

Conscious experience in sleep and wakefulness

Francesca Siclari^a, Claudio Bassetti^b, Giulio Tononi^a

^a Department of Psychiatry, University of Wisconsin-Madison, Madison, USA

^b Department of Neurology, University Hospital Bern, Switzerland

Funding / potential competing interests: No financial support and no other potential conflict of interest relevant to this article were reported.

Summary

Consciousness in the course of the sleep-wake cycle varies considerably, ranging from its near-complete absence shortly after sleep onset to its re-appearance in the form of vivid, hallucinatory experiences in dreams. Phenomenological studies have shown that conscious experience in different states of being (sleep, wakefulness, and sleep-wake transitions) displays state-specific features. More recent studies have provided new approaches for the study of mental experiences during sleep and wakefulness. In particular, they have shown that sleep is not a global phenomenon, as generally thought, but a local one, and that in particular instances, patterns of sleep and wakefulness can occur simultaneously in the same individual. The present work describes common conscious experiences during sleep and wakefulness and discusses potential neurobiological correlations in view of these recent findings.

Key words: sleep; consciousness; dreams; daydreaming

Introduction

Every human being knows what it is like to be conscious. We have all experienced losing consciousness when we fall into deep, dreamless sleep, and regained it during a dream or upon awakening. Not only does consciousness vanish and reappear on a nightly basis, it can also assume a surprising variety of forms, encompassing brief images that flash by as sleep sets in, hallucinatory experiences in dreams later in the night and vivid memories that emerge during wakefulness. Investigating conscious experiences necessarily implies that one has to rely on subjective retrospective reports that can be influenced by a variety of factors including memory. Despite these methodological challenges, studies in this field have convincingly demonstrated that conscious experiences bear specific state-dependent features (see table 1 for a summary). Recent advances in the field of sleep and consciousness have provided new approaches for the study of the neurobiological basis of these features. The present work aims at describing conscious experiences that are commonly encountered during sleep and wakefulness by

healthy individuals and at outlining their distinguishing features. Potential neurobiological correlations and future directions are discussed.

Conscious experience during sleep

Sleep as a physiological and every-night phenomenon offers a unique opportunity for the study of consciousness. Within the same night, consciousness can completely disappear (typically early in the night during slow wave sleep) and reappear later in the form hallucinatory experiences in dreams. Dreaming can in fact be seen as a particular form of consciousness that occurs during sleep. Considering this assumption, one is faced with an apparent paradox [1]: On the one hand, the dreamer is conscious. He experiences a world that is imaginary, but bears so much resemblance to reality that it is, in fact, taken for real. On the other hand, the dreamer is asleep, and by definition does not react to external stimuli unless these are strong enough to wake him up. This sensory disconnection implies that every experience in a dream is generated internally and is, in neurological jargon, a hallucination (see Table 2 for definitions).

Rapid eye movement (REM) sleep

REM sleep, characterised by fast-frequency, activated EEG-activity, rapid eye movements and muscle atonia, is the physiological sleep stage in which conscious experiences are most likely to occur (in 71–93% of cases [2]). Although dreams are well known for their bizarre characteristics, they also share a large amount of similarities with waking consciousness. Dreams are experienced through the same sensory modalities as waking experiences [1]. They are highly visual, in full colour and contain the same categories as our waking life (people, objects, faces, etc.). Auditory experiences, including speech and conversation, are often indistinguishable from those experienced during wakefulness, and, although less frequently, touch, taste and olfaction can also be part of dreams. There appears to be a high correspondence between our waking and dreaming lives in terms of current concerns, personality traits and interpersonal relationships. On the other hand, dreams, especially during REM sleep, bear some distinguishing characteristics [1]. To start with, dreaming is typically delusional, as the dreamer takes experiences for real and often accepts impossible events or objects, as well as sudden transformations or inconsistent scene switches. He is often uncertain about place and time, and may even hold contradictory

Correspondence:
Giulio Tononi, MD PhD
Department of Psychiatry
University of Wisconsin – Madison
6000 Research Park Blvd
53519 Madison, Wisconsin
USA
gtononi[at]wisc.edu

Table 1 Table summarising conscious experiences in different states of being and their characteristics.

State of being	Conscious experience	Frequency (upon questioning)	Content	Distinguishing features
Wakefulness	Daydreaming (mind-wandering)	80%	Mainly thoughts. Dreamlike in up to 25%.	Independent of external stimuli (by definition). Compared to REM sleep dreams: more abrupt topic changes.
REM sleep	Dreaming	71–93%	Vivid, hallucinatory experiences.	Delusional quality compared to wakefulness: Single-mindedness Reduced self-awareness Reduced executive control High degree of emotionality altered mnemonic processes
NREM sleep	Dreaming	23–75%	Early in the night: thought-like and conceptual. Later in the night vivid and hallucinatory experiences.	Compared to REM sleep dreams: – shorter – less dreamlike, more thought-like – less vivid – more conceptual – under greater volitional control – more plausible – more related to current concerns – less emotional Late in the night sometimes indistinguishable from REM sleep reports.
Transition from wakefulness to sleep	Hypnagogic hallucinations	80–90%	Short static images ('snapshots'), or brief sequences of disconnected frames. Sensation of falling. Sometimes influenced by activities performed prior to sleep.	Compared to conscious experience in other sleep stages: – fewer emotions – fewer characters – less self-representation – less bizarre – closer to reality
Transition from sleep to wakefulness	Hypnopompic hallucinations	13%	Flying or floating sensations. Autoscopic or out-of body experiences. Perception of distorted objects. Sensed presence hallucinations.	Compared to sleep onset experiences: more bizarre and more spatio-temporal distortions.

beliefs. There is also a tendency for thoughts and images to persist without interruption, a characteristic that has been referred to as single-mindedness [3]. Consistent with this observation is the fact that word counts of reports obtained from awakenings during REM sleep often contain more words than reports obtained during wakefulness [3]. Dream content can be highly emotional, sometimes to a degree that is rare in waking life [4]. Other features that distinguish dreaming from wakefulness include reduced self-awareness (the dreamer typically does not know that he is asleep), and diminished executive control (the dreamer has no voluntary control over the content of the dream and cannot pursue goals). Finally, dreaming is associated with altered mnemonic processes since upon awakening, dream recall typically vanishes rapidly, unless it is instantly recorded.

Neurobiology

At first sight, the EEG during REM sleep resembles the EEG during waking or stage N1, with its activated, low-voltage, fast activity-pattern. Absolute levels of blood flow and meta-

bolic activity are high during REM sleep, similar to levels seen during wakefulness. There are however, regional differences, and some areas are even more active during REM sleep than in wakefulness. These include limbic areas (amygdala and parahippocampal cortex), and the cortical areas that receive limbic projections, such as the anterior cingulate, the parietal lobule, as well as the extrastriate areas. The rest of the parietal cortex, precuneus, posterior cingulate and dorsolateral frontal cortex, are relatively deactivated [5]. These regional activations and deactivations are consistent with differences between waking and dreaming cognition. Reduced voluntary control for instance might be related to deactivation of the right inferior parietal cortex (Brodmann's Area 40), an area that is active in waking volition [6, 7] but deactivated during REM sleep [8, 9]. Diminished self-monitoring on the other hand may reflect deactivation of the posterior cingulate cortex, inferior parietal cortex, orbitofrontal cortex and dorsolateral prefrontal cortex [9] [8]. Deactivation of prefrontal cortex has indeed been shown to be associated with reduced self-awareness in highly en-

Table 2 Definitions of important terms used throughout the text.

Phenomenon	Definition
Hallucination	Perception of something that is not present.
Dream	Any form of conscious experience during sleep. Can be hallucinatory.
Sensory disconnection	Term referring to the fact that sensory stimuli are generally not incorporated into conscious experience during sleep.

gaging sensory perception in wakefulness [10]. The intense emotions often encountered in dreams are possibly related to the marked activation of limbic and para-limbic structures [8, 11, 12]. It remains unclear why mnemonic processes are altered during REM sleep, considering that limbic circuits in the medial temporal lobe, which are implicated in memory processes, are highly active during REM sleep [8, 9, 13]. It is conceivable that dream amnesia is related to hypoactivity of the prefrontal cortex, which also plays a role in mnemonic processes [1]. Another possibility is that dream amnesia is linked to hypoactivity of the posterior cingulate cortex, which appears to play a role in memory processing and in distinguishing real from imagined events [14–16]. Finally, specific patterns of local activation and deactivation might underlie features of dream bizarreness. Delusional misidentification or hyper-identification are common features of dreams. Someone might for instance be recognised as one's brother, although he has the physical appearance of someone else. In clinical practice, this phenomenon (called Fregoli syndrome) is seen after ventral temporal lesions (most often on the right side) or lesions in the prefrontal cortex. In dreaming, delusional misidentification has been suggested to underlie the concomitant activation of temporal areas underlying face recognition and of the amygdala (providing a feeling of familiarity) in the absence of prefrontal activation that normally exerts a "monitoring function" [17]. This and other reports [18, 19] illustrate how neurological and neuropsychological observations can contribute to the understanding of the mechanisms underlying dreaming.

Non-REM (NREM) sleep

Early in the night, the EEG in NREM sleep is characterised by numerous slow waves that reflect 0.5–4 Hz alternations of the membrane potential of cortical neurons between up- and down states. Slow waves decline in the course of the night, and are a marker of the homeostatic process inherent to sleep. Another hallmark of NREM sleep are sleep spindles, 12–16 Hz waxing and waning oscillations that result from reciprocal interactions between inhibitory cells in the thalamic reticular nucleus and bursting thalamocortical relay neurons. NREM sleep early in the night is the moment when consciousness is most likely to be absent. At other moments during NREM sleep, conscious experiences are more likely to occur, although on the whole less frequently than in REM sleep. Depending on the study, between 23 and 75% of awakenings during NREM sleep yield reports of mental activity [2]. Mental experiences in NREM sleep are typically shorter, less dreamlike, more thought-like, less vivid, more conceptual, under greater volitional control, more plausible, more related to current concerns, and less emotional than reports obtained from awakenings during REM sleep [1, 20] [21, 22]. However, at the end of the night, reports tend to be more frequent, longer and have more hallucinatory character, and in a number of cases appear indistinguishable from reports obtained from REM sleep [23, 24]. The following examples, taken from an unpublished study conducted by two of the authors in two healthy subjects, illustrate this difference:

"I was thinking of a frying pan going hot on the stove, like when you cook something." (Stage N2, 1:25 am)

"I was a wizard I think, or a magician. I was wearing a wizard's hat, I think I was trying to cast a spell and I remember I saw myself wearing a hat like that." (Stage N2, 7:06 am)

Neurobiology

Although sleep is generally thought of as a global phenomenon, affecting the whole brain at the same time, recent studies have proven otherwise. Slow waves and spindles, representing the hallmarks of NREM sleep, have been shown to occur locally, independently from other brain regions. For slow waves, this is especially true towards the end of the night [25], as if upon the dissipation of sleep pressure, only a few areas of the brain were "still asleep", while others already displayed patterns more akin to waking activity. Considering that the frequency and dreamlike hallucinatory character of mental experiences appear to increase in the course of the night during NREM sleep, it is tempting to hypothesise that the brain's capacity to generate conscious experiences is reduced in the presence of slow waves. It has been suggested that the level of consciousness depends on the brain's capacity to integrate a large amount of information [26]. TMS-EEG studies, measuring how brain activity is evoked by TMS propagates through the brain, have shown that during slow wave sleep the response remains either local (reflecting a loss of integration) or spreads non-specifically (loss of information), while during wakefulness and REM sleep changing patterns of activation across distant interconnected brain regions are observed [27]. A possible explanation for the reduction of differentiated patterns of activation during sleep is bistability in thalamocortical circuits, the same mechanism that underlies spontaneous slow waves [28]. When falling asleep, brainstem activating systems decrease their firing, increasing the influence of depolarisation-dependent K⁺ currents in thalamic and cortical neurons [29], causing neurons to become bistable and to fall into a silent, hyperpolarised state (down-state) after a short period of activation (up-state). Changes in neurotransmitters may also contribute to bistability [30]. As a result, any local activation, occurring spontaneously or induced by a stimulus (like TMS), will evolve into a silent neuronal down-state and into a slow wave on the EEG [31]. The bistability with frequent and prolonged off periods during early NREM sleep [32] is likely to prevent the occurrence of sustained depolarisation and of complex thalamocortical interactions. Considering the recent demonstration that off periods in NREM sleep are mostly local, especially in distant cortical areas [25], then interactions among distant cortical areas are especially susceptible to disruption by bistability. If information integration among cortical regions is necessary for consciousness, then consciousness during sleep should be lowest when off periods are frequent and long, as in early NREM sleep, and minimally so when off periods are mostly absent as in REM sleep, or rare and short as in late NREM sleep [32].

Evidence for a negative association between slow waves and sleep consciousness comes from a recent study demon-

strating that dreaming during NREM sleep is associated with lower power in the slow wave frequency band over frontal brain regions [33]. Along the same line, another study showed that the number of individual slow waves and sleep spindles is lower during sleep associated with conscious experiences [34].

Conscious experience during transitions between sleep and wakefulness

Falling asleep

While falling asleep, one typically experiences so-called hypnagogic hallucinations (Greek for “leading into sleep”). These are frequent in the healthy population (80–90%), usually short and consist of static images (“snapshots”) or brief sequences of disconnected images. Compared to mental activity in other stages, reports obtained at sleep onset typically contain fewer emotions, fewer characters, less self-representation, are less bizarre and closer to reality [35, 36]. Activities that have been performed prior to sleep may influence the content of hypnagogic imagery [37, 38]. The following examples, taken from the same study mentioned above, represent reports of conscious experiences at sleep onset (stage N1):

“I saw a hockey player. No one in particular.”

“I saw the headline of a newspaper story, saying that 24 had been burnt in a fire.”

Awakening

In contrast to hypnagogic hallucinations, which are a common phenomenon, hallucinations at the transition from sleep to wakefulness, called hypnopompic hallucinations, are less frequently encountered in the healthy population [39]. They are, however, reported by 25–30% of individuals with narcolepsy [40] and constitute one of the defining features of the illness. Compared to hypnagogic hallucinations, conscious experiences upon awakening are more bizarre and contain more spatio-temporal distortions [41]. Hypnopompic hallucinations are often accompanied by sleep paralysis, an inability to move upon awakening despite being conscious. In the presence of sleep paralysis, conscious experiences sometimes assume a nightmarish quality. Individuals commonly experience a “sensed-presence”, frequently interpreted as coming from an imaginary intruder, and suffer intense fear. Breathing difficulties, the impression of choking and feeling a pressure on the chest are also common experiences in this constellation. These sensations are often associated with the perception of a person or animal sitting or pushing on the chest. In other instances, non-frightening, floating or flying sensations are experienced, which may or not be accompanied by out-of-body or auto-scopic experiences.

Neurobiology

Recent studies have shown that in particular instances, different brain regions can be in different states at the same

time, a condition termed “state dissociation” [42]. During some sleep disorders such as NREM parasomnias, including sleepwalking and confusional arousals, some brain regions have been shown to display activity similar to wakefulness, while others show patterns that are closer to sleep [43, 44]. Interestingly, fragments of dreams are sometimes reported in association with sleepwalking [45]. It is conceivable that in transitional states, when sleep and wake replace each other, state dissociation is particularly likely to occur. Indeed, recent studies have demonstrated that the transition from wake to sleep and vice versa is not a spatially and temporally uniform process. The thalamus for instance, has been shown to undergo deactivation well before the cortex when falling asleep, and even within the cortex deactivation is topographically heterogeneous [46]. As outlined before, hallmarks of NREM sleep (spindles and slow waves) occur locally (i.e. asynchronously), especially in distant cortical areas. It is conceivable that the heterogeneous cortical activation, related to the local occurrence of sleep, might underlie hypnagogic hallucinations in the falling asleep process. It might also explain why mental activity at sleep onset shares features with dreams encountered in other sleep stages (i.e. the hallucinatory character) but also why they are much closer to waking consciousness (i.e. more thought-like and closer to reality).

The process of awakening also seems to occur in different brain regions at different times. A PET study for instance has shown that upon awakening from NREM sleep, cerebral blood flow is most rapidly established in centrencephalic regions (brainstem and thalamus), and only in the following 15 minutes in anterior cortical regions [47]. This suggests that in the course of the awakening process, some parts of the brain may still be partially “asleep”, while others are already “awake”. Awakenings out of REM sleep characterised by sleep paralysis and hypnopompic hallucinations also reflect this dissociation. Polysomnographic recordings in these instances have revealed both features of wakefulness and REM sleep, including alpha-theta EEG activity, decreased muscle tone interrupted by bursts of muscular activity (reflecting attempts to move) and a mixture of saccadic and rapid eye movements [48]. Commonly experienced phenomena in the hypnopompic state are likely related to simultaneously present features of wakefulness and REM sleep. Individuals appear to lose the sensory disconnection characteristic of sleep and thus perceive their actual environment. On the other hand, hallucinatory and delusional experiences characteristic of REM sleep continue. Sleep paralysis likely underlies persisting muscle atonia from REM sleep, and the inability to recruit accessory respiratory muscles to deepen inspiration has been suggested to result in a sensation of pressure on the chest [49]. Fear and terror are likely related to heightened amygdala activity, which is characteristic of REM sleep. Finally, the absence of proprioceptive feedback caused by persisting muscle atonia might underlie the sensation of weightlessness that accompanies flying and floating experiences that are also encountered in these instances [5].

Conscious experience during wakefulness

The term daydreaming is commonly used to describe “dreamlike” mental activity that occurs during wakefulness. In experimental conditions, it is often defined as mentation that is independent of external stimuli or the task in question. When asked about conscious experiences during wakefulness, healthy subjects report thoughts in up to 80% of cases [50]. In up to 20–25% of cases, experiences are even described as dreamlike and hallucinatory [51, 52]. When compared with dream reports from REM sleep, mental activity during wakefulness appears to contain more abrupt topic changes [53].

The amount of “mind-wandering” has been shown to correlate with activity of the default mode network, consisting of regions that are normally active during passive, resting test conditions compared to demanding cognitive tasks [54]. Areas that exhibit greater activity during mind-wandering include the medial prefrontal cortex, the anterior cingulate, precuneus, insula, left angular gyrus and superior temporal cortex [54]. Another study found a similar association between activity in parts of the default mode network and stimulus-independent thoughts, and also showed that anti-correlated stimulus-dependent thoughts were associated with activity in lateral fronto-parietal cortices [55]. The default mode network has also been shown to be related to self referential mental activity [56], thinking about the past [57, 58], envisioning the future [59] and visual and auditory imagery [60]. The fact that daydreaming and mental imagery appears to be related to activity of the default mode network raises the question as to whether this is also true for dreaming [61]. Although connectivity between the core regions of the default-mode network appears to be maintained during REM sleep [62], the fact that it is also preserved in deep slow wave sleep, anaesthesia and coma [63, 64], when conscious experiences are considered absent or minimal, argues against a primary involvement of the default mode network in dreaming. Also, posterior regions of the default mode network, including the posterior cingulate, precuneus and lateral parietal cortex, are typically deactivated during REM sleep [5]. In the future, studies comparing cerebral activity patterns between daydreaming and dreaming in the same subject could be of value in clarifying similarities and differences in the neural substrates of these states.

Conclusion

Recent advances in consciousness research have provided new approaches for the study of mental experiences during sleep and wakefulness. Most importantly, sleep should not be considered as a global phenomenon anymore, affecting the whole brain at the same time, since it occurs and is regulated locally. Changing patterns of local activity in the course of the night might underlie particular characteristics of dreaming. Additionally, recent studies have shown that in particular instances, some parts of the brain can be asleep, while others are simultaneously awake. Such dissociated phenomena likely occur during sleep-wake transitions and

might account for intriguing features of mental activity while falling asleep or awakening.

References

- Nir Y, Tononi G. Dreaming and the brain: from phenomenology to neurophysiology. *Trends Cogn Sci*. 2010;14(2):88–100.
- Nielsen TA. A review of mentation in REM and NREM sleep: “covert” REM sleep as a possible reconciliation of two opposing models. *Behav Brain Sci*. 2000;23:851–66.
- Rechtschaffen A. The single-mindedness and isolation of dreams. *Sleep*. 1978;1(1):97–109.
- Nielsen TA, Deslauriers D, Baylor GW. Emotions in dreams and waking event reports. *Dreaming*. 1991;1:287–300.
- Tononi G. Sleep and Dreaming. In: Laureys S, Tononi G, eds. *The neurology of consciousness*: Elsevier; 2009.
- Goldberg I, Ullman S, Malach R. Neuronal correlates of “free will” are associated with regional specialization in the human intrinsic/default network. *Conscious Cogn*. 2008;17(3):587–601.
- Desmurget M, Reilly KT, Richard N, Szathmari A, Mottolese C, Sirigu A. Movement intention after parietal cortex stimulation in humans. *Science*. 2009;324(5928):811–3.
- Maquet P, Peters J, Aerts J, Delfiore G, Degueldre C, Luxen A, et al. Functional neuroanatomy of human rapid-eye-movement sleep and dreaming. *Nature*. 1996;383(6596):163–6.
- Braun AR, Balkin TJ, Wesenten NJ, Carson RE, Varga M, Baldwin P, et al. Regional cerebral blood flow throughout the sleep-wake cycle. An H2(15)O PET study. *Brain*. 1997;120 (Pt 7):1173–97.
- Goldberg, II, Harel M, Malach R. When the brain loses its self: prefrontal inactivation during sensorimotor processing. *Neuron*. 2006;50(2):329–39.
- Maquet P, Laureys S, Peigneux P, Fuchs S, Petiau C, Phillips C, et al. Experience-dependent changes in cerebral activation during human REM sleep. *Nat Neurosci*. 2000;3(8):831–6.
- Nofzinger EA, Mintun MA, Wiseman M, Kupfer DJ, Moore RY. Forebrain activation in REM sleep: an FDG PET study. *Brain Res*. 1997;770(1–2):192–201.
- Maquet P. Functional neuroimaging of normal human sleep by positron emission tomography. *J Sleep Res*. 2000;9(3):207–31.
- Summerfield JJ, Hassabis D, Maguire EA. Cortical midline involvement in autobiographical memory. *Neuroimage*. 2009;44(3):1188–200.
- Foster BL, Dastjerdi M, Parvizi J. Neural populations in human postero-medial cortex display opposing responses during memory and numerical processing. *Proc Natl Acad Sci U S A*. 2012;109(38):15514–9.
- Vannini P, O'Brien J, O'Keefe K, Pihlajamäki M, Laviolette P, Sperling RA. What goes down must come up: role of the posteromedial cortices in encoding and retrieval. *Cereb Cortex*. 2011;21(1):22–34.
- Schwartz S, Dang-Vu T, Ponz A, Duhoux S, Maquet P. Dreaming: a neuropsychological view. *Schweiz Arch Neurol Psychiatr*. 2005;156(8):426–39.
- Bassetti CL, Bischof M, Valko PO. Dreaming: a neurological view. *Schweiz Arch Neurol Psychiatr*. 2005;156:399–414.
- Bischof M, Bassetti CL. Total dream loss: a distinct neuropsychological dysfunction after bilateral PCA stroke. *Ann Neurol*. 2004;56(4):583–6.
- Antrobus JS. REM and NREM sleep reports. *Psychophysiology*. 1983;20:562–8.
- Hobson JA, Pace-Schott EF, Stickgold R. Dreaming and the brain: toward a cognitive neuroscience of conscious states. *Behav Brain Sci*. 2000;23(6):793–842; discussion 904–1121.
- Foulkes D. Dream reports from different stages of sleep. *The Journal of Abnormal and Social Psychology*. 1962;65(1):14–25.
- Monroe LJ, Rechtschaffen A, Foulkes D, Jensen J. Discriminability of Rem and Nrem Reports. *J Pers Soc Psychol*. 1965;12:456–60.
- Antrobus J, Kondo T, Reinsel R, Fein G. Dreaming in the late morning: summation of REM and diurnal cortical activation. *Conscious Cogn*. 1995;4(3):275–99.
- Nir Y, Staba RJ, Andrillon T, Vyazovskiy VV, Cirelli C, Fried I, et al. Regional slow waves and spindles in human sleep. *Neuron*. 2011;70(1):153–69.
- Tononi G. Consciousness as integrated information: a provisional manifesto. *Biol Bull*. 2008;215(3):216–42.
- Massimini M, Ferrarelli F, Huber R, Esser SK, Singh H, Tononi G. Breakdown of cortical effective connectivity during sleep. *Science*. 2005;309(5744):2228–32.
- Massimini M, Tononi G, Huber R. Slow waves, synaptic plasticity and information processing: insights from transcranial magnetic stimulation and high-density EEG experiments. *Eur J Neurosci*. 2009;29(9):1761–70.
- McCormick DA, Wang Z, Huguenard J. Neurotransmitter control of neocortical neuronal activity and excitability. *Cereb Cortex*. 1993;3(5):387–98.
- Esser SK, Hill S, Tononi G. Breakdown of effective connectivity during slow wave sleep: investigating the mechanism underlying a cortical gate using large-scale modeling. *J Neurophysiol*. 2009;102(4):2096–111.
- Hill S, Tononi G. Modeling sleep and wakefulness in the thalamocortical system. *J Neurophysiol*. 2005;93(3):1671–98.
- Vyazovskiy VV, Olcese U, Lazimy YM, Faraguna U, Esser SK, Williams JC, et al. Cortical firing and sleep homeostasis. *Neuron*. 2009;63(6):865–78.

- 33 Chellappa SL, Frey S, Knoblauch V, Cajochen C. Cortical activation patterns herald successful dream recall after NREM and REM sleep. *Biol Psychol.* 2011;87(2):251–6.
- 34 Siclari F, LaRocque J, Postle BR, Tononi G. Slow waves and sleep consciousness. Society for Neuroscience; New Orleans 2012.
- 35 Cicogna PC, Natale V, Occhionero M, Bosinelli M. A comparison of mental activity during sleep onset and morning awakening. *Sleep.* 1998;21(5):462–70.
- 36 Rowley JT, Stickgold R, Hobson JA. Eyelid movements and mental activity at sleep onset. *Conscious Cogn.* 1998;7(1):67–84.
- 37 Stickgold R, Malia A, Maguire D, Roddenberry D, O'Connor M. Replaying the game: hypnagogic images in normals and amnesics. *Science.* 2000;290(5490):350–3.
- 38 Wamsley EJ, Perry K, Djonlagic I, Reaven LB, Stickgold R. Cognitive replay of visuomotor learning at sleep onset: temporal dynamics and relationship to task performance. *Sleep.* 2010;33(1):59–68.
- 39 Ohayon MM, Priest RG, Caulet M, Guilleminault C. Hypnagogic and hypnopompic hallucinations: pathological phenomena? *Br J Psychiatry.* 1996;169(4):459–67.
- 40 Broughton R. Neurology and Dreaming. *Journal of the University of Ottawa.* 1982;7:101–10.
- 41 Cicogna P. Dreaming during sleep onset and awakening. *Percept Mot Skills.* 1994;78(3 Pt 1):1041–2.
- 42 Mahowald MW. What state dissociation can teach us about consciousness and the function of sleep. *Sleep Med.* 2008;10(2):159–60.
- 43 Bassetti C, Vella S, Donati F, Wielepp P, Weder B. SPECT during sleepwalking. *Lancet.* 2000;356(9228):484–5.
- 44 Terzaghi M, Sartori I, Tassi L, Didato G, Rustioni V, LoRusso G, et al. Evidence of dissociated arousal states during NREM parasomnia from an intracerebral neurophysiological study. *Sleep.* 2009;32(3):409–12.
- 45 Oudiette D, Leu S, Pottier M, Buzarre MA, Brion A, Arnulf I. Dreamlike mentations during sleepwalking and sleep terrors in adults. *Sleep.* 2009;32:1621–7.
- 46 Magnin M, Rey M, Bastuji H, Guillemant P, Mauguire F, Garcia-Larrea L. Thalamic deactivation at sleep onset precedes that of the cerebral cortex in humans. *Proc Natl Acad Sci U S A.* 2010;107(8):3829–33.
- 47 Balkin TJ, Braun AR, Wesensten NJ, Jeffries K, Varga M, Baldwin P, et al. The process of awakening: a PET study of regional brain activity patterns mediating the re-establishment of alertness and consciousness. *Brain.* 2002;125(Pt 10):2308–19.
- 48 Pizza F, Moghadam KK, Franceschini C, Bisulli A, Poli F, Ricotta L, et al. Rhythmic movements and sleep paralysis in narcolepsy with cataplexy: a video-polygraphic study. *Sleep Med.* 2010;11(4):423–5.
- 49 Cheyne JA, Rueffer SD, Newby-Clark IR. Hypnagogic and hypnopompic hallucinations during sleep paralysis: neurological and cultural construction of the nightmare. *Consc Cogn.* 1999;8:319–37.
- 50 Fosse R, Stickgold R, Hobson JA. Brain-mind states: reciprocal variation in thoughts and hallucinations. *Psychol Sci.* 2001;12(1):30–6.
- 51 Foulkes D, Fleisher S. Mental activity in relaxed wakefulness. *Journal of Abnormal Psychology.* 1975;84(1):66–75.
- 52 Foulkes D, Scott E. An above-zero waking baseline for the incidence of momentarily hallucinatory mentation. *Sleep Research.* 1973;2.
- 53 Reinsel R, Antrobus J, Wollman M. Bizarreness in dreams and waking fantasy. . In: Antrobus J, Bertini M, editors. *The neuropsychology of sleep and dreaming.* Hillsdale, NJ: Erlbaum 1992. p. 157–84.
- 54 Mason MF, Norton MI, Van Horn JD, Wegner DM, Grafton ST, Macrae CN. Wandering minds: the default network and stimulus-independent thought. *Science.* 2007;315(5810):393–5.
- 55 Vanhaudenhuyse A, Demertzi A, Schabus M, Noirhomme Q, Bredart S, Boly M, et al. Two distinct neuronal networks mediate the awareness of environment and of self. *J Cogn Neurosci.* 2011;23(3):570–8.
- 56 Gusnard DA, Akbudak E, Shulman GL, Raichle ME. Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proc Natl Acad Sci U S A.* 2001;98(7):4259–64.
- 57 Daselaar SM, Fleck MS, Cabeza R. Triple dissociation in the medial temporal lobes: recollection, familiarity, and novelty. *J Neurophysiol.* 2006;96(4):1902–11.
- 58 Hassabis D, Kumaran D, Maguire EA. Using imagination to understand the neural basis of episodic memory. *J Neurosci.* 2007;27(52):14365–74.
- 59 Szpunar KK, Watson JM, McDermott KB. Neural substrates of envisioning the future. *Proc Natl Acad Sci U S A.* 2007;104(2):642–7.
- 60 Daselaar SM, Porat Y, Huijbers W, Pennartz CM. Modality-specific and modality-independent components of the human imagery system. *Neuroimage.* 2010;52(2):677–85.
- 61 William Domhoff G. The neural substrate for dreaming: is it a subsystem of the default network? *Conscious Cogn.* 2011;20(4):1163–74.
- 62 Koike T, Kan S, Misaki M, Miyauchi S. Connectivity pattern changes in default-mode network with deep non-REM and REM sleep. *Neurosci Res.* 2011;69(4):322–30.
- 63 Boly M, Phillips C, Tshibanda L, Vanhaudenhuyse A, Schabus M, Dang-Vu TT, et al. Intrinsic brain activity in altered states of consciousness: how conscious is the default mode of brain function? *Ann N Y Acad Sci.* 2008;1129:119–29.
- 64 Vincent JL, Patel GH, Fox MD, Snyder AZ, Baker JT, Van Essen DC, et al. Intrinsic functional architecture in the anaesthetized monkey brain. *Nature.* 2007;447(7140):83–6.