could have provided a more comprehensive understanding of the mechanisms underlying sleep sensory-dependent variations in the aperiodic slope. Future investigations should encompass the entire sleep cycle, including finer distinctions between sleep states, such as tonic and phasic REM. Tonic REM has been associated with lower arousal thresholds and more thought-like conscious experiences, while phasic REM has been linked to higher levels of sensory disconnection and more vivid, hallucinatory-like conscious content (Ermis et al., 2010; Sallinen et al., 1996; Simor et al., 2018, 2020; Takahara et al., 2002; Wehrle et al., 2007). Therefore, in view of the observed behaviour of ΔS regarding dreaming

activity in NREM, it is likely that ΔS also presents within-stage fluctuations in REM sleep.

Another significant limitation is that our stimulation trials systematically included an eKC, which prevented a direct comparison between trials with and without eKCs regarding ΔS and associated variations in subjective experiences. This constraint complicates the interpretation of ΔS independently of the eKC effect. However, our exploratory models suggested that the effects of ΔS did not seem to depend on the presence of an eKC. This implies that the brain's response to external stimuli during sleep is likely a complex, multicomponent process, of which the eKC is just one part. Therefore, ΔS may provide a more comprehensive measure of this response, capturing broader dynamics beyond those reflected by the eKC alone.

By focusing solely on the aperiodic spectral slope of the EEG signal, our aim was to propose a single measure that could serve as a snapshot of the general brain state at a particular point in time. However, other aperiodic measures, such as the offset (Favaro et al., 2023) or 'knee' frequency (Ameen et al., 2024), also appear promising for the study of sleep. Furthermore, it may be beneficial to compare results using different frequency ranges, as several authors have evaluated aperiodic activity in sleep data with various cutoff values (Alnes et al., 2021; Andrillon et al., 2020; Colombo et al., 2019; Favaro et al., 2023; Miskovic et al., 2018). This variation is partly due to the presence of a 'knee' around 20 Hz, which, however, has been shown to be less prominent in NREM sleep (Ameen et al., 2024). Nonetheless, the frequency ranges selected in the present study have been previously used in the literature and have proven informative about E/I balance, arousal, and conscious states across the sleep-wake cycle (R. Gao et al., 2017; Höhn et al., 2024; Kozhemiako et al., 2022; Lendner et al., 2020; Maschke et al., 2023).

### 4.4.5. Conclusion

In summary, our findings suggest that stimulus-dependent slope variations can effectively probe underlying brain states, providing valuable insights into subjective experiences during sleep. To our knowledge, this is the first study to evaluate aperiodic slope variations in response to auditory, tactile, and visual stimulation during N2 sleep. This approach may offer a useful tool for exploring sleep-dependent variations in consciousness and arousal, particularly in relation to associated subjective experiences, enhancing our understanding of how these experiences may fluctuate within sleep stages, and allowing for a more precise distinction of transient brain states. Furthermore, our results suggest potential links between the background aperiodic neural landscape, the presence and nature of ongoing conscious experiences, and subjective sleep appraisal, extending beyond typical stimulus-dependent evoked responses.

# Chapter 5.
# General Discussion

The research presented in this thesis aimed to characterise the effects of sensory stimulation during sleep in relation to subjective conscious experiences. The findings challenge the traditional view of sleep as a state of sensory disconnection, demonstrating that a significant number of stimuli can penetrate conscious awareness during sleep, serving both to probe and to shape ongoing subjective experiences. This suggests that the concept of dreams as a form of 'disconnected consciousness,' where subjective experiences arise independently of external stimuli, needs reconsideration.

## 5.1. Summary of Findings

A systematic review of the current literature on the influence of sensory stimulation on dreams (see Chapter 2) highlighted the significant heterogeneity among existing experimental protocols. The review's findings suggest that stimulus-dependent dream changes (SDDCs) can be categorized into three main types: direct incorporations, indirect incorporations, and dream modulations. Direct incorporations involve the seamless integration of stimuli into the dream narrative or their recognition as external elements, which can sometimes trigger dream lucidity, as demonstrated in one of the presented experimental studies (see Chapter 3). In contrast, indirect incorporations occur through semantic or mnemonic associations and often require the dreamer's subjective input for identification. Dream modulations encompass all other types of SDDCs; however, due to the high diversity of cases included in this category, these changes are more difficult to predict and objectively measure.

Among the various sensory modalities, somatosensory stimuli appear to be the most effective at inducing SDDCs, with saliency emerging as a particularly important factor in determining their impact. However, research directly comparing the effects of different

sensory modalities remains limited, and cross-study comparison is hindered by the variability of reported findings. To address this gap, a methodological assessment tool was developed to provide a reliable measure of empirical quality, which may serve as a guideline for prospective studies to adhere to state-of-the-art scientific standards in the field of dream engineering (see Appendix I: Supplementary Text 1). This tool revealed that most SDDC-related research presents several methodological shortcomings, further hindering interpretation and robustness of findings. Therefore, experimental work was conducted to provide additional empirical evidence to the field: two multimodal sensory stimulation sleep studies were performed to investigate the effects of auditory, visual, and tactile stimuli on sleep subjective experiences.

The first experimental study included a within-subject early morning nap protocol based on a minimal laboratory-based setup, involving portable EEG devices and open-source software, in view of validating a dream lucidity induction technique (see Chapter 3). The findings demonstrate that the implemented targeted-lucidity reactivation (TLR) protocol, which combined cognitive training with sensory stimulation during wake and subsequent REM sleep, effectively enhanced dream awareness and control. Sensory stimuli presented during REM sleep successfully elicited voluntary predefined eye movement responses from the dreamer, enabling real-time communication with the experimenter and serving as an objective measure of both lucidity and stimulus awareness during sleep. These outcomes suggest that multimodal stimulation protocols offer a valuable approach for directly investigating sensory (dis)connection during sleep and its influence on the qualitative aspects of ongoing conscious experiences.

Notably, this study is part of a collaborative, multi-centric research project involving three leading international sleep laboratories in Italy, the Netherlands, and Canada. The protocol was pre-registered before data collection commenced at any of the participating centres, ensuring a high level of methodological consistency across sites. This

approach will allow for the pooling of datasets, resulting in the largest experimental study of lucid dream induction with EEG data collection to date, showcasing robust methodological rigor, replicability, and effective collaboration. Furthermore, the protocol was designed to be cost-effective and rely on minimal technical requirements by using commercially available, ready-to-use portable EEG devices and open-source dream engineering software (Esfahani, Daraie, et al., 2023; Esfahani, Sikder, et al., 2023). The pooled data will also be openly shared in public repositories, in compliance with current scientific best practices.

The second experimental study employed an overnight serial awakening protocol over multiple nights, following a within-subject design (see Chapter 4). This study focused exclusively on N2 awakenings, examining stimulus-dependent variations in the aperiodic spectral slope (ΔS) and their relationship to various subjective sleep measures, including the presence and content of conscious experiences, as well as subjective assessments of sleep depth and sleepiness. The findings revealed that aperiodic slopes consistently steepened after stimulation compared to sham conditions, with the steepest slopes observed following auditory stimulation, particularly in the high-frequency range (30-45 Hz). These results align with inter-modality differences in the amplitude of the evoked K-complexes (eKCs)—a low-frequency response consistently elicited in our study—suggesting that the modality-specific effects observed in both high-frequency ΔS and eKCs likely reflect independent mechanisms that may interact with each other.

Regarding conscious experiences, auditory ΔS emerged as a predictive marker for the presence and type of dream activity during N2 sleep. Specifically, contentful dream trials exhibited less high-frequency slope steepening at Cz compared to trials without dreams, likely indicating an association between dreaming and increased wake-like high-frequency power. Additionally, thought-like reports were linked to reduced low-frequency ΔS (0.5-30 Hz) at Fz compared to perceptual experiences, suggesting reduced low-frequency activity in

frontal regions in case of thought-like content. These findings align with previous research which related NREM dreaming to relatively heightened high-frequency activity in a posterior cortical 'hot zone', further showing that thought-like experiences were associated with greater wake-like activity in frontal areas (Siclari et al., 2017, 2018). Together, these results suggest that ΔS represents a valuable marker of within-stage fluctuations in sleep conscious activity.

Subjective sleep ratings also demonstrated a significant relationship with post-stimulation slope variations across sensory modalities. Both subjective sleep depth and sleepiness ratings were positively associated with broadband and low frequency ΔS, respectively. This indicates that smaller ΔS values, likely reflecting decreased low-frequency power, correspond to lighter subjective sleep and lower sleepiness ratings. These observations are consistent with previous findings that correlated lower subjective sleep depth and higher rates of sleep state misperception to increased wake-like activity during sleep (Andrillon et al., 2020; Fasiello et al., 2024; Stephan et al., 2021; Zhao et al., 2021). Thus, ΔS proves to be informative about within-stage variations in subjective sleep appraisal.

## 5.2. Future Research Directions

The findings presented in this thesis open several avenues for future research in the field of dream engineering, particularly in exploring the complex interplay between sensory stimulation, neural activity, and conscious experiences during sleep. This evidence challenges the traditional view of sleep and dreaming as states of sensory disconnection, advocating for a more fine-grained understanding of brain state dynamics across the sleep-wake cycle. Traditional sleep scoring methods, with their broad categorizations, often overlook significant within-stage variability and micro-structural heterogeneity (e.g., N1: Tanaka et al., 1996; N2: Brandenberger et al., 2005; Decat et al., 2022; REM: Simor et al., 2016, 2018, 2019). In recent years, research has underscored the shifting nature of sleep, characterized by local and temporal fluctuations in brain activity, environmental responsiveness,

and associated subjective experiences (Andrillon & Oudiette, 2023; Avvenuti & Bernardi, 2022; Siclari & Tononi, 2017). This calls for more precise tracking of transient changes in arousal and consciousness during sleep, which may be orchestrated by the same naturally oscillating infra-slow time course previously demonstrated for fluctuations in neural excitability, environmental responsiveness, and autonomic activity during sleep (Bueno-Junior et al., 2023; Lázár et al., 2019; Lecci et al., 2017; Vanhatalo et al., 2004).

The outcomes reported through this work highlight the potential of sensory stimulation-based measures as useful tools for assessing these changes, enabling a more granular approach of sleep physiology and phenomenology. Future research should focus on developing new frameworks that use sensory processing markers to characterize these dynamics, including arousal thresholds (Picchioni et al., 2024), behavioural responsiveness (Türker et al., 2023; cf. Chapter 3), event-related potentials (Moyne et al., 2022), or stimulus-dependent variations in aperiodic activity (Alnes et al., 2024; Ameen et al., 2024; cf. Chapter 4). Moreover, it would be interesting to evaluate whether such measures follow the previously mentioned infra-slow time course through highly recurrent overnight sampling. Importantly, these insights may have practical implications for enhancing the accuracy of automated sleep staging algorithms, particularly by identifying periods of heightened conscious activity or sensory awareness, thereby refining dream engineering techniques. Additionally, they may be clinically relevant for conditions such as sleep misperception and paradoxical insomnia, offering non-invasive markers for within-stage fluctuations in subjective experience.

A promising future direction involves combining the lucid dream induction protocol validated in this thesis with aperiodic slope measurements to explore whether $\Delta S$ varies with the degree of dream lucidity or can predict the dreamer's perception and response to stimuli. Furthermore, measures like $\Delta S$ may serve as sensitive markers of stimulus-dependent changes in conscious activity. Previous studies on SDDCs suggest that dream modifications may be influenced by

arousal or other indicators of 'cortical registration' (Conduit et al., 1997; Fedyszyn & Conduit, 2007; Koulack, 1969; Nielsen et al., 1993; Zimmerman, 1970), but conclusive evidence is still lacking. Follow-up studies should evaluate the neural correlates of SDDCs, their relation to (micro)arousals, and their association with ΔS. Moreover, while the focus of the current dissertation was restricted to external stimulation, future research should also consider interoceptive signals (H.-D. Park & Tallon-Baudry, 2014; Wei & Van Someren, 2020), further expanding the range of possible SDDCs and evaluating their influence on sleep subjective experiences.

The role of SDDCs in maintaining sleep continuity is also significant, as dreams may protect sleep by either preventing external stimuli from entering awareness—through competition for attentional resources—or by integrating these stimuli into the dream narrative, thereby reducing their arousing effects. However, fundamental questions about SDDCs remain unanswered, particularly regarding the factors that determine the type of SDDC elicited by a given stimulus. To address these gaps, future research should establish standardized definitions for SDDCs and dreams, as well as refine the queries used to probe conscious experiences upon awakening. Moreover, the identification of SDDCs should leverage automated computational linguistics to ensure objective and reproducible quantification of dream content, alongside the implementation of rigorous control conditions.

Finally, to overcome the current limitations in dream engineering studies, large-scale research efforts will be essential. These should involve multi-laboratory collaborations, pre-registered protocols of high methodological quality, and open data sharing. Additionally, increasing the spatial resolution of data in future studies, particularly through high-density EEG or functional neuroimaging, is advisable. Such improvements would enable the identification of modality-specific regional variations in brain responses to sensory stimulation and their connection to the qualitative aspects of ongoing subjective experiences. Enhanced topographical resolution would also facilitate more precise source modelling, deepening our understanding

of subcortical contributions to sensory-dependent changes in sleep and dream activity, and clarifying the time-course of neural responses to sensory stimulation across the sleep-wake cycle.

## 5.3. Concluding Remarks

In summary, sensory stimulation offers valuable insights into the dynamics of the dreaming brain. The investigation of SDDCs, the development of lucid induction techniques that enable objective measures of behavioural responsiveness to experimental stimuli, and the analysis of stimulus-dependent aperiodic slope variations in relation to subjective experiences all contribute to a deeper understanding of the 'fluid boundaries' of sleep and their connection to conscious experiences. It is now clear that dreaming does not represent a state of complete sensory disconnection per se, but rather exists on a continuum—from full awareness of both the external environment and the internally generated experiences, as in lucid dreaming, to the total absence of subjective experience, when the sleeper is reportedly unconscious.

Despite considerable progress in characterizing the neural correlates of dreaming, the development of a reliable 'Dream Catcher' formula remains elusive (Wong et al., 2020). This difficulty likely arises from the inherently complex nature of subjective experiences, which may not be fully captured by spontaneous electrophysiological patterns alone. These patterns are likely to reflect a broad array of ongoing processes, including potential noise from different sources and spontaneous or random activity fluctuations, which limit their utility as definitive indicators of dreaming activity. A more effective approach might involve using neural and phenomenological permeability to external stimuli as a marker of state-like fluctuations in consciousness.

More generally, the conceptualization of dreaming has progressively been rooted in the philosophical framework of predictive processing (Bucci & Grasso, 2017; Clark, 2012; Hobson & Friston, 2012; Simor et al., 2020, 2022). This framework posits that the brain functions as a Bayesian inferential machine, constantly striving to optimize the

match between its internally generated predictions and the sensory input it receives. This matching process is influenced by how attentional resources are allocated and the precision of perceptual processing. In this context, the brain's access to reliable sensory information—dictated by levels of sensory disconnection and information integration—becomes a key determinant of subjective experiences, including those during sleep. During periods of heightened sensory processing, the brain may reduce predictive errors by aligning internal conscious experiences with available sensory input, leading to more stimulus-oriented content and SDDCs, as observed in hypnagogic dream incubation (Haar Horowitz et al., 2023). In contrast, periods of increased sensory thresholds, such as phasic REM sleep, may allow the brain to generate purely internal experiences, creating novel scenarios that could help prevent or mitigate future waking prediction errors, as suggested by prospective coding and dream simulation theories (Revonsuo, 2000; Revonsuo et al., 2016; Simor et al., 2020, 2022; Tuominen et al., 2019; Valli & Revonsuo, 2009).

Overall, it becomes increasingly clear that dreams should not be regarded as isolated bubbles of consciousness. As philosophers and pioneering dream researchers have theorised for centuries, sensory perception appears to play a fundamental role in shaping subjective experiences during sleep. The intricate relationships between sensory disconnection, the presence and content of conscious experiences, and the underlying patterns of brain activity hold great promise for advancing our understanding of dreams, likely offering valuable insights into their functional aspects. However, these claims warrant further empirical investigation. Therefore, it may be time to shift our focus toward developing stimulation-based 'Dream Prober' protocols that can more accurately discern the intricacies of sleep consciousness, eventually shedding light on the long-standing mysteries of dreaming.

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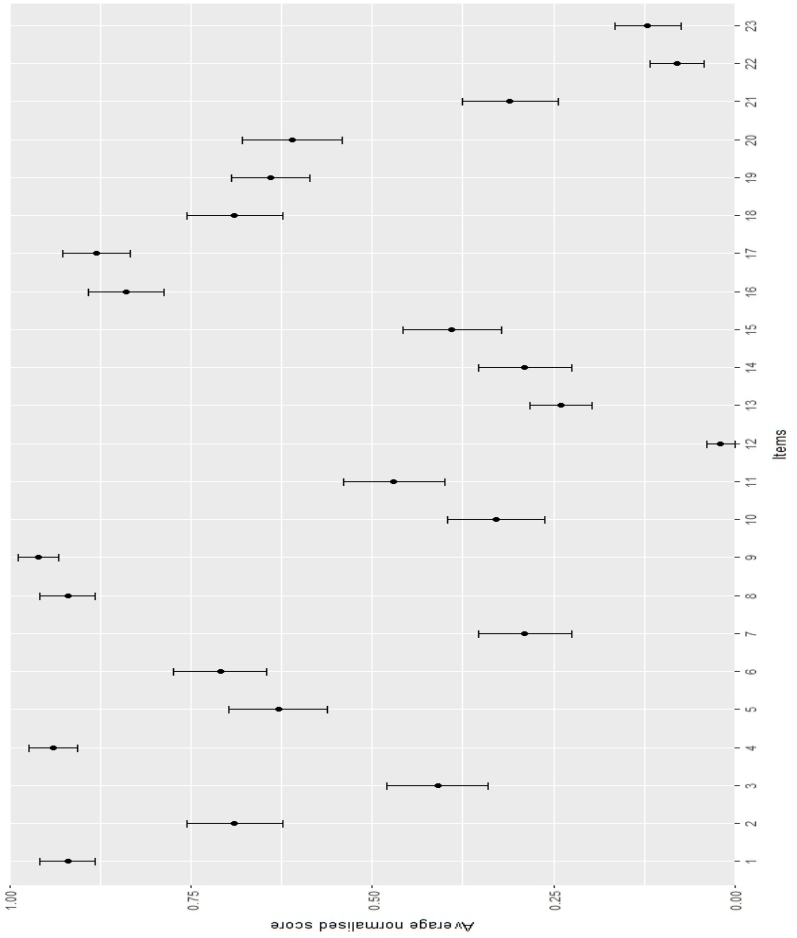
# Appendices

## Appendix I.

**Supplementary Figure I.1. Methodological assessment checklist item-by-item score distribution (m ± std) for selected studies.**



**Supplementary Table I.1. Articles excluded following pre-selection criteria.**

| Article | Not research article (e.g., review article, comment…) | Brain stimulation | Other sensory modalities (e.g., internal stimulation) | Not in English | Drug administration |
|---|---|---|---|---|---|
| Oswald (1965) | X | | | | |
| Baldridge (1966) | X | | | | |
| Koulack (1987) | X | | | | |
| Stickgold (1999) | X | | | | |
| Stickgold (2001) | X | | | | |
| Schredl & Stuck (2009) | X | | | X | |
| Braun & Cheok (2014) | X | | | | |
| Wiseman (2014) | X | | | | |
| Carr et al. (2020a) | X | | | | |
| Carr et al. (2020b) | X | | | | |
| Siclari (2020) | X | | | | |
| Fazekas et al. (2021) | X | | | | |
| Baird et al. (2021) | X | | | | |
| Heijden et al. (2022) | X | | | | |

| | | | | | |
|---|---|---|---|---|---|
| Vitali et al. (2022) | X | | | | |
| Jakobson et al. (2012a) | | X | | | |
| Jakobson et al. (2012b) | | X | | | |
| Jakobson et al. (2012c) | | X | | | |
| Voss et al. (2014) | | X | | | |
| Blanchette-Carrière et al. (2020) | | X | | | |
| Noreika et al. (2020) | | X | | | |
| Finley (1921) | | | X | | |
| Yazmajian (1967) | | | X | | |
| Gross & Lavie (1994) | | | X | | |
| Schredl et al., (1999) | | | X | | |
| Raymond et al. (2002) | | | X | | |
| Canziani (1950) | | | | X | |
| Angeleri & Ferroni (1965) | | | | X | |
| Leuschner (1986) | | | | X | |
| Stuck (2010) | | | | X | |

| | | | | | |
|---|---|---|---|---|---|
| Moore & Seymour (1987) | | | | | X |
| Aceto et al. (2007) | | | | | X |
| Radek et al. (2018) | | | | | X |

**Supplementary Table I.2. Articles excluded following final selection criteria.**

| **Article** | **No dream data reported** | **No sleep measure** (i.e., EEG or actigraphy) | **Pooled data** (e.g., across modalities, LD & non-LD…) | **(Post-) Hypnotic 'dream' states** | **Only LD data** | **Results published elsewhere** |
|---|---|---|---|---|---|---|
| Loomis et al. (1937) | X | | | | | |
| Ornitz et al. (1967) | X | | | | | |
| Salamy (1971) | X | | | | | |
| Oltman et al. (1977) | X | | | | | |
| Zepelin et al. (1984) | X | | | | | |
| Miyauchi et al. (1990) | X | | | | | |
| Sallinen et al. (1996) | X | | | | | |
| Lavie et al. (1998) | X | | | | | |
| Perrin et al. (2002) | X | | | | | |
| Blagrove et al. (2006) | X | | | | | |
| Ruby et al. (2008) | X | | | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Rihm & Rasch (2015) | X | | | | | |
| Watt et al. (2015) | X | | | | | |
| Züst et al. (2019) | X | | | | | |
| Koroma et al. (2020) | X | | | | | |
| Neumann et al. (2020) | X | | | | | |
| Fogel et al. (2022) | X | | | | | |
| Moyne et al. (2022) | X | | | | | |
| Max (1935) | | X | | | | |
| LaBerge & Levitan (1995) | | X | | | | |
| Kamal et al. (2010) | | X | | | | |
| Kamal et al. (2012) | | X | | | | |
| Vitinius et al. (2014) | | X | | | | |
| Horowitz et al. (2020) | | X | | | | |
| Moiseeva (1975) | | | X | | | |
| Carr et al. (2020c) | | | X | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Konkoly et al. (2021) | | | X | | | |
| Schjelderup (1960) | | | | X | | |
| Arkin et al. (1966) | | | | X | | |
| Stross & Shevrin (1968) | | | | X | | |
| Torda (1975) | | | | X | | |
| Kumar et al. (2018) | | | | | X | |
| Koulack (1968) | | | | | | X |

**Supplementary Table I.3. Methodological assessment checklist scores for selected studies.**

| Article | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | Total score |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ackerley et al. (2020) | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 18 |
| Bastuji et al. (2008) | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 10 |
| Berger (1963) | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 13 |
| Bloxham & Durrant (2014) | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| Borghese et al. (2022) | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 20 |
| Bradley & Meddis (1974) | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 10 |
| Bruck & Horasan (1995) | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| Burton et al. (1988) | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 11 |
| Castaldo & Holzman (1967) | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 16 |
| Castaldo & Holzman (1969) | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 16 |

| | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Castaldo & Shevrin (1970) | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 12 |
| Conduit & Coleman (1998) | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 8 |
| Counduit et al. (1997) | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 12 |
| De Koninck & Koulack (1975) | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 19 |
| Dement & Wolpert (1958) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Erlacher, Schmid, Bischof, et al. (2020) | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 13 |
| Erlacher, Schmid, Schuler, et al. (2020) | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 11 |
| Fedyszyn & Conduit (2007) | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 14 |
| Flo et al. (2011) | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 13 |
| Goodenough et al. (1965) | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 9 |
| Hoelscher et al. (1981) | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 16 |
| Horowitz et al. (2018) | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 7 |

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Koulack (1969) | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 11 |
| Lavigne et al. (2004) | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 11 |
| Leslie & Ogilvie (1996) | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 14 |
| Lewin et al. (1973) | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 12 |
| Martinec Nováková, Kliková, et al. (2021) | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 20 |
| Martinec Nováková, Miletínová, et al. (2021) | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 1 | 18 |
| Nielsen (1993) | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 16 |
| Nielsen et al. (1993) | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 8 |
| Nozoe et al. (2020) | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 12 |
| Okabe et al. (2018) | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 1 | 16 |
| Okabe et al. (2020) | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 18 |
| Paul et al. (2014) | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 12 |
| Picard-Deland et al. (2021) | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 19 |
| Picard-Deland & | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 18 |

| | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nielsen (2022) | | | | | | | | | | | | | | | | | | | | | | | | |
| Rahimi et al. (2015) | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 19 |
| Rechstaffen & Foulkes (1965) | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 13 |
| Sauvageau et al. (1998) | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 16 |
| Schäfer et al. (2019) | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 22 |
| Schmid & Erlacher (2020) | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 12 |
| Schredl et al. (2009) | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 20 |
| Schredl et al. (2014) | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 18 |
| Shapiro et al. (1963) | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 9 |
| Shapiro et al. (1965) | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 10 |
| Strauch (1988) | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 13 |
| Stuart & Conduit (2009) | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | 0 | 18 |
| Tilley et al. (1987) | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 12 |
| Trotter et al. (1988) | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 9 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ziegler (1973) | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 12 |
| Zimmerman (1970) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |

**Supplementary Text I.1. Historical overview: Early work and preliminary findings about sensory-dependent dream changes.**

Observations regarding the influence of external stimuli on oneiric experiences have been recorded for millennia. Early writings about the effect of sensory perceptions on ongoing dreams date back to ancient Greece, with Aristotle mentioning how "*dreamers fancy that they are affected by thunder and lightning, when in fact there are only faint ringings in their ears; or that they are enjoying honey or other sweet savours, when only a tiny drop of phlegm is flowing down [the oesophagus]; or that they are walking through fire, and feeling intense heat, when there is only a slight warmth affecting certain parts of the body*." (Aristoteles. Parva Naturalia / De Divinatione per Somnum - Chapter I, Section 463a). The philosopher introduces this by observing that "*in sleep [...] even trifling movements seem considerable [to the dreamers]*", yet "*when they are awakened, these things appear to them in this their true character*", already making assumptions about state-dependent perceptual variations that would be unravelled experimentally over 20 centuries later (Cubberley, 1923; Nielsen et al., 1993).

In fact, we need to jump forward to the late nineteenth century to find the first documented accounts of systematic dream manipulation by the hand of Hervey de Saint-Denys (1867), whose pioneering work paved the way for modern dream science. He reported that olfactory stimuli could lead to the incorporation into the dream of memories associated with that particular odour, setting the premises for what we now know as TMR. He was also one of the first to describe a potential link between the emotional tone of an odour and declarative memory. Later, Cane (1889) published a short essay in The Lancet where he wrote that "*all the phenomena of dreams are fully accounted for by the auto-sensations physiologically developed within the body, and which are sometimes increased by pathological or semi-pathological conditions and modified by external impressions or stimuli. […] The external influences which are well known to affect the sleeper are noises, voices,*

*touches, lights, and changes of temperature*", further underlining the core, long-held belief that dreams naturally involve and even originate from both internal and external perceptual events – although, as can be seen below, the truthfulness of this kind of statement has been challenged over time.

Another dream researcher who focused more extensively on this topic was Weygandt (1893), a disciple of Wundt (as cited in Schredl, 2010) who also defended the opinion that all dreams emerge from sensory impressions, whether internal ("*tiredness*"; "*urge to urinate*", "*sexual arousal*"; "*breathing*"; "*blood circulation*"; "*hunger/thirst*"; "*vestibular system*") or external ("*visual/auditory stimuli*"; "*olfactory/gustatory stimuli*"; "*tactile/temperature stimuli*"). Furthermore, he hypothesised that the emotional tone of these sensory impressions determines the overall emotional tone of the dream and that the affective tone of dreams is actually linked to the waking mood. He provided a few examples to illustrate how these sensory impressions could act upon the dream content, namely reporting a dream about being in a train in the mountains with snow all around and the air getting colder and colder, which upon awakening was associated with the fact that a cold breeze was flowing into the bedroom. Although the claim that all oneiric experiences originate from perceptual events has been disproved, certain statements remain true. They are the base upon which we have built up our current knowledge about dream incorporation events, such as that "*impressions of external sensory perception being above the perceptual threshold are merged into the dream images and can give the dream a new turn*" (Weygandt, 1893).

Calkins (1893) examined over three hundred dream reports from two subjects who performed multiple awakenings per night and then immediately wrote down any dreams they had experienced. This work allowed for a general overview of what dreams are typically made of, providing valuable insight into the qualitative and quantitative aspects of oneiric experiences, and establishing the well-known continuity between waking and dreaming (Schredl & Hofmann, 2003) over a century ago. Concerning dream elements, Calkins stated

that they may be considered either as presentations — "*connected through sense excitation with the immediate present*" - or as representations — "*connected though the fact of association with the waking life of the past*" (Calkins, 1893; p. 319). The first category seems to relate to the matter at hand, including perception and physical sensation in the dream. Calkins found out that only about 10% (33/335) of the recorded dreams could be linked to a physical or perceptual event of the sleeping body, with auditory events being the most frequent (14/33; ~42%), followed by thermal (6/33; ~18%) and somatosensory (5/33; ~15%) events.

Two follow-up studies attempted to replicate these findings: the first attempted to experimentally modulate the dream experience by stimulating subjects with music, odours, and cool surfaces, but all stimulation events resulted in the subject's premature awakening, preventing any result from being achieved (Andrews, 1900). The second evaluated several aspects of a large set of dream reports from two subjects, much like in Calkins' study. Following the above definition, the occurrence of 'presentation' events –where there is "*consciousness within the dream of actual external stimuli*"– remained infrequent. However, one subject reported twenty dreams supposedly caused by external stimuli and 13 in which stimulation was taken up into an ongoing dream (out of 150 reports). About a third of these dreams were 'experimentally' induced; the subject had fragrant elements placed by her bedside or was sprinkled with water drops, or noise was presented during her sleep (Weed & Hallam, 1896).

Without any surprise, Freud, one of the pioneers in what we may call 'early dream science', is also to be mentioned for his contribution to theorising about the interaction between the dreaming self and the external environment. His take on the numerous clinical observations and oneiric self-reports he collected throughout his career is still almost systematically cited as one of the cornerstones of our knowledge about dreaming. Freud hypothesised that dreams have a protective function and serve as 'guardians of sleep' by disguising the meaningfulness of external stimuli, which could otherwise provoke arousal and disturb the normal course of the sleeping episode (Freud,

1997). Therefore, dreams would be used by the sleeping mind to 'deny' the stimulus. Nevertheless, he also admitted that external stimuli could be incorporated into the dream if they are coherent with the sleeper's ongoing subjective experience and current preoccupations (Freud, 1997), the latter having been proven to be a major determinant of dream content (Cartwright et al., 2006; Domhoff, 2010; Eichenlaub et al., 2018; van Rijn et al., 2015).

To provide evidence to these statements, Freud mentioned several pre-existing examples of both spontaneous and provoked sensory events that influenced the realm of dreams (Freud, 1997): over a century before, Meier reported a dream in which he felt he was being stretched out by some men who then planted a stake into the ground in-between his two toes, which upon awakening was linked to the fact that a straw was stuck between his toes (Meier, 1758); instead, Hildebrant's dreams involved the ringing of an alarm clock that was incorporated sometimes as the bells of a church, sometimes as the clinking of breaking china plates (Hildebrandt, 1881). However, the most famous example is Maury's 'guillotine dream': set in Paris during the Reign of Terror, Maury witnesses the trial and decapitation of fellow citizens only to end up getting murdered by guillotine himself – the decapitation being the dream interpretation of the fact that the top of his bed had fallen on his neck during his sleep (Maury, 1861). The latter has often been cited as a demonstration that dreams may emerge at the time of stimulation and that the dreamed timeline does not correspond to the equivalent sleep time lapse. It is to be noted, however, that the episode was not recorded until more than ten years after it happened (Ellis, 1922), and numerous reconstructions and false memories may have tainted the report (Clavière, 1897). Clavière tried to evaluate the time-lapse assumption on his own by comparing the timing of incorporation into the dream of an alarm clock that was set to ring twice: the first alarm was incorporated into the dream in the form of a ringing telephone, and the second one woke up the author. Having access to the exact interval between these two alarms, he could

successfully closely match the 'real' time-lapse and the approximated dream time-lapse, invalidating Maury's claim (Clavière, 1897).

Cubberley (1923) also counts among the first researchers who tried to explain how physical sensations could influence dreams: he explored the effects of continuous somatosensory sensation on various regions of the body by applying what he called 'tensors' (elements which induce tightness or contraction; e.g., a small piece of gummed paper) or 'detensors' (elements which induce relaxation or loosening, such as cream or oily matter). Among the hundreds of post-stimulation dream reports he collected, he declared that when proper dream recall was possible, the effect of the light tensors systematically appeared in the dreams and even represented the central theme of the dream plot. Examples from the transcribed oneiric extracts include dreaming about clumsy dancers when applying tensors to the soles of the feet, or dreaming of being examined by a doctor with a stethoscope when the tensor was located on the chest area. 'Detensor' incorporation into the dream scenery appeared less clear-cut, with examples including dreaming of sliding on the stomach with the feet raised in the air when the stimulus was applied to the sole of the feet or not finding any free seat at a theatre when applied to the buttocks.

Interestingly, the author stated that "*tensor experiments upon almost all parts of the trunk and head, while in other respects strictly in line with those on the limbs, are apt to be attended by affects*" (Cubberley, 1923; p. 249). In other words, a stronger emotional component was associated with external stimuli targeting core and vital body parts. This observation suggests that the processing of environmental stimuli during sleep may be partially related to their potentially harmful or disturbing effect on the sleeper. Another interesting observation made by Cubberley is an apparent magnification effect, such that light to moderate external stimuli appeared to be represented in a much more intense way once integrated into the dream. The author concluded by stating that "*the development of the dream is governed by the configuration of tensions in the dreamer's body*," in line with previous accounts on the hypothetical sources of dream elements. Of course, we must take great

caution when interpreting this data, as auto-suggestion is a major hindrance to any experimental design where the experimenter is his own subject.

Around a decade later, Max (1935) made some interesting observations while researching motor activity during sleep in deaf-mute individuals. Based on myographic activity recorded from the upper limbs, he attempted to establish varying consciousness and sleep depth states. He awakened the subjects after identifying spontaneous variations in muscle activity or after applying external stimuli, such as light flashes, tactile vibrations, or objects placed on the body. The author noticed that awakenings were often accompanied by a dream report when preceded by sustained muscular activity (without overt body movement), whether spontaneous or in response to stimulation. In fact, out of 33 cases of spontaneously increased arm or finger muscle activity, 30 resulted in a dream report upon awakening. As for awakenings following stimulation, those with a dream report also showed higher muscular activity than those without a dream recall. Interestingly, this increased activity seems specific to deaf-mutes compared to control subjects and to upper-limb activity compared to lower-limb activity. Following the author's rationale, this may be explained by the fact that for deaf individuals, the upper limbs are one of the main seats of linguistic abilities and, therefore, one of the key sites for conscious expression, which would arguably be more operative while dreaming than while dreamlessly sleeping.

Canziani (1950) suggested that external stimulation events could adopt different values for the sleeping consciousness, depending on how the interaction between the stimulus features and the physiological state of the sleeper unfolds. He provided an original classification of dream states, which could be interpreted as what we refer to as SDDCs: (a) "*dissociated atonite states*", in which the perceptual features of the stimulus are perceived but do not seem to have any effect on the intellectual-emotional state of the dreamer, so the sleeper perceives the sensory information but is not able to process its meaning; (b) "*seemingly unjustified emotional states*", in which the subject

wakes up without any awareness of the stimulus (or of any related dream) while appearing to be in an emotional state of confusion that may have been initiated by the stimulus through subliminal associative processes; (c) "*oneiric confusion states with illusory transformation of the scenery and adjustment of the stimulus to the scenery*", that is, an inclusion of the perceived stimulus into the dream in a form which is coherent to the plot; and (d) "*states of immediate or gradual recognition of the stimulus*", in which the stimulus is perceived and accurately recognised, provoking the cessation of the dream and sleep episode.

Furthermore, Canziani defended the idea that dreams that incorporate external stimuli are initiated at the time of stimulation, with the ensuing dream scenario elaborated through three successive phases. The first would represent, as the author calls it, a 'generic premise': an introductory phase of the dream plot that does not seem to relate to the stimulus particularly; here, the stimulus excites the sensory system and is unconsciously processed while disturbing the equilibrium of the oneiric consciousness. This is followed by the 'specific premise' phase, where the scenery is adapted and transformed into some specific situation that may allow the inclusion of the stimulus into the dream plot; at that point, the stimulus is closely reaching the dream consciousness threshold, with the consequent activation of associative networks that allow for the dream setting to adapt to the stimulus. The final phase would then consist of the dream scene's conclusion, in which the stimulus reaches the dream consciousness threshold and is more or less transformed to be included in the plot; this third phase may or may not be followed by an arousal. He illustrated this with a few examples, namely using Maury's 'guillotine dream': the first phase would correspond to the French Revolution scenery, the second to the conviction and condemnation to guillotine, and the last would correspond to the decapitation.

During the first half of the past century, the democratisation of EEG as a tool for measuring scalp electrical activity in humans, paired with the discovery of REM sleep in the 1950s by Aserinsky & Kleitman, marked the transition towards a more neurophysiological approach to

sleep and dream science (Aserinsky & Kleitman, 1953; Berger, 1929). Sleep studies started very early to include sensory stimulation protocols to study their effects on conscious experiences and time perception during dreams (e.g., Baldridge, 1966; Dement & Wolpert, 1958; Loomis et al., 1937; Max, 1935). Since then, methodological approaches, including clearly defined experimental and control conditions, have allowed us to progressively build up evidence about the phenomenological aspects and physiological correlates of SDDC, which we tried to summarise in our systematic review (see Chapter 2).

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**Supplementary Text I.2. Methodological assessment checklist**

Methodological assessment checklist adapted from Downs & Black (1998). Modified items are marked with an asterisk (*). Score choices for each item are indicated within brackets. Total scores may range from 0 to 25. Definitions and/or examples are provided in italics.

- **Reporting**

1. Is the hypothesis/aim/objective of the study clearly described? [0] – [1]

2. Are the main outcomes to be measured clearly described in the Introduction or Methods section? [0] – [1]
   *If the main outcomes are first mentioned in the Results section, the question should be answered "0".*

3. Are the characteristics of the subjects included in the study clearly described? [0] – [1]
   *Inclusion and/or exclusion criteria should be given.*

4. Are the interventions of interest clearly described? [0] – [1]
   *Experimental manipulations should be clearly described.*

5. Is there an adequately defined baseline or control condition? * [0] - [1]
   *Baseline and/or control conditions (where relevant) that are to be compared to experimental interventions should be clearly described.*

6. Are the main findings of the study clearly described? [0] - [1]
   *Simple outcome data (e.g., denominators/numerators, group averages) should be reported for all major findings so that the reader can check the major analyses and conclusions. NB: This question does not cover statistical tests, which are considered below.*

7. Does the study provide estimates of the random variability in the data for the outcomes of interest? [0] - [1]

*In non-normally distributed data, the interquartile range of results should be reported. In normally distributed data, the standard error, standard deviation, or confidence intervals should be reported. It must be assumed that any used estimates were appropriate, and the question should be answered "1".*

8. In cases where experimental trials have been excluded from the analyses, have the exclusion criteria been provided? * [0] – [1]
   *In cases where no trials have been excluded post-hoc, this question should be answered "1". In cases where trials have been excluded without any proper justification (including number and reason for rejection), this question should be answered "0". Ex: "8 trials were excluded from main analyses because the EEG signal preceding the awakening included signs of arousal (alpha bursts or major body movements)" would be rated "1".*

9. In cases where subjects have been excluded from the analyses, have the exclusion criteria been provided? * [0] – [1]
   *In cases where no subjects have been excluded post hoc, this question should be answered "1". In data where subjects have been excluded without any proper justification (including number and reason for rejection), this question should be answered "0". Ex: "2 subjects were excluded because they were unable to maintain sleep", "1 subject was excluded from main analyses because he couldn't provide any dream report" would both be rated "1".*

10. Have actual probability values been reported (e.g., 0.035 rather than < 0.05) for the main outcomes except where the probability value is < 0.001? [0] – [1]

- **External validity**

All the following criteria attempt to address the representativeness of the findings of the study and whether they may be generalised to the population from which the study subjects were derived.

11. Is the sampling procedure described? * [0] - [1]
    *The study must identify the source population for subjects and describe how they were selected (e.g., random sampling, convenience sampling).*

12. Is the sampling procedure unbiased? * [0] - [1]
    *Whenever the previous item (11) has been answered "0", this item will be answered "0" too. If any potential confounding effects are inherent to the sampling procedure, the answer should be "0". If the study states that it is evaluating certain characteristics of the general population, but the sample is composed only of members of a specific population, the answer should be "0". Ex: "the sample included the authors of the study", "all subjects were 1st year medical students" would both be rated "0".*

13. Is the experimental setting representative of the natural context targeted by the study? * [0] - [1] - [2]
    *The question should be answered "2" for home-based studies, "1" for studies that include at least one habituation session in the laboratory, and "0" for studies that do not report or consider the ecological factor of the experimental setting.*

- **Internal validity / Bias**

14. Was an attempt made to blind study subjects to the intervention they have received? [0] - [1]
    *For studies where the patients would have no way of knowing which intervention they received and no way of predicting the type of manipulation for each trial, this should be answered "1". For studies that explicitly mentioned which methods they applied to minimise the risk that subjects were aware of the intervention, this should be*

*answered "1". When no blinding strategies are mentioned, this question should be answered "0". Ex: "The study compared randomly presented trials, either with or without stimulation, collected from the same night following a within-subject design" would be rated "1".*

15. Was an attempt made to blind those measuring the main outcomes of the intervention? [0] - [1]
    *The blinding procedure must be clearly described. When only independent judges were involved in rating the outcome measures, the answer should be "1". If the experimenters are involved in the analyses in any way, the anonymization and randomization of the data must be explicitly stated. If the subjects were included in the analyses to provide additional personally relevant insight, the answer should be "0".*

16. If any of the results of the study were based on "data dredging", was this made clear? [0] - [1]
    *Any analyses that had not been planned at the outset of the study should be clearly indicated. If no retrospective, unplanned subgroup analyses were reported, then answer "1".*

17. Is the experimental duration (e.g., number of experimental sessions, number of trials, etc.) comparable for all subjects? * [0] - [1]
    *For studies where the total duration of the study is closely similar for all subjects, the answer should be "1". For studies where there are differences in duration, but these are reported and accounted for using appropriate models, the answer should be "1".*

18. Were the statistical tests used to assess the main outcomes appropriate? [0] - [1]
    *The statistical techniques used must be appropriate to the data. For example, non-parametric methods should be used whenever assumptions allowing the applicability of parametric tests are not met. Where little statistical analysis has been undertaken but there is no evidence of bias, the question should be answered "1". If the distribution of the data (normal or not) is not described, it must be*

*assumed that the estimates used were appropriate, and the question should be answered "1". When no statistical testing has been done, the answer should be "0".*

19. Were the main outcome measures accurately defined, valid, and reliable? * [0] - [1] – [2]
*For studies where the outcome measures are clearly described and objective scoring criteria that ensure potential replicability are provided, the question should be answered "2". For studies where information about outcome measures is provided but details remain insufficient to ensure exact replication, the question should be answered "1". Studies in which the scoring criteria for the outcome measures are not provided should be scored "0". Ex: "an automatic scoring algorithm was used" or "the scoring grid may be found in the supplementary material" would both be scored "2"; "stimulus incorporation was rated as direct when an unambiguous representation of the stimulus was present in the report and as indirect when elements semantically associated with the stimulus were present in the report" would be scored "1"; "stimulus incorporation was rated by 2 independent judges" would be scored "0".*

- **<u>Internal validity / Confounding (selection bias)</u>**

20. Were appropriate randomization procedures applied to the experimental conditions/groups? * [0] - [1]
*Unless the method of randomization would not ensure random allocation, studies that state that subjects were randomised to intervention groups or that the trial order was randomised and properly counterbalanced should be answered "1". For example, an alternate allocation would score "0" because it is predictable.*

21. Was there an adequate adjustment for relevant confounding variables in the analyses from which the main findings were drawn? * [0] - [1]
*This question should be answered "0" for trials if the distribution of known confounders in the different treatment groups was not*

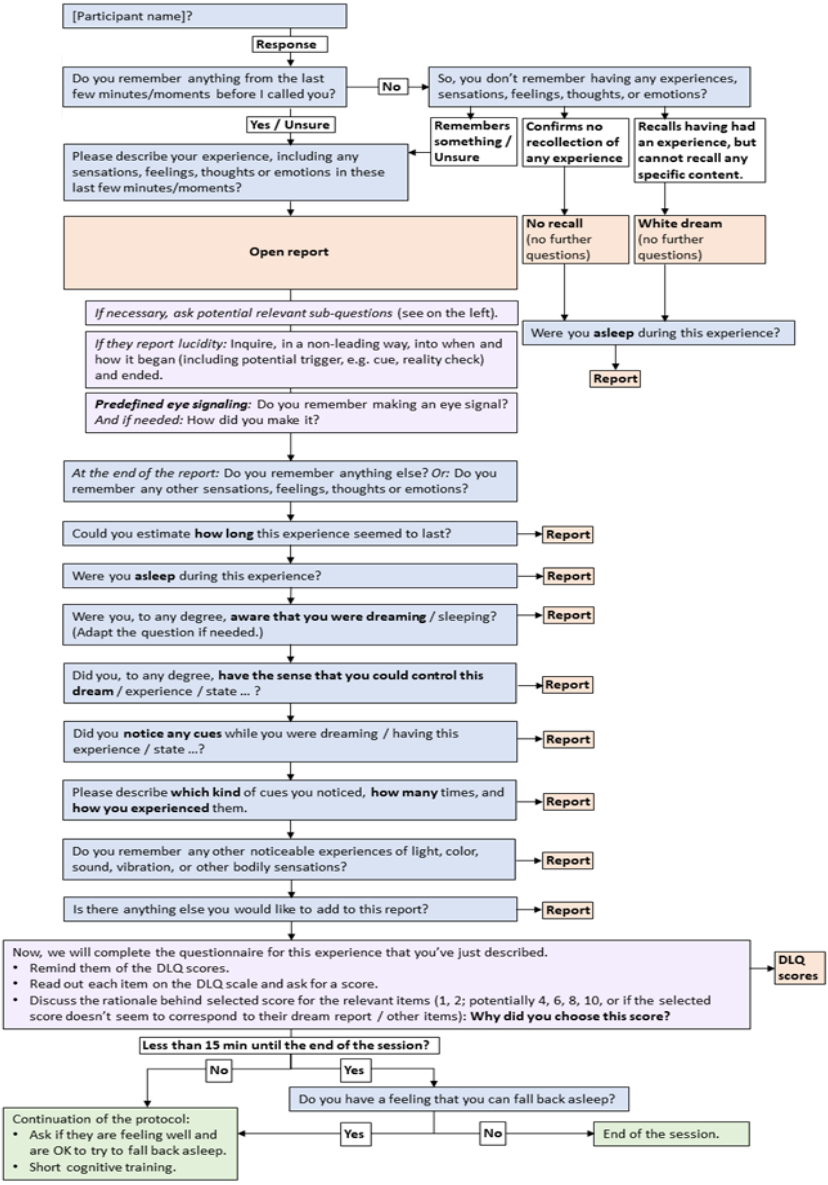
*described or the distribution of known confounders differed between the treatment groups but was not considered in the analyses. In the case of group-level design, at least age and gender should have been evaluated.*

- **<u>Power</u>**

22. Has any power calculation been performed and described? * [0] - [1]
23. Have appropriately chosen effect sizes been reported? * [0] - [1]
    *Ex: r-scores, Cohen's d*

# Appendix II.

## Supplementary Figure II.1. Dialogic flow of the semi-structured dream interview.



**Supplementary Table II.1. Item-by-item scores for the adapted methodological assessment checklist.**

| | | Item | Score | (max score) |
|---|---|---|---|---|
| R | 1 | Is the hypothesis/aim/objective of the study clearly described? | 1 | 1 |
| R | **2** | Are the main outcomes to be measured clearly described in the Introduction or Methods section? | 1 | 1 |
| R | **3** | Are the characteristics of the subjects included in the study clearly described? | 1 | 1 |
| R | **4** | Are the interventions of interest clearly described? | 1 | 1 |
| R | **5** | Is there an adequately defined baseline or control condition? | 1 | 1 |
| R | **6** | Are the main findings of the study clearly described? | 1 | 1 |
| R | **7** | Does the study provide estimates of the random variability in the data for the outcomes of interest? | 1 | 1 |
| R | **8** | In cases where experimental trials have been excluded from the analyses, have the exclusion criteria been provided? | 1 | 1 |

| | | | | |
|---|---|---|---|---|
| R | **9** | In cases where subjects have been excluded from the analyses, have the exclusion criteria been provided? | 1 | 1 |
| R | **10** | Have actual probability values been reported (e.g. 0.035 rather than <0.05) for the main outcomes except where the probability value is < 0.001? | 1 | 1 |
| EV | **11** | Is the sampling procedure described? | 1 | 1 |
| EV | **12** | Is the sampling procedure unbiased? | 1 | 1 |
| EV | **13** | Is the experimental setting representative of the natural context targeted by the study? | 0 | 2 |
| IV/B | **14** | Was an attempt made to blind study subjects to the intervention they have received? | 1 | 1 |
| IV/B | **15** | Was an attempt made to blind those measuring the main outcomes of the intervention? | 0 | 1 |
| IV/B | **16** | If any of the results of the study were based on “data dredging”, was this made clear? | 1 | 1 |
| IV/B | **17** | Is the experimental duration (e.g. number of experimental sessions, number of trials, etc.) comparable for all subjects? | 1 | 1 |

| | | | | |
|---|---|---|---|---|
| IV/B | **18** | Were the statistical tests used to assess the main outcomes appropriate? | 1 | 1 |
| IV/B | **19** | Were the main outcome measures accurately defined, valid, and reliable? | 2 | 2 |
| IV/C | **20** | Were appropriate randomization procedures applied to the experimental conditions/groups? | 1 | 1 |
| IV/C | **21** | Was there adequate adjustment for potential/known confounding effects in the analyses from which the main findings were drawn? | 1 | 1 |
| P | **22** | Has any power calculation been performed and described? | 0 | 1 |
| P | **23** | Have appropriately chosen effect sizes been reported? | 0 | 1 |
| **TOTAL SCORE** | | | **20** | 25 |

R: Reporting; EV: External Validity; IV-B: Internal Validity (Bias); IV-C: Internal Validity (Confounding); P: Power.

**Supplementary Table II.2. Evaluation of sleep metrics for valid participants.**

| | Experimental Session | |
|---|---|---|
| **Metrics** | **REM Cueing** | **REM Sham** |
| **TIB (min)** | 196.3 ± 13.83 | 190.68 ± 15.12 |
| **SPT (min)** | 164.03 ± 16.13 ** | 151.65 ± 16.2 ** |
| **WASO (min)** | 45.68 ± 19.33 | 41.43 ± 15.58 |
| **TST (min)** | 117.93 ± 26.82 | 109.85 ± 22.49 |
| **N1 (min)** | 37.2 ± 25.04 | 27.13 ± 16.32 |
| **N2 (min)** | 55.2 ± 19.59 | 60.78 ± 19.31 |
| **SWS (min)** † | 9.23 ± 11.31 | 6 ± 10.44 |
| **REM (min)** | 16.3 ± 10.97 | 15.95 ± 10.87 |
| **NREM (min)** | 101.63 ± 28.15 | 93.9 ± 19.42 |
| **SOL (min)** | 24.55 ± 10.89 | 30.75 ± 17.03 |
| **Latency N1 (min)** | 24.55 ± 10.89 | 32.2 ± 19.34 |
| **Latency N2 (min)** | 42.93 ± 24.85 | 41.43 ± 14.35 |

| | | |
|---|---|---|
| **Latency SWS (min)** † | 119.7 ± 46.08 | 124.72 ± 49.21 |
| **Latency REM (min)** | 91.6 ± 38.63 | 84.08 ± 41.43 |
| **N1 (%)** | 31.95 ± 20.41 | 25.86 ± 17.29 |
| **N2 (%)** | 46.49 ± 11.78 * | 54.95 ± 14.51 * |
| **SWS (%)** † | 7.32 ± 9.33 | 5.25 ± 8.82 |
| **REM (%)** | 14.25 ± 10.08 | 13.94 ± 8.57 |
| **NREM (%)** | 85.75 ± 10.08 | 86.06 ± 8.57 |
| **SE (%)** | 59.71 ± 12.11 | 57.76 ± 11.6 |
| **SME (%)** | 71.37 ± 13.25 | 72.12 ± 11.67 |

Values are represented in the form of mean ± standard deviation. SPT: Sleep Period Time; TST: Total Sleep Time; SE: Sleep Efficiency; SME: Sleep Maintenance Efficiency; SOL: Sleep Onset Latency; WASO: Wake After Sleep Onset.

**: P < 0.05; **: P < 0.01; † Only 9 sessions in the REM sham and 10 in REM cueing condition included SWS. Therefore, measures related to SWS were excluded from statistical analysis.*

**Supplementary Text II.1. SSILD-based cognitive-sensory training protocol.**

The cognitive training was delivered through a ~30-minute vocal recording, organized into distinct blocks. Each centre used different languages for the recording (NL: English; IT: Italian; CA: French and English) while keeping the content, length, and structure identical. The English version is presented here (see also Supplementary Figure II.1).

The audio track starts with a general definition of lucid dreaming, provides a summary of the cognitive training protocol, and then describes the different fast (2-3 seconds of focus on each of the senses in cyclic order, i.e., vision, hearing, and bodily-sensation exercises) and slow (20 seconds of focus on each of the senses in cyclic order, i.e., vision, hearing, and bodily-sensation exercises) cycles of SSILD training in detail.

The first training block instructs participants to perform 4 uncued fast cycles, followed by 4 uncued slower cycles (Block 1). Afterward, the audio track describes the association of the stimuli with the SSILD cycles: light cues with the vision exercises, audio cues with the hearing exercises, and vibration cues with bodily-sensation exercises (Block 2). Each SSILD exercise (vision, hearing, and bodily sensations, respectively) lasts one minute and concludes with the administration of the corresponding sensory cue by the experimenter to remind the participant to keep a lucid mindset. The cues also mark the transition from one exercise to the next, with a light cue indicating the end of the vision exercise and the start of the hearing exercise, an audio cue signalling the completion of the hearing exercise and the initiation of the bodily-sensation exercise, and a tactile cue marking the conclusion of the cycle and the start of a new one. During this block, each sensory cue is accompanied by a verbal prompt describing the targeted lucid mindset, as in Carr et al. (2020).

Finally, the last block of the cognitive training consists of a repetition of the previous cued SSILD section, with the sole exception that no verbal prompts are played after each cue (Block 3). Consequently, participants are expected to transition autonomously from one exercise to another whenever they perceive a cue. Participants are also reminded to perform the predefined LRLR eye movement signalling in cases of lucidity or stimulus perception after falling asleep.

The transcription of the audio track is provided below:

*"[Introduction]:*

*A lucid dream is a dream in which you are aware of the fact that you are dreaming while you are still asleep. With this realization, you can sometimes influence or control what happens in a dream. In this experiment, you'll get instructions on how to practice becoming lucid while awake.*

*For lucid dreams to occur, you need to train your mind and body into a subtle state that is optimised for lucid dreaming. This involves focusing on your vision, hearing, and bodily sensations in cycles. From this point, we guide you through the training process and describe the practicing cycles. The cycles always start with a vision exercise, then continue towards the hearing exercise, and finally end with the bodily-sensation practices. We describe each of the vision, hearing, and bodily-sensation exercises now:*

*[Vision exercise]*

*For the vision exercise, you should keep your eyes closed and focus all your attention on the darkness behind your closed eyelids. Keep your eyes completely still and totally relaxed. You might see coloured dots, complex patterns, images, or maybe nothing at all. It doesn't matter what you can or cannot see – just pay attention in a passive and relaxed manner and don't try to see anything.*

*[Hearing exercise]:*

*For the hearing exercise, we want you to shift all of your attention to your ears. You might be able to hear the faint sounds of traffic or the wind from*

*outside. You might also be able to hear sounds from within you, such as your own heartbeat or a faint ringing in your ears. It doesn't matter what, if anything, you can hear – just focus all of your attention on your hearing.*

*[Bodily sensations exercise]:*

*For the bodily sensations exercise, you should shift all of your attention to sensations from your body. Feel the weight of your blanket, your heartbeat, the temperature of the air, etc. You might also notice some unusual sensations such as tingling, heaviness, lightness, spinning sensations, and so on. If this happens, simply relax, observe them passively and try not to get excited.*

*Before starting with the first exercise, I would like to mention that you may have intrusive thoughts during this process. For instance, you may think of what you need to buy or do after this experiment. It doesn't matter if the intrusive thoughts come to your mind, but what matters is that you can intentionally let them go and focus on your body and mind."*

Then, the SSILD training (Block 1) started, comprising 1 minute of fast cycles practice followed by 4 minutes of short cycles practice:

*"Now you should start with the first step of the training. Practice four fast cycles during which you spend only 2-3 seconds focusing each on the vision, hearing, and bodily sensations. You don't have to count the seconds, but you should complete at least 4 cycles during this time. You can start now.*

*[After 1 min]:*

*You can stop now. At this point, you should perform four to six slower cycles that approximately take 20 seconds focusing each on the vision, hearing, and bodily sensation steps. Again, you don't have to count the seconds, but you should complete at least 4 cycles during this time. You can start now.*

*[Silence continues for 4 minutes]"*

During the following 12 minutes, the combined SSILD and sensory cueing with additional verbal prompts were presented (Block 2):

*"Now, I want to train your mind to recognize the flashing lights, beeping sounds, and vibration cues as lucidity cues so that when one is played during your sleep, you will become lucid in a dream. While you rest here, we are going to play the cues at intervals. Whenever you hear, see, or feel one of the cues, you should remain in the same position with your eyes closed, but you will become lucid by attending to where your mind has been, attending to your body, and attending to your surroundings. The same as before, each cycle starts with vision training. You should continue the vision practice until you see a light cue. Then a prompt will be played to help you focus. Once the prompt is ended you should move forward to the hearing exercise. You should continue the hearing practice until you hear an audio cue. Again, a prompt will be played to help you focus. Once the prompt is ended you should move forward to the bodily-sensations exercise. The vibration cue will indicate when the exercise is ended and then you should start a new cycle. Please note that, as a response to the cues, you do not need to do the Left-right-left-right eye signals while training, only do the eye signals when you become lucid in a dream. You can start with vision practice, now …"*

The prompted cueing included 6 cues (Light-Audio-Tactile-Light-Audio-Tactile) with 1-minute inter-stimulus intervals. The prompt after each cue was the following:

*"[Cue]*

*As you notice the cue, you become lucid. Bring your attention to your thoughts ... [pause] ..., notice where your mind has wandered ...[pause]... Now observe your body ... [pause] ..., your sensations ... [pause] ..., and your feelings... [pause] ... Observe your breathing...[pause]... remain critically aware, lucid, and notice how aspects of this experience are in any way different from your normal waking experience. [pause]*

*[The next exercise will be started by mentioning the type of the exercise, i.e., vision, hearing, or bodily sensation.]"*

After the last cue, the final block started, consisting in 8 minutes of cueing without vocal prompts (Block 3), during which the participant was expected to transition independently to the next exercise following each cue. The participant was also reminded of doing the predefined LRLR eye movement in case of lucidity during sleep. The instructions were the following:

*"The cues will continue to be played in intervals over the next 6 minutes. The prompts, however, will not be played anymore. You should continue to practice becoming lucid by focusing on your vision, hearing, and bodily sensations, the same as before and again in cycles. We keep sending you the cues when you need to move from one exercise to another. Pay attention to your mind, your body, and your surroundings. Notice how aspects of your experience are in any way different from your normal waking experience. At the end of this block, when the cues are stopped, you can fall asleep normally and you don't have to do the exercises anymore. Please keep in mind that when the cognitive training is ended, you should do the left-right-left-right eye signalling in three cases: 1/ when you become lucid in a dream, 2/ as a response to the cues while being lucid, and 3/ approximately every 30 seconds while you are lucid, even though you do not perceive any cue.*

*Now you can start with the vision exercise…"*

*[6 cues (2 from each modality: Light-Audio-Tactile-Light-Audio-Tactile) should be played in 1-min intervals, then the recording ends and the 2.5h nap window begins]"*

# Appendix III.

**Supplementary Table III.1. Stimulus-dependent aperiodic slope variation (ΔS) comparison between modalities for all evaluated frequency ranges and channels.**

| Frequency range | EEG Channel | ΔS A | ΔS T | ΔS V | Test | Statistics | P-value | |
|---|---|---|---|---|---|---|---|---|
| Low | Fz | 0.27 ± 0.42 | 0.43 ± 0.19 | 0.43 ± 0.23 | A-T | t(24) = -2.15 | 4.21E-02 | |
| | | | | | A-V | t(24) = -1.64 | 1.13E-01 | |
| | | | | | T-V | t(24) = -0.02 | 9.83E-01 | |
| Low | Cz | -0.03 ± 0.34 | 0.25 ± 0.19 | 0.30 ± 0.20 | A-T | t(24) = -5.54 | 1.08E-05 | * |
| | | | | | A-V | t(24) = -4.69 | 9.17E-05 | * |
| | | | | | T-V | t(24) = -1.13 | 2.71E-01 | |
| Low | Pz | 0.09 ± 0.41 | 0.27 ± 0.19 | 0.25 ± 0.19 | A-T | t(24) = -2.68 | 1.31E-02 | |
| | | | | | A-V | z = -1.68 | 9.26E-02 | |
| | | | | | T-V | t(24) = 0.38 | 7.10E-01 | |
| Low | Oz | 0.20 ± 0.40 | 0.42 ± 0.20 | 0.39 ± 0.21 | A-T | t(24) = -3.21 | 3.76E-03 | * |
| | | | | | A-V | z = -1.79 | 7.36E-02 | |
| | | | | | T-V | t(24) = 0.50 | 6.19E-01 | |
| High | Fz | 0.75 ± 0.36 | 0.44 ± 0.27 | 0.48 ± 0.35 | A-T | t(22) = 4.20 | 3.71E-04 | * |
| | | | | | A-V | t(22) = 3.27 | 3.47E-03 | * |
| | | | | | T-V | z = -0.31 | 7.57E-01 | |
| High | Cz | | | | A-T | t(22) = 2.66 | 1.44E-02 | |
| | | | | | A-V | t(23) = 2.39 | 2.56E-02 | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | 0.69 ± 0.28 | 0.47 ± 0.31 | 0.43 ± 0.44 | T-V | t(23) = 0.54 | 5.97E-01 |
| High | Pz | 0.74 ± 0.32 | 0.45 ± 0.28 | 0.37 ± 0.41 | A-T | t(22) = 4.57 | 1.50E-04 * |
| | | | | | A-V | t(22) = 3.99 | 6.23E-04 * |
| | | | | | T-V | z = 1.04 | 3.00E-01 |
| High | Oz | 0.47 ± 0.33 | 0.16 ± 0.30 | 0.26 ± 0.33 | A-T | z = 3.62 | 2.95E-04 * |
| | | | | | A-V | t(21) = 2.74 | 1.23E-02 |
| | | | | | T-V | t(24) = -1.28 | 2.14E-01 |
| Broadband | Fz | 0.37 ± 0.42 | 0.45 ± 0.19 | 0.46 ± 0.22 | A-T | z = -0.87 | 3.82E-01 |
| | | | | | A-V | t(24) = -0.92 | 3.68E-01 |
| | | | | | T-V | t(24) = -0.15 | 8.86E-01 |
| Broadband | Cz | 0.05 ± 0.35 | 0.28 ± 0.16 | 0.35 ± 0.18 | A-T | t(24) = -4.16 | 3.50E-04 * |
| | | | | | A-V | t(24) = -3.78 | 9.18E-04 * |
| | | | | | T-V | t(24) = -1.57 | 1.30E-01 |
| Broadband | Pz | 0.18 ± 0.40 | 0.29 ± 0.17 | 0.29 ± 0.18 | A-T | t(24) = -1.69 | 1.04E-01 |
| | | | | | A-V | z = -0.87 | 3.82E-01 |
| | | | | | T-V | z = 0.47 | 6.38E-01 |
| Broadband | Oz | 0.24 ± 0.38 | 0.37 ± 0.20 | 0.37 ± 0.19 | A-T | t(24) = -2.09 | 4.74E-02 |
| | | | | | A-V | z = -1.06 | 2.88E-01 |
| | | | | | T-V | t(24) = 0.02 | 9.85E-01 |

Low frequency: 0.5-30 Hz; High frequency: 30-45 Hz; Broadband: 0.5-45 Hz. A: Auditory; T: Tactile; V: Visual. ΔS values correspond to m ± std.
* statistical significance at Bonferroni-corrected threshold ($p < 0.042$)

# Research Data Management

This thesis is based on the results of human experimental studies, which were conducted in accordance with the principles of the Declaration of Helsinki. The joint local ethical committee of Scuola Superiore Sant'Anna and Scuola Normale Superiore has given approval to conduct the studies related to Chapters 3 (n. 31/2022) and 4 (n. 12/2021).

**Ethics and Privacy**

Informed consent was obtained from participants for data collection, processing, and sharing of pseudonymized data after the research. Participants' anonymity and privacy were ensured using unique individual subject codes, which corresponded with codes on paper and electronic forms. The correspondence between these codes and participant identities was stored separately from any participant data, with access restricted to the researchers involved.

**Data Collection and Storage**

Paper materials are securely stored in the repositories of the Sleep, Plasticity, and Conscious Experience laboratory. The electronic data reported in Chapter 3 were collected using the CastorEDC data management software and are stored in a project archive folder within the servers of the Donders Centre for Cognitive Neuroimaging (code: 3013102.01). Data management and monitoring for this study were also performed within CastorEDC. The datasets analysed during these studies are available from the corresponding author upon reasonable request. All studies are, or will be, published as open access. Datasets suitable for reuse will be made available online upon publication of the main outcomes. The study in Chapter 3 is part of a multi-centric, pre-registered research project, and the research protocol was made available online prior to data collection at any participating centres (https://osf.io/zfs57/).

# IMT School for Advanced Studies Lucca

The IMT School for Advanced Studies Lucca is dedicated to cultivating the next generation of leading researchers and scholars. Central to this mission is the IMT PhD program, which is recognized nationally and internationally for its rigorous academic training and interdisciplinary approach. The PhD programs at IMT cover a broad spectrum of fields, including economics, computer science, engineering, cognitive and social neuroscience, cultural heritage, and political history. This diversity reflects the school's commitment to addressing complex global challenges through a combination of theoretical and applied research.

The PhD curriculum at IMT is designed to be closely integrated with the research activities of the school's research units. Students benefit from a rich academic environment, where they are encouraged to engage in collaborative projects that often span multiple disciplines. The IMT School's research centres are equipped with state-of-the-art facilities and resources, providing an ideal setting for cutting-edge research.

The IMT School closely monitors the career progression of its PhD graduates, with many securing prestigious postdoctoral positions and faculty roles at top academic institutions globally. Alumni have continued their academic careers at universities such as Harvard University, University of Oxford, MIT, and the University of Cambridge. Outside of academia, graduates have found success in various sectors including governmental agencies, international organizations, and private industry, particularly in fields such as data science, public policy, technology, and cultural management.

The comprehensive training provided at IMT ensures that graduates are well-prepared for high-level positions that contribute significantly to both the academic community and the broader knowledge economy.

For more detailed information about the IMT PhD program, including application procedures and upcoming thesis defences, please visit: http://www.imtlucca.it

# Donders Graduate School for Cognitive Neuroscience

For a successful research institute, it is vital to train the next generation of young scientists. To achieve this goal, the Donders Institute for Brain, Cognition and Behaviour established the Donders Graduate School for Cognitive Neuroscience (DGCN), which was officially recognized as a national graduate school in 2009. The Graduate School covers training at both Master's and PhD levels and provides an excellent educational context fully aligned with the research program of the Donders Institute.

The school successfully attracts highly talented national and international students in biology, physics, psycholinguistics, psychology, behavioural science, medicine, and related disciplines. Selective admission and assessment centres guarantee the enrolment of the best and most motivated students.

The DGCN tracks the careers of PhD graduates carefully. More than 50% of PhD alumni continue in academia with postdoc positions at top institutes worldwide, such as Stanford University, University of Oxford, University of Cambridge, UCL London, MPI Leipzig, Hanyang University in South Korea, NTNU Norway, University of Illinois, Northwestern University, Northeastern University in Boston, ETH Zürich, and the University of Vienna. Positions outside academia are spread among the following sectors: specialists in a medical environment (mainly in genetics, geriatrics, psychiatry, and neurology), specialists in a psychological environment (e.g., as specialists in neuropsychology, psychological diagnostics, or therapy), and positions in higher education as coordinators or lecturers. A smaller percentage enters business as research consultants, analysts, or heads of research and development. Fewer graduates stay in a research environment as lab coordinators, technical support, or policy advisors. Upcoming possibilities include positions in the IT sector and management

positions in the pharmaceutical industry. In general, the PhD graduates almost invariably continue with high-quality positions that play an important role in our knowledge economy.

For more information on the DGCN as well as past and upcoming defences, please visit: http://www.ru.nl/donders/graduate-school/phd/