Spontaneous thoughts and experiences across wakefulness and sleep

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Abstract

Consciousness research is commonly divided into two main areas: the study of states of consciousness and the study of contents of consciousness. States of consciousness refer to discrete modes of awareness elicited by normal states of the brain, such as those associated with wakefulness and sleep, and by abnormal factors, including brain lesions, pharmacological agents and other external interventions. Contents of consciousness refer what we are conscious *of*. In this chapter, we emphasize the dynamic nature of consciousness in terms of both its states and contents. First, we first observe that our life constantly alternates between different conscious and unconscious states, namely, sleep and wakefulness. Then, within each state, we note an inherent dynamism in content, with conscious experience ranging from content-full to content-less. By surveying the variety of conscious experiences across wakefulness and sleep, we highlight the similarities in reported contents across these states. We further discuss how the possibility of having conscious experiences without specific content challenges the idea that being conscious necessarily involves being conscious *of* something. Finally, by reviewing the literature on the neural correlates of consciousness, we propose a potential convergence in the study of conscious states and contents.

1. Consciousness is a dynamic phenomenon

1.1 Being conscious and being conscious *of*

Consciousness can be described both as a state of being (being conscious), but also in terms of the contents that are being experienced (being conscious *of* something). Studying consciousness in its intransitive sense (awake/asleep) means exploring the global "states" or "modes" that allow the formation of various experiences (e.g. dreaming). Studying consciousness in its transitive sense (i.e., being conscious *of*) means describing particular contents of consciousness, that is the phenomenal properties of specific experiences (Figure 1a). There have been numerous attempts to examine the relationship between conscious states and contents (see Figure 1b for example).

The state and content approaches are not orthogonal. Being conscious and being conscious *of something* are often presented as two sides of the same coin, in that, if you are conscious of something then you are by definition conscious and vice versa. However, recent investigations have uncovered so-called "contentless" states, which include certain type of meditative practices or low-arousal states that are described by individuals as having a "blank mind" (Andrillon et al., 2025). These states suggest a more complex relationship between states and contents of consciousness.

1.2 Conscious contents as a stream

Consciousness is a highly dynamic phenomenon. Throughout our days and nights, we cycle across many different types of states and contents (Figure 1c) as conscious states can be influenced by the levels of arousal. Large fluctuations in arousal can determine large changes in the overall conscious state, such as transitions between wakefulness and dreamless sleep (Tononi et al., 2024). At the same time, within a given conscious state, there can be nested fluctuations in the conscious contents that individuals experience.

For example, during wakefulness, individuals often fluctuate between contents oriented to a specific goal or task, and self-generated, task-unrelated contents such as those occurring during mind wandering (Smallwood & Schooler, 2015). Likewise, during sleep, individuals can alternate between dreaming and dreamless sleep, even within physiological states that are considered fairly homogenous such as Non Rapid Eye-Movement (NREM) sleep stage 2 (Siclari et al., 2013; Wong et al., 2023) (Figure 1c). The fluctuations in contents are, thus highly dynamic, a feature captured by William James' metaphor of "the stream of consciousness" (James, 1890).

Wakefulness is typically associated with rich conscious experiences, whereas sleep is more often associated with no or oneiric contents (e.g., (Siclari et al., 2013)). However, the wide palette of dreams, which can range from vivid features to minimal contents (Windt, 2015) showcases the variability of content within a given state. Besides, there is also some continuity between the contents belonging to different states. For example, the transition between wakefulness and sleep cannot be summarized to a specific tipping point (Lacaux et al., 2023) and individuals themselves frequently fail to notice that they have fallen asleep. This implies that individuals can move from one conscious state to another without necessarily having experienced a break in their stream of thoughts, further stressing the importance of examining states and contents of consciousness jointly.

1.3 Arousal and attention shape the dynamics of consciousness

Specific brain states are necessary for *any* content to be made conscious, providing background conditions that constrain conscious contents and their reportability. These background conditions include brain anatomy, homeostatic regulation, but also the general arousal level and attentional state of an individual (Koch et al., 2016). We here define arousal as the physiological processes determining an individual's level of alertness, wakefulness and responsiveness. Attention here refers to the neural mechanisms allowing an

individual to select (top-down attention) or leading to the selection (bottom-up attention) of specific information.

Neuronally, both arousal and attentional mechanisms can be identified as changes in cortical excitability, which refers to the strength of the response of cortical neurons to a given stimulation. In turn, the strength of neuronal response can be more or less favorable for conscious states or contents (Koch et al., 2016). Regarding conscious states, global changes in cortical excitability can determine the overall state of consciousness, accounting for the transition from wakefulness to sleep (Tononi & Massimini, 2008). Regarding the contents of consciousness, attentional orientation can modulate the encoding of specific sensory inputs (Harris & Thiele, 2011) and their incorporation into the stream of consciousness (Dehaene et al., 2006).

In the next section, we will see how neuro-physiological states shape the dynamics of conscious states and contents in wakefulness.

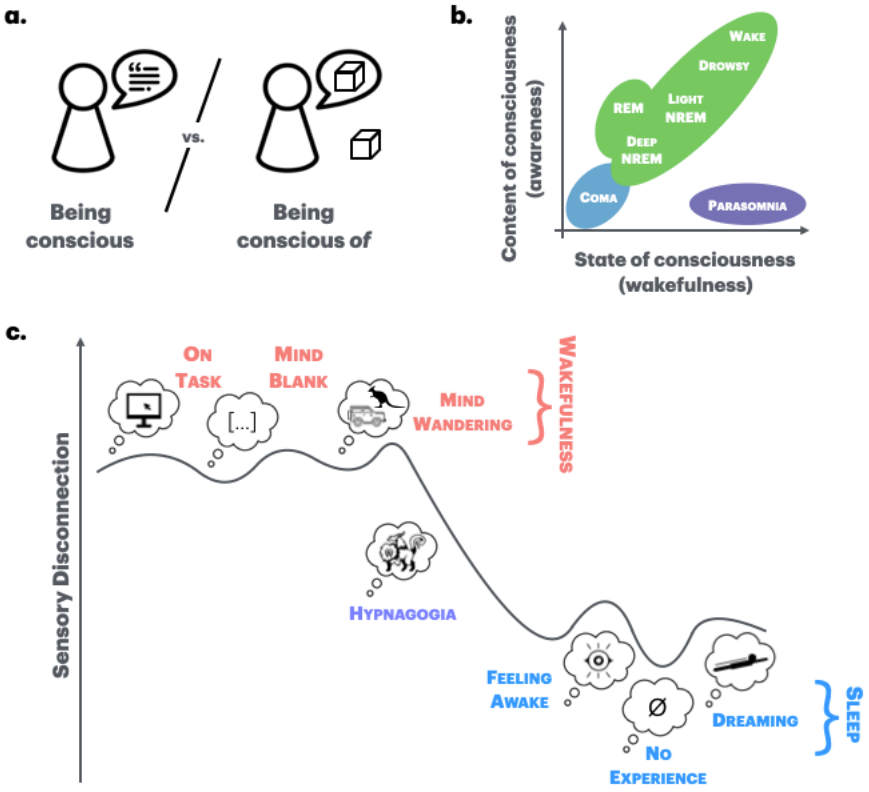

Figure 1. Consciousness as a dynamic phenomenon.

a: Consciousness can be investigated as a state (being conscious) or through its contents (being conscious of something). b: Standard 2D model of consciousness used in disorders of consciousness (DoC) that distinguished states and contents of consciousness (from (Laureys, 2005)). c: We rather propose that, within a given conscious state, there can be nested fluctuations in the conscious contents that an individual can experience. For example, during wakefulness, consciousness often fluctuates between contents oriented to a specific task, task-unrelated contents (such as those occurring during mind wandering) or mind blanks. Likewise, during sleep

individuals can alternate between dreaming and dreamless sleep, with the ability to later report on the dream content or not.

2. Spontaneous thoughts and experiences during wakefulness

2.1 Emergence of the concept of mind wandering

A defining feature of wakefulness is that our minds stray away from the here and now of the things we do. As a result, we spend a big part of our mental lives delving into spontaneous thoughts that do not necessarily reflect our current environment (Killingsworth & Gilbert, 2010; Seli et al., 2018a). These spontaneous thoughts and experiences are largely freewheeling, in that they are elicited by the absence of constraints. Two types of constraints have been proposed: deliberate constraints, where cognitive control regulates the stream of thought in a goal-directed fashion, and automatic constraints, which typically reflect salient environment cues or physiological demands (Christoff et al., 2016).

Among different types of spontaneous thoughts, mind-wandering has been extensively studied over the past two decades (Smallwood & Schooler, 2015). Mind wandering is operationalized as thoughts unrelated to the task at hand (task-unrelated thoughts) or being decoupled from the current environmental stimuli (stimulus-irrelevant thoughts) (Stawarczyk et al., 2011). Mind-wandering spans multiple cognitive, emotional and clinical domains, intertwining with processes like attention, mood, and memory, often playing a dual role in daily life by either disrupting focus or facilitating creative thinking (Smallwood & Schooler, 2015). However, there are ongoing debates about the nature of mind-wandering as to whether it refers to a unitary phenomenon or a family of phenomena with overlapping and non-overlapping features (Christoff et al., 2018; Seli et al., 2018b). Yet, all the different models of mind wandering tend to agree on its core dynamic features, its centrality for wakeful cognition and consciousness, and, at the mechanistic level, its association with activations of the default mode network (DMN).

2.2 The Default Mode Network and its implication in mind wandering and consciousness

This DMN refers to a set of brain regions comprising the posterior cingulate cortex and adjacent precuneus, the medial prefrontal cortex, the inferior parietal lobule, the angular gyrus, the temporal poles, the hippocampus, the parahippocampal gyrus and the retrosplenial cortex (Raichle et al., 2001) (Figure 2). The DMN is widely known, among others, thanks to its paradoxical discovery: using functional neuroimaging (PET) studies, which compared task activations to resting periods, revealed that the abovementioned regions showed systematic deactivations (Shulman et al., 1997). Using fMRI later on, these regions were found to be active by default during rest only, and hence they were named as default mode network[1]. Convergent evidence suggests that DMN might be directly implicated in self-referential or internally focused thought processes, such as prospective or autobiographical thinking, mental simulations and emotional appraisal (Andrews-Hanna et al., 2014). Overall, research on the default mode network (DMN) and mind-wandering has developed in parallel, with the DMN offering a consistent neural substrate, and mind-wandering serving as a stable cognitive phenomenon through which to interpret DMN fluctuations

[1] It is important to note that since these early observations the DMN has been shown to also recruit different sets of brain regions when engaging in task performance, therefore it is not merely a resting state network.

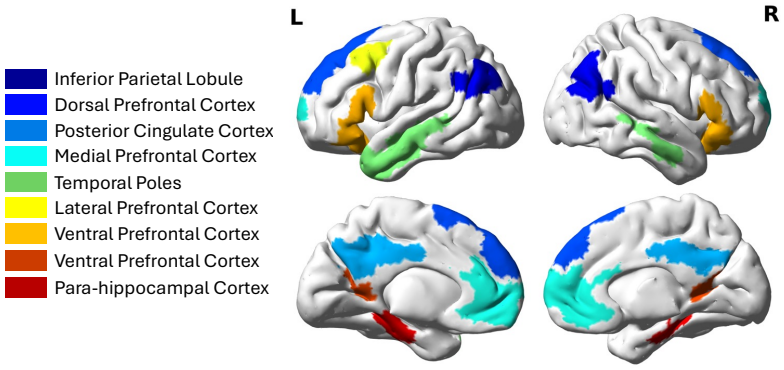

Figure 2. Topology of the DMN
Representations of the main brain regions of the Default Mode Network based on the Schaefer atlas (Schaefer et al., 2018).

An interesting way by which our brains work is an antagonistic mode of functioning. The shifts from external perception to internal thinking are paralleled by shift in the activation of cortical networks. Shifts from the external environment encompass the recruitment of frontoparietal regions, while inward attention is associated with activations in the DMN (Fox et al., 2005; Vanhaudenhuyse et al., 2011). On a broader scope, it appears that brain activity during wakefulness organizes in a push-pull manner, mapped by these distinct and antagonistic functional networks. Given that the presence of such anticorrelations decreases across states of lower arousal, such as sleep (Chow et al., 2013), sedation (Luppi et al., 2019), anesthesia (Boveroux et al., 2010), hypnosis (Demertzi et al., 2011) and disorders of consciousness (Di Perri et al., 2016), it was recently proposed that such anticorrelations might be a central organizational feature of wakeful experiences without which consciousness cannot be supported (Demertzi et al., 2022).

Importantly, mind wandering is also associated with the activation of a medio-temporal cluster of the DMN, spanning the hippocampus and the parahippocampal cortex (Fox et al., 2015). As the hippocampus can spontaneously replay sequences of neural activity that resemble previous experiences, a process known as memory replay (Pfeiffer, 2020), it has been proposed the hippocampus might serve as a source of context-relevant thoughts.

This “thought variability” provided by the hippocampus might be utilized by medial subdivisions of the DMN to construct a coherent stream of thought (Christoff et al., 2016). Hippocampal ripples, a specific pattern of brain activity associated with memory replays, have been proposed as a brain mechanisms triggering instances of mind wandering (Iwata et al., 2024; O’Callaghan et al., 2021). Interestingly, hippocampal ripples are also observed during sleep (Girardeau & Zugaro, 2011) and the DMN is also activated during dreaming, suggesting some continuity between mind wandering and dreaming (Domhoff & Fox, 2015; Fox et al., 2013).

2.3 Mind blanking and seemingly “contentless” states

It is important to note that our mind does not always move from thought to thought. Occasionally, we cannot report or have nothing to report about our immediate past experiences (Boulakis & Demertzi, 2025; Ward & Wegner, 2013), a phenomenon called mind blanking. This experience is accompanied by a metacognitive feeling that something went missing from our stream of thought (Efklides & Touroutoglou, 2010).

What does mind blanking actually reflect? Is it about the absence of available content, akin to a moment of unconsciousness during wakefulness, or does it concern a failure to introspect and evaluate mental content, akin to a failure of meta-awareness and memory (Andrillon et al., 2025)? As it currently stands, there is no consensus to define or capture the variant properties of mind-blanking episodes (Fell, 2022). Indeed, mind blanking has been described as inattention to anything (Andrillon et al., 2021), as the absence of reportable content (Boulakis et al., 2025; Mortaheb et al., 2022), or the voluntary act of thinking of nothing (Kawagoe et al., 2019). However, by examining how the brain, body, and behavior organize during mind blanking periods, we can come closer to acquiring insights into how the brain, body, and behavior organize during mind blanking periods.

During studies that probe participants to report their thoughts, mind blanking is typically reported 10-15% of the time (Andrillon et al., 2021; Mortaheb et al., 2022; Ward & Wegner, 2013). Periods of mind-blanking are associated with reduced vigilance (Andrillon et al., 2021) and reduced physiological arousal (Unsworth & Robison, 2018). At the behavioral level, mind blanking differs from other types of attentional lapses like mind wandering, because it has a unique impact on task performance (Andrillon et al., 2021).

Brain-wise, mind blanking was associated with widespread deactivations in parietal, occipital, and thalamic areas as well as in the anterior cingulate cortex. Contrasting mind-blanking reports with content-oriented mental states revealed deactivations in the left angular gyrus as well, potentially representing periods of reduced neuronal resource allocation to mental faculties associated with mental state reportability, namely attentional and semantic processes (Boulakis et al., 2023).

What could these deactivations represent? Previous investigations in the same dataset showed that mind blanking was associated with a brain pattern where all brain regions were functionally connected to one another (Mortaheb et al., 2022) (Figure 3), a pattern previously found during sleep (El-Baba et al., 2019), suggesting a global state of reduced arousal. At the same time, it was shown that the amplitude of the fMRI BOLD global signal[2] was higher during mind blanking reports compared to content-oriented reports, which had also been previously linked to reduced arousal levels (Wong et al., 2013). Complementary results from electroencephalography (EEG) corroborate the link between low arousal and mind blanking. Sleep-like slow waves, akin to those observed in sleep, have been observed prior to attentional lapses, including before reports of mind blanking (Andrillon et al., 2021).

Together, these results emphasize the relationship between global brain dynamics (defining arousal and conscious states) and the generation of conscious contents or lack thereof.

[2] The fMRI BOLD (Blood Oxygen Level Dependent) global signal is a measure representing the average BOLD signal across all brain voxels at a given time, reflecting widespread, synchronized fluctuations in neural and physiological activity. It captures global changes in blood oxygenation levels that may arise from neural processes as well as non-neuronal sources such as respiration, heart rate, and other systemic physiological factors.

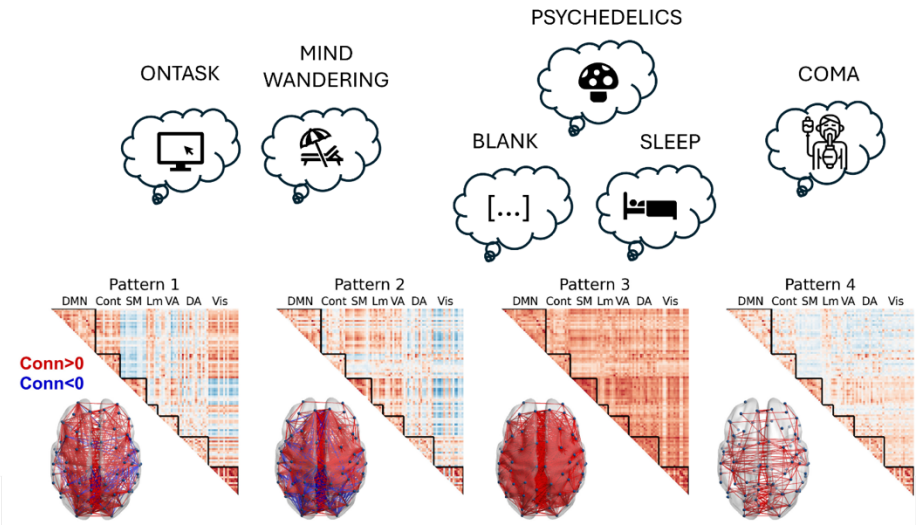

Figure 3. Brain connectivity patterns and subjective experience

Across wakefulness and sleep, the brain explores connectivity patterns of different integration (cortical communication) and segregation (cortical specialization). These patterns could help describe consciousness states and contents. Content-oriented experiences are typically associated with a balance between segregation and integration (Patterns 1 and 2), which is expressed through a pattern of positive and negative connectivity, and contrasts with the overall positive connectivity present in Pattern 3. However, states such as mind-blanking, sleep, and psychedelics are characterized by high inter-areal connectivity, and hence low of functional segregation (Pattern 3). Finally, patients with disorders of consciousness show more frequent exploration of a pattern characterized by reduced integration and segregation, which mostly reflects the underlying anatomy (Pattern 4). To our knowledge, data about dreaming have not yet been reported. Modified from (Mortaheb et al., 2022).

3. Consciousness during sleep

3.1 Sleep as a natural modulation of consciousness

Sleep is usually characterized by a period of immobility or rest, a typical posture, and a decreased responsiveness to external stimuli (Andrillon & Oudiette, 2023). Contrary to death or coma, sleep is easily reversed, and we can quickly regain our ability to react and respond to environmental demands. These behavioral signs reflect physiological changes orchestrated by the brain, to such an extent that sleep has been described as “of the brain, for the brain, by the brain” (Hobson, 2005).

Yet, sleep is not a monolith. In humans, there are two forms of sleep: Rapid Eye-Movement (REM) sleep (also called Paradoxical Sleep) and Non Rapid Eye-Movement (NREM) sleep (Carskadon & Dement, 2005). In terms of cortical activity, NREM sleep is characterized by an increase in neural synchronization, evidenced by the presence of large-amplitude slow waves (1-4Hz, delta range) across the entire cortex. This contrasts with the small-amplitude desynchronized activity typically observed in wakefulness but also in REM sleep.

Sleep does not only affect behavior and physiology. It also impacts subjective experience (Andrillon & Oudiette, 2023). Indeed, during REM sleep individuals can report conscious experiences following ~85%

of forced awakenings (Siclari et al., 2013; Wong et al., 2023). Yet, if REM sleep is associated with a form of consciousness (dreams), these conscious experiences differ from wakeful experiences: they are largely dissociated from the environment and are characterized by a reduced, if not absent, meta-awareness and sense of agency (Nir & Tononi, 2010; Windt, 2015). Even in NREM sleep, which has often been associated with a state of unconsciousness, ~35% of forced awakenings are associated with reports of conscious experiences (Siclari et al., 2013; Wong et al., 2023).

Sleep can also be associated with a feeling of being awake, while individuals show clear physiological signs of sleep. These discrepancies between the subjective experience and the current electrophysiological signature of sleep are commonplace (Valko et al., 2021), particularly in insomnia (Bastien et al., 2014). Part of these discrepancies can be attributed to the common misconceptions that consciousness disappears at sleep onset and that subjective experiences during sleep are all dream-like (e.g., bizarre, fantastic storylines) (Andrillon, 2021). However, consciousness does not always fade after the first electrophysiological signs of sleep. Rather, it can transform into specific experiences called hypnagogia (Lacaux et al., 2023), which can share features with dreams but also with mind-wandering, potentially making them hard to distinguish from wakeful experiences. Furthermore, sleep onset is a gradual process that does not occur synchronously in all the brain at once (Magnin et al., 2010). Cortical regions (e.g., the hippocampus) transition to sleep before other subcortical regions (e.g., the thalamus), leading to very specific dissociated states that individuals themselves do not necessarily associate with sleep.

Finally, there are also dissociations between the physiological state of sleep and behavior. If responsiveness drastically reduces following sleep onset, it is not completely abolished (Strauss et al., 2022) and sleepers can process sensory inputs overtly or covertly in a surprisingly complex way (Andrillon & Kouider, 2020; Lacaux et al., 2023).

3.2 Neural dynamics associated with conscious and unconscious reports during sleep

Because sleep jointly alters behavior, brain activity and subjective experience, it has been recognized as a unique opportunity to explore the neural correlates of conscious and unconscious states and to identify the background conditions necessary for consciousness (Revonsuo, 2009; Wong et al., 2020). Normal individuals can report having no conscious experience following a forced or spontaneous awakening from NREM sleep. These reports of unconsciousness are associated with the apparition of cortical slow waves and an increase in local synchrony (Tononi & Massimini, 2008). Interventional studies relying on TMS[3] or electrical stimulation showed that these slow waves lead to a breakdown of cortico-cortical connectivity (Massimini et al., 2005; Pigorini et al., 2015). This is because these slow waves reflect a phenomenon of cortical bistability, which represents an alternance between periods of neuronal activity (ON) and silence (OFF) (Vyazovskiy & Harris, 2013) (Figure 4). Neuronal silencing especially seems to prevent the kind of sustained activity and integration of information that appear so central to consciousness (Koch et al., 2016; Mashour et al., 2020). The fact that reports of dreams and conscious experiences are so prevalent in REM sleep, a state deprived of the sort of global slow waves observed in NREM sleep, support the notion that a desynchronized brain is required for the formation of conscious experiences.

Beyond the coarse division between wakefulness, NREM and REM sleep, a subdivision of NREM sleep exists. This is called Stage 2 NREM (NREM2) which is characterized by intermittent slow waves (Carskadon & Dement, 2005). This form of light sleep represents an exceptional opportunity to study how subtle changes in brain activity can support the formation of conscious experiences. Indeed, when awoken from NREM2 individuals can report drastically different experiences: no conscious experience, conscious

[3] Transcranial Magnetic Stimulation (TMS) is a non-invasive neuromodulation technique that uses magnetic fields to stimulate specific areas of the brain, altering neural activity in targeted regions.

experience, or even conscious experience without recall of the content itself (Siclari et al., 2013). Contrasting these different types of reports revealed that consciousness can be predicted by a decrease in slow wave activity (1-4Hz) over a “hot spot” of cortical brain regions, and an increase of fast activity (25-50Hz) over cortical areas more centrally distributed (Siclari et al., 2017). Going into further detail, this approach also revealed that specific contents of the conscious experience are associated with a decrease in slow wave power in the same networks that are activated by experiencing these contents while awake (Siclari et al., 2017).

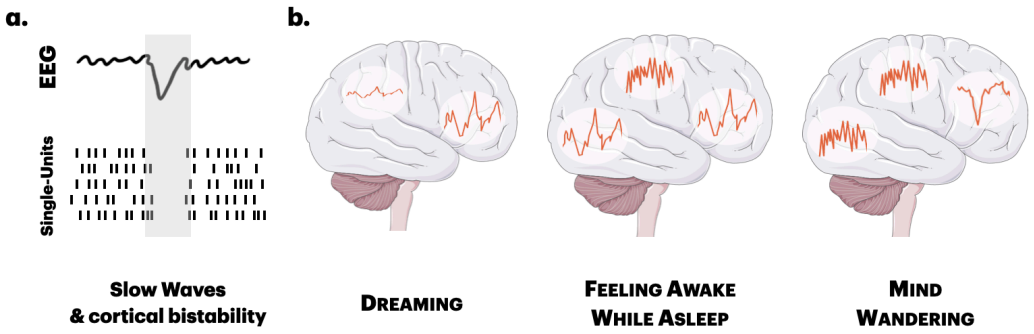

Figure 4. Local aspects of sleep and conscious experiences.

(a) Slow waves are high-amplitude low-frequency patterns of EEG activity and a hallmark of NREM sleep. Slow waves result from the synchronization of neuronal activity with a period of silence (OFF) followed by a period of neuronal activity (ON). b: Local and global modulations of slow/fast activity can predict fluctuations in subjective experience. A decrease of slow waves over parietal cortices predicts dreaming. An increase in fast activity over widespread cortical networks are associated with the feeling of being awake while sleep. In wakefulness, the presence of sleep-like slow waves can predict lapses of attention, like mind wandering.

Sleep research has, thus, moved beyond the simplistic association of NREM sleep with unconsciousness and REM sleep with consciousness. As in wakefulness, conscious experiences during sleep are highly varied and dynamic. Dreams can encompass a wide range of experiences, showing intriguing parallels with waking phenomena, such as mind-wandering and mind-blanking. These phenomenological similarities are echoed in shared neural correlates, suggesting the possibility of a unified framework to account for the dynamics of consciousness across both sleep and wakefulness (Vyazovskiy & Andrillon, 2025).

4. Markers and mechanisms of spontaneous experiences

4.1 The search for the Neural Correlates of Consciousness

The scientific study of consciousness requires tools to objectively assess someone’s else conscious state or content of experience. Markers of consciousness can be verbal or behavioural as humans have most of the time the ability to directly communicate about the content of their subjective experience. There are obviously many exceptions that can make such correlates of consciousness debatable. For example, consciousness can be sometimes present in the absence of the ability to immediately report on this experience or without any behavior associated with this experience (e.g., dreaming or anesthesia). This situation can become a relevant clinical challenge in patients with disorders of consciousness who suffer of a cognitive motor dissociation (Bodien et al., 2024).

A complementary approach is, thus, to examine brain activity associated with specific states or contents of consciousness. This search for Neural Correlates of Consciousness (NCCs) represents a foundational challenge for the science of consciousness (Crick & Koch, 1990; Koch et al., 2016). NCCs are classically

defined as the "*minimal neuronal mechanisms jointly sufficient for any one specific conscious percept*" (Crick & Koch, 2003). In practice, the concept of NCCs can be understood in varied ways. NCCs can be specific to a given subjective experience, or the phenomenal dimension of that experience such as the redness of an apple (content-specific NCC). But NCCs can also refer to the mechanisms or brain structures that are directly conducive to conscious experiences in general (full NCC). NCCs and the investigation of spontaneous conscious experiences in wakefulness and sleep are tightly associated for two reasons: (1) NCCs can help track fluctuations in subjective experience without requiring participants to report on these fluctuations, (2) in return, these fluctuations can help understand the strengths and limits of NCCs.

4.2 State and content-specific the Neural Correlates of Consciousness

Contrasting different states of consciousness, such as wakefulness or dreaming on the one hand and dreamless sleep or anesthesia on the other hand has allowed to identify several "full NCCs". For example, activated and desynchronized patterns of activity are characteristic of wakefulness, but also states in which individuals might be unresponsive but conscious, such as REM sleep or certain types of anesthesia (e.g., after ketamine intake) (Koch et al., 2016). On the contrary, the presence of large-amplitude slow waves is typically associated with unconscious states (Tononi et al., 2024) although the presence of slow waves is not always a reliable indicator that consciousness is absent (Frohlich et al., 2021).

Content-specific NCCs target contents or phenomenal dimensions of conscious experience. For example, the conscious processing of a new image or sound is typically associated with a widespread and sustained pattern of activation in cortical areas (Dehaene et al., 2006). There are intense debates to better specify the minimal set of neuronal mechanisms necessary and sufficient for the formation of a content-specific conscious experience (Mashour et al., 2020; Tononi et al., 2016). It is worth noting that content-specific NCCs can reflect prerequisites or cognitive functions associated with conscious processing rather than the conscious representation itself. Strategies have been proposed to distill the neural correlates of the conscious representation from its prerequisites and consequences (Aru et al., 2012) but even when conflating these different types of correlates, NCCs can prove extremely useful to detect the presence of consciousness. For example, the sensitivity to the violation of simple or complex auditory rules as in the Oddball or Local/Global paradigms[4] allowed the identification of specific EEG signatures including the Mismatch Negativity (MMN) or P300. These signatures can provide invaluable information about the (un)conscious state of an individual and its (un)connectedness to the environment even when the said individual is not responsive, such as in sleep (Strauss et al., 2015), anesthesia (Uhrig et al., 2016), or in disorders of consciousness (Bekinschtein et al., 2009).

Koch and colleagues stress nonetheless the importance of establishing NCCs that are "directly" associated with conscious experience to distinguish NCCs from background conditions necessary for consciousness, such as arousal (Koch et al., 2016). Accordingly, structures promoting arousal, like as the Ascending Reticular Activating System would not be considered a NCC because it is mainly associated with the regulation of arousal, which is itself a background condition for consciousness. Some NCCs used in basic or clinical research (e.g., slow waves, alpha oscillations, etc.) (Sitt et al., 2014) could thus reflect changes in arousal rather than direct changes in conscious states or contents, although clinical categories such as Minimally Conscious State (MCS) and Unconscious Wakefulness Syndrome (UWS) partially account for this confounding factor since they are similar in terms of arousal.

[4] The Local/Global Paradigm is an experimental framework used to study how individuals process hierarchical stimuli by focusing on either the local details or the overarching global shape, therefore providing insights into selective attention and conscious processing.

NCCs can also reflect consequences of conscious processing. Content-specific NCCs, such as the P300 could at least partially reflect report (including self-report) rather than the formation of a conscious mental representation per se (Sergent et al., 2021). Examining how these NCCs are impacted in states in which individuals are conscious but not necessarily in a reflective way (such as during dreaming) can provide a unique window to dissociate the neural processes associated with the formation of a conscious mental representation and its cognitive consequences (Tsuchiya et al., 2015).

4.3 State and contents of consciousness, reunited at last?

Searching for the NCCs has long been structured along the level/content dichotomy of consciousness science. Yet, there are recent attempts at operating a convergence between the level and state approach of consciousness through the NCCs. First, content-specific NCCs can help address questions about states of consciousness because being conscious of something logically implies being conscious. Accordingly, as mentioned earlier, markers of conscious processing of sensory information provide interesting tools to identify consciousness in sleep (Strauss et al., 2015; Türker et al., 2023) or disorders of consciousness[5] (Rohaut et al., 2024). These tools typically have a good specificity but a more limited selectivity (King et al., 2013; Sitt et al., 2014) as states of consciousness disconnected of the environment can exist (Sanders et al., 2012). Conversely, NCCs of states can also inform on the types of conscious contents than an individual can experience. For example, the presence of sleep-like slow waves (a marker that is usually associated with unconsciousness when observed globally) or patterns of high inter-areal functional connectivity can help predict the occurrence of specific experiences, such as mind wandering, mind blanking or dreaming in wakefulness and sleep (Andrillon et al., 2021; Mortaheb et al., 2022; Perogamvros et al., 2017).

Two influential classes of markers of consciousness regards complexity (Lempel-Ziv, Kolmogorov, Perturbational Complexity Index etc.) and connectivity measures (weighed Symbolic Mutual Information, Phase Lag Index, etc.) (Sitt et al., 2014). These metrics try to estimate the richness of neural activity. Their relationship with consciousness is still debated, but is motivated by the notion that consciousness depends on a balance between integration and segregation, order and chaos (Bassett & Gazzaniga, 2011; Carhart-Harris et al., 2014). Interestingly, some complexity and connectivity measures can differentiate between different states of consciousness (Sitt et al., 2014) and, in some cases, are even sensitive to changes in consciousness that are pharmacologically induced or associated with neuro-psychiatric disorders (Fernández et al., 2013; Scott & Carhart-Harris, 2019).

Yet, a more systematic investigation of the sensitivity of NCCs to both states and contents of consciousness indicates that these relationships are complex (Pérez et al., 2024). Pérez and colleagues found that many NCCs, such as EEG alpha and beta power, complexity or entropy were found to positively correlate with conscious states (e.g., larger in wakefulness than in NREM sleep) but were eventually negatively correlated with conscious contents (larger for unseen stimuli than for seen stimuli). This reversal is striking although it is mitigated by the fact that "content" effects are typically much smaller that "state" effects. This means that if a variable X is positively associated with a state of consciousness but negatively associated with conscious access of a specific content, the value of X will still be higher for a participant experiencing a content than the same participant when unconscious. Yet, it could be argued that an ideal NCC should be sensitive to both state and contents with the same directionality. A more systematic mapping of how NCCs behave in different contexts, especially during fluctuations of consciousness throughout wakefulness and

[5] Disorders of consciousness are neurological conditions following trauma-related or anoxic accidents ranging from coma to vegetative and minimally conscious states, where patients have limited or no interaction with their environment as a result of impaired awareness and behavioral responsiveness.

sleep, could help understand what these NCCs are indexing (e.g., pre-requisites, mechanisms, consequences, or functions of consciousness).

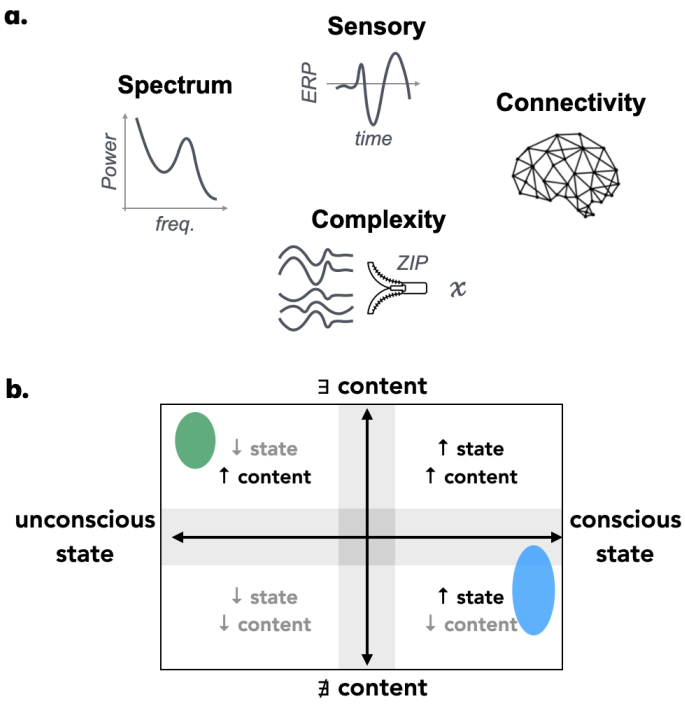

Figure 4: Neural correlates of consciousness across states and contents

a: Neural correlates of consciousness include markers of sensory processing (event-related potentials, ERPs), signal complexity, connectivity, or spectral features. They are derived from neural recordings. b: Neural correlates of consciousness can be compared regarding their sensitivity to conscious states and contents. Circles show the area in which most of the known correlates have been found. From (Pérez et al., 2024).

Conclusions

The dichotomy between states and levels of consciousness profoundly shaped the way consciousness is studied. However, recent works focusing on the fine-grained fluctuations in conscious contents in wakefulness and sleep, particularly relative to the phenomenal properties and temporal dynamics of conscious experiences, draw interesting parallels between these states. These findings stress the continuity between wakeful and sleep experiences, blurring the distinction between states and contents of consciousness. This movement is reinforced by the examination of neural correlates and mechanisms of consciousness, which show a convergence of general principles regarding the kind of neural dynamics that are conducive or unfavorable for the formation of conscious experiences. For example, markers of cortical (de)synchronization can be extracted at the whole-brain or network level, allowing a finer prediction of consciousness. This reunion of the state and content approach of consciousness might have important implications for our conceptualization of the conscious experiences that constitute our days and nights but also for our understanding of consciousness in clinical populations.

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