

## Feature Review

# Dreaming and the brain: from phenomenology to neurophysiology

Yuval Nir and Giulio Tononi

Department of Psychiatry, University of Wisconsin, Madison, WI 53719, USA

**Dreams are a remarkable experiment in psychology and neuroscience, conducted every night in every sleeping person. They show that the human brain, disconnected from the environment, can generate an entire world of conscious experiences by itself. Content analysis and developmental studies have promoted understanding of dream phenomenology. In parallel, brain lesion studies, functional imaging and neurophysiology have advanced current knowledge of the neural basis of dreaming. It is now possible to start integrating these two strands of research to address fundamental questions that dreams pose for cognitive neuroscience: how conscious experiences in sleep relate to underlying brain activity; why the dreamer is largely disconnected from the environment; and whether dreaming is more closely related to mental imagery or to perception.**

## Contemporary dream research

Although dreams have fascinated humans since the dawn of time, their rigorous, scientific study is only a recent development [1–4] (Online Supplementary Figure 1). In *The interpretation of dreams* [5], Freud predicted that ‘Deeper research will one day trace the path further and discover an organic basis for the mental event.’ Recent work, which we review here, is beginning to fulfill Freud’s prediction.

The study of dreams is a formidable task, because dream consciousness is only accessible via report rather than direct observation (Box 1) and because it is difficult to manipulate dream content experimentally, whether by exposure to stimuli before [6,7] or during sleep [7,8]. Therefore, it is difficult to predict the contents of specific dreams [9], and most modern dream research tries to relate neuronal activity retrospectively to dream form rather than to dream content (i.e. to focus on properties of all dreams rather than to investigate the neural correlates of a particular dream). Yet, encouraging progress has been made in relating the phenomenology of dreams to underlying brain activity, and to studies of brain damage and development.

## Phenomenology of dreams and their relation to brain activity

The level and nature of one’s conscious experience varies dramatically in sleep. During slow wave sleep (SWS; see Glossary) early during the night, consciousness can nearly vanish despite persistent neural activity in the

thalamocortical system [10]. Subjects awakened from other phases of sleep, especially but not exclusively during REM sleep, report ‘typical’, full-fledged dreams (vivid, sensorimotor hallucinatory experiences that follow a narrative structure) [3,11]. The dreamer is highly conscious (has vivid experiences), is disconnected from the environment (is asleep), but somehow the brain is creating a story, filling it with actors and scenarios, and generating hallucinatory images. How does the brain accomplish this feat? And, conversely, what do dreams reveal about the organization and working of the brain?

Given that awakenings from REM sleep regularly yield reports of typical dreams, we focus first on neural activity during REM sleep, to gain insight into brain states that are compatible with dreaming. However, dreams can occur in other brain states, such as late NREM sleep, as discussed below.

## Similarities between dreaming and waking

To gain insight into the phenomenology and neural basis of dreams, it is useful to consider both similarities and differences between waking consciousness and dreaming consciousness, and to relate these differences to changes in brain activity and organization [11]. Perhaps the most striking feature of conscious experiences in sleep is how similar the inner world of dreams is to the real world of wakefulness. Indeed, at times, the dreamer might be uncertain whether they are awake or asleep. Certainly, dreams are not created in a vacuum but closely reflect the organization and functions of the brain.

## Glossary

**Non-Rapid Eye Movement (NREM) sleep:** sleep comprising stages N1, N2 and N3 (slow wave sleep), characterized by slow waves and spindles in the EEG.

**Ponto-Geniculo-Occipital (PGO) waves:** phasic field potentials occurring immediately before and during REM sleep (originally discovered in cats). They propagate from the pontine brainstem via the lateral geniculate nucleus of the thalamus to the occipital visual cortex.

**Rapid Eye Movement (REM) sleep:** sleep occurring mostly late at night, with low amplitude EEG as in wake, presence of theta activity (4–7 Hz), reduced muscle tone and involuntary saccadic rapid eye movements.

**Slow waves:** oscillations of cortical origin that have frequencies <4 Hz.

**Spindles:** waxing and waning oscillations of thalamic origin that have frequencies in the sigma band (12–15 Hz)

**Stage N1 (NREM1):** sleep where the EEG is intermediate between wake and deep sleep, with presence of theta activity (4–7 Hz), occasional vertex sharp EEG waves, and slow eye movements.

**Stage N2 (NREM2):** sleep occurring throughout the night, where the EEG can contain spindles and occasional slow waves.

**Stage N3 (NREM3) / Slow Wave Sleep (SWS):** sleep occurring mostly early at night, with many large slow waves in the EEG.

Corresponding author: Tononi, G. (gtononi@wisc.edu).

**Box 1. Can reports be trusted to convey internal experiences in sleep accurately?**

Do dream reports, obtained by awakening a sleeping subject, accurately convey subjective experiences in sleep? At one extreme, one could be fully conscious throughout sleep but remember dreams well, little, or not at all, depending on the brain state when one is awakened. Indeed, researchers know that dreaming often goes unreported: some people claim they rarely dream, but systematic awakenings in sleep labs have revealed that people greatly underestimate how often and how much they are conscious during sleep. By contrast, neurological patients who report loss of dreaming are no more likely to have memory disorders than are those who report dreaming [22], suggesting that a lack of dream reports reflects lack of experience rather than changes in memory alone. Further studies could illuminate this issue as, for example, memory-related regions in the medial temporal lobe are highly active in REM sleep (Figure 1, main text).

At the other extreme, one could claim that humans are unconscious throughout sleep and merely have a tendency to confabulate during the transition into wakefulness. Although such a claim is hard to refute conclusively (just as it is hard to prove conclusively that one is not a zombie when awake), it seems implausible; when one has just experienced a vivid dream, it seems hard to believe that it was made up in a flash during an awakening. Indeed, (i) the estimated time in dream report correlates well with the time elapsed in REM sleep

before awakening [62]; and (ii) in REM sleep behavior disorder (where muscle atonia is disrupted), movements appear to match the reported dream [112].

Reports obtained upon awakenings from deep NREM sleep are more difficult to evaluate because of disorientation associated with increased sleep inertia [113]. However, evidence indicates that dream consciousness can occur in NREM sleep and does not merely reflect recalls of earlier REM sleep dreams [59]: (i) it is sometimes possible to influence dream content by sounds delivered in NREM sleep, and to ‘tag’ NREM reports [59]; (ii) Some NREM parasomnias (sleep talking and sleep terrors) correspond with reported dream experiences [114]; and (iii) ‘full-fledged’ dreams are sometimes reported upon awakening from the first NREM episode, before any REM sleep occurred [59,66], and even in naps consisting of only NREM sleep [67].

Nevertheless, several factors might render dream reports less trustworthy when compared with reports of waking experience, including: (i) a dramatic state change, because one reports about a sleep experience when awake; (ii) considerable time delay, because dream reports are obtained after the experience, possibly leading to passive forgetting and interference; (iii) difficulties in verbally describing experiences that are mainly visual and emotional; and (iv) censorship of embarrassing, immoral, sexual and aggressive material.

In most dreams, perceptual modalities and submodalities that dominate in wakefulness are heavily represented. Dreams are highly visual, in full color, rich in shapes, full of movement and incorporate typical wakefulness categories, such as people, faces, places, objects and animals [3]. Dreams also contain sounds (including speech and conversation) and, more rarely, tactile percepts, smells and tastes, as well as pleasure and pain [4,12–14]. Experiences in typical dreams have a clear sensory character (i.e. they are seen, heard and felt) and are not mere thoughts or abstractions.

These phenomenological similarities are reflected in neurophysiological similarities between waking and dreaming. For historical and methodological reasons, most electroencephalogram (EEG) and neuroimaging studies have contrasted brain activity during quiet wakefulness with that observed during REM sleep, when subjects are most likely to report dreams [15–20]. At least superficially, the EEG looks similar in active waking and REM sleep. Positron emission tomography (PET) studies have shown that global brain metabolism is comparable between wakefulness and REM sleep [11,20]. Such studies have also revealed a strong activation of high-order occipito-temporal visual cortex in REM sleep, consistent with the vivid visual imagery during dreams (Figure 1) [16,17,19].

There is also consistency between a subject’s cognitive and neural organization in dreaming and waking [13,14]. For instance, studies of children demonstrate that dream features show a gradual development that parallels their cognitive development when awake [21] (Box 2). Patients with brain lesions that impair their waking cognition show corresponding deficits in dreams. For example, subjects with impaired face perception also do not dream of faces [22,23] (Box 3).

Dreams also reflect one’s interests and personality, just like mental activity during wakefulness. Formal content analysis has revealed that mood, imaginativeness, individuals of interest and predominant concerns are

correlated between one’s waking and dreaming self [12–14]. Personal anxieties experienced in wake, such as being inappropriately dressed, lost, or late for an examination, can appear in dreams that involve social interactions [24]. Dreams, similar to one’s personality in general, are quite stable over time in adulthood [12–14], and share many characteristics across cultures [12–14]. In addition, one feels that one is personally participating in many dream events.

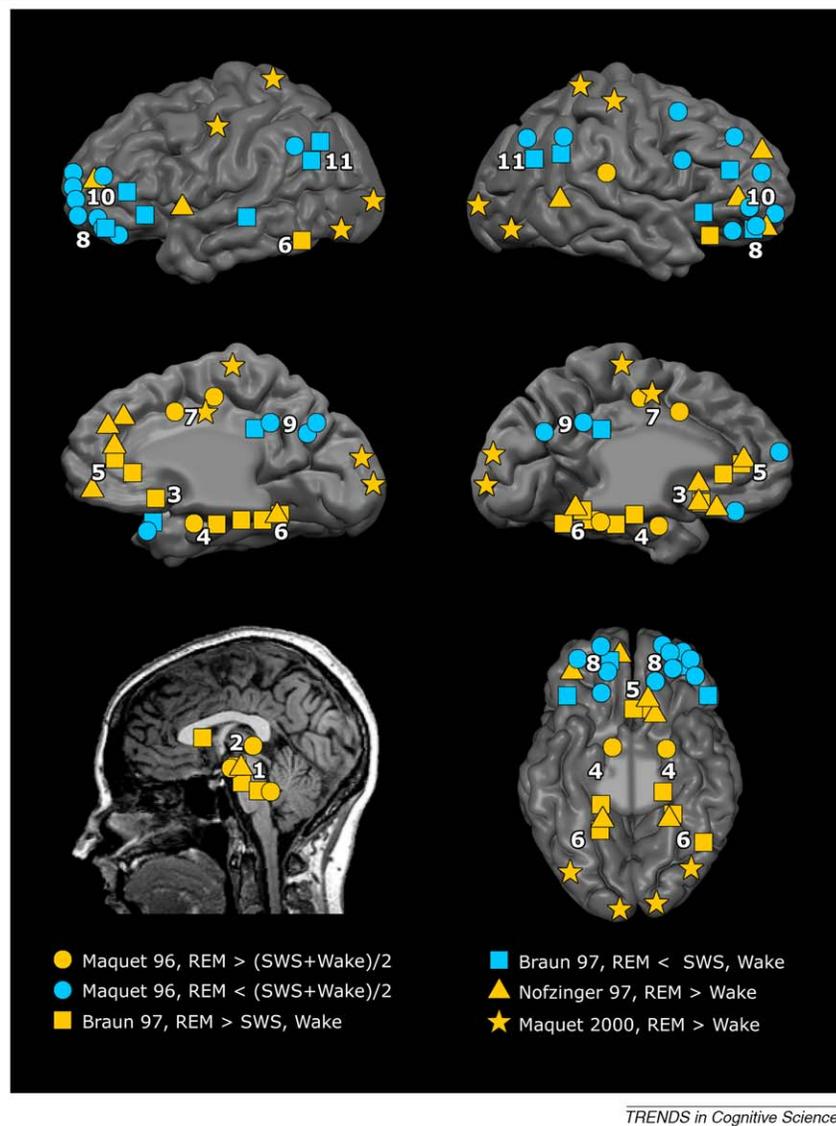
Despite these similarities, what makes dream consciousness so fascinating are the ways in which it differs from waking experience. Some of these phenomenological differences are accompanied by consistent neurophysiological differences.

*Reduced voluntary control and volition*

One is generally surprised on awakening from a dream (‘it was only a dream’) mainly because one did not consciously will that one would dream it. In fact, during dreaming, there is a prominent reduction of voluntary control of action and thought. One cannot pursue goals, and one has no control over the content of the dream. The fact that one is so surprised, excited and even skeptical about lucid dreaming (possibly a way to control some dreams [25]) illustrates how dreams normally lack voluntary control [9]. Interestingly, recent evidence points to the role of the right inferior parietal cortex (Brodmann’s Area 40) in waking volition [26,27], an area that is deactivated during REM sleep [15,16] (Figure 1).

*Reduced self-awareness and altered reflective thought*

Dreaming consciousness consists of a single ‘track’: one is not contextually aware of where one is (in bed) or of what one is doing (sleeping and dreaming). There is a strong tendency for a distinct narrative of thoughts and images to persist without disruption (‘single-mindedness’ [28]). Indeed, reports of mental activity in REM sleep are longer than reports obtained from awake subjects [28]. Dreaming



**Figure 1.** Functional neuroanatomy of human REM sleep: a meta-analysis of PET results. Meta-analysis of relative increases and decreases in neuronal activity during REM sleep as seen with PET imaging using  $H_2^{15}O$  measurements of regional cerebral blood flow (rCBF) [15,16,19] or [ $^{18}F$ ]-flurodeoxyglucose measurements of glucose metabolism [17]. Top row: cortical surface, lateral view. Middle row: cortical surface, medial view. Bottom row: subcortical foci (left) and ventral view of cortical surface (right). Analysis is based on published Talairach coordinates of foci whose activity was significant at  $p < 0.001$  corrected (Z-score  $> 3.09$ ). Circles, squares, triangles and stars denote activity foci as reported in Refs [15–17,19], respectively. Each symbol marks the center-of-mass of a region regardless of its spatial extent. Yellow symbols denote increased regional activity in the (1) mesopontine tegmentum and midbrain nuclei, (2) thalamus, (3) basal forebrain and diencephalic structures, (4) limbic MTL structures including amygdala and hippocampus, (5) medial prefrontal cortex, (6) occipito-temporal visual cortex, and (7) anterior cingulate cortex. Cyan symbols denote decreased activity in the (8) orbitofrontal cortex, (9) posterior cingulate and precuneus, (10) dorsolateral prefrontal cortex, and (11) inferior parietal cortex.

is typically delusional because events and characters are taken for real. Reflective thought is altered in that holding contradictory beliefs is common, and a dreamer easily accepts impossible events, such as flying, inconsistent scene switches, sudden transformations and impossible objects [29], such as a pink elephant. There is often uncertainty about space, time and personal identities [30]. For example, a character might have the name, clothes and hairstyle of a male friend, but have the face of the dreamer's mother. Reduced self-monitoring in dreams might be related to the deactivation of brain regions, such as posterior cingulate cortex, inferior parietal cortex, orbitofrontal cortex and dorsolateral prefrontal cortex [15,16] (Figure 1). Indeed, deactivation of prefrontal cortex has been shown to accompany reduced self-awareness during

highly engaging sensory perception in wakefulness [31]. However, some dreams might have conserved reflective thought processes, such as thoughtful puzzlement about impossible events [32], contemplating alternatives in decision-making [32], reflecting during social interactions [32] and 'theory of mind' [33], demonstrating that individual dreams can differ from each other substantially.

#### Emotionality

Some dreams are characterized by a high degree of emotional involvement, including joy, surprise, anger, fear and anxiety [34–36]. Interestingly, sadness, guilt and depressed affect are rare [11], possibly owing to reduced self-reflection. Some claim that fear and anxiety are enhanced in dreams to a degree that is rare in waking life

### Box 2. The development of dreams in children

When do children start dreaming, and what kind of dreams do they have? Given that children often show signs of emotion in sleep, many assume that they dream a great deal. However, a series of studies by David Foulkes showed that children under the age of 7 reported dreaming only 20% of the time when awakened from REM sleep, compared with 80–90% in adults [21].

Preschoolers' dreams are often static and plain, such as seeing an animal or thinking about eating. There are no characters that move, no social interactions, little feeling, and they do not include the dreamer as an active character. There are also no autobiographic, episodic memories, perhaps because children have trouble with conscious episodic recollection in general, as suggested by the phenomenon of infantile amnesia. Preschoolers do not report fear in dreams, and there are few aggressions, misfortunes and negative emotions. Children who have night terrors, in which they awaken early during the night from SWS and display intense fear and agitation, are probably terrorized by disorientation owing to incomplete awakening rather than by a dream [115]. Thus, although children of age 2–5 years can see and speak of everyday people, objects and events, they apparently cannot dream of them.

Between the ages of 5–7 years, dream reports become longer, although they are still infrequent. Dreams might contain sequences of events in which characters move about and interact, but narratives are not well developed. At around 7 years of age, dream reports become longer and more frequent, contain thoughts and feelings, the child's self becomes an actual participant in the dream, and dreams begin to acquire a narrative structure and to reflect autobiographic, episodic memories.

It could be argued that perhaps all children dream, but some do not yet realize that they are dreaming, do not remember their dreams, or cannot report them because of poor verbal skills. Contrary to these intuitive suggestions, dream recall was found to correlate best with abilities of mental imagery rather than with language proficiency. Mental imagery in children is assessed by the Block Design Test of the Wechsler intelligence test battery [116]. In this task, children look at models or pictures of red and white patterns, and then recreate those patterns with blocks. Crucially, scores on this test are the one

parameter that correlates best with dream report in children. Put simply, it is children with the most developed mental imagery and visuo-spatial skills (rather than verbal or memory capabilities) that report the most dreams, suggesting a real difference in dream experience. Visuo-spatial skills are known to depend on the parietal lobes, which are not fully myelinated until 7 years of age. Thus, linking visuo-spatial cognitive development with brain maturation studies [117] is an important field of further research.

The static nature of preschoolers' dreams is also in accord with the notion that preoperational children can not imagine continuous visual transformations [118]. In the 'mental rotation' test [119], a subject is asked to determine whether two figures are the same or different. In adults, reaction times (which are used as the score) increase linearly with the degree of rotation, but children do not show this relationship and do not seem to be mentally imagining movement using visuo-spatial imagery. This is consistent with their dream reports lacking movement [21].

Along the same lines, people who are blinded after the age of 5–7 years appear to have visual imagination and dream with visual imagery throughout life, whereas becoming blind at an earlier age leads to absence of visualization in both waking and dreaming [120,121] (dreaming in blind individuals is, however, a subject of debate [122,123]). Overall, dreaming appears to be a gradual cognitive development that is tightly linked with the development of visual imagination.

The slow development of full-fledged dreams and their intimate relation with imagination cast doubts on whether animals can dream as humans do. It is likely that animals can also be conscious during sleep. For instance, lesions in parts of the brainstem that control movements cause cats to seemingly act out their dreams [124], similar to humans with REM sleep behavior disorder [112]. However, although a cat might experience images and emotions in sleep, it is less likely that these experiences are tied together by a narrative as is the case in the typical dreams of humans [125]. Altogether, the kind of dreaming consciousness that an animal has might reflect the extent to which it is conscious in general, and both waking and dreaming consciousness are best viewed as graded phenomena [79].

[37], in line with Freud's suggestion that dream narratives originate in perceived threats or conflicts [5]. Whether this interpretation has merits, REM sleep is in fact associated with a marked activation of limbic and paralimbic struc-

tures, such as the amygdala, the anterior cingulate cortex and the insula [15,17,19] (Figure 1). However, emotions are feeble in other dreams, and are absent altogether in 25–30% of REM sleep reports [34–36], including in situations

### Box 3. Lesion studies of dreaming

The primary source on neuropsychology of dreaming is a study by Solms [22], who examined 361 neurological patients and asked them in detail about their dreaming. Overall, lesion studies indicate that dreaming depends on specific forebrain regions rather than on the brainstem REM sleep generator [22,126,127]. In most cases, global cessation of dreaming follows damage in or near the temporo-parieto-occipital junction (around Brodmann's Area 40), more often unilaterally than bilaterally [23,126]. This region supports various cognitive processes that are essential for mental imagery [128]. Accordingly, patients with such damage typically show a parallel decline in waking visuo-spatial abilities [108]. These results suggest that mental imagery is the cognitive ability most related to dreaming (although a link between loss of dreaming and aphasia has also been suggested [129]).

Less frequently, global cessation of dreaming follows bilateral lesions of white matter tracts surrounding the frontal horns of the lateral ventricles, underlying ventromedial prefrontal cortex [22]. Many of these nerve fibers originate or terminate in limbic areas, in line with increased limbic activity in REM sleep, as revealed by functional imaging [15–18]. The ventromedial white matter contains dopaminergic projections to the frontal lobe, which were severed in prefrontal leucotomy, once performed on many schizophrenic patients [53]. Most leucotomized patients (70–90%) com-

plained of global cessation of dreaming as well as of lack of initiative, curiosity and fantasy in waking life [23]. Given that dopamine can instigate goal-seeking behavior, these data have been interpreted as supporting the classical psychodynamic view of dreams as fulfillment of unconscious wishes related to egoistic impulses [130].

Apart from global cessation of dreaming, more restricted lesions produce the cessation of visual dreaming [22,108], or the disruption of particular visual dimensions in dreams. For example, lesions in specific regions that underlie visual perception of color or motion are associated with corresponding deficits in dreaming [23,108]. In general, it appears that lesions leading to impairments in waking have parallel deficits in dreaming.

Some lesions, especially those in medial prefrontal cortex, the anterior cingulate cortex and the basal forebrain, are associated with increased frequency and vividness of dreams and their intrusion into waking life [22]. Importantly, many brain-damaged patients report no changes in dreaming, indicating that the neural network supporting dreaming has considerable specificity. For example, lesions of dorsolateral prefrontal cortex, sensorimotor cortex and V1 do not appear to affect dreaming [22]. The fact that patients with V1 lesions report vivid dreaming argues against the notion that reentry to early retinotopic cortex is a necessary condition for visual awareness [131].

where emotions would probably be present in waking [34], once again highlighting the variability in dream phenomenology.

#### *Altered mnemonic processes*

Memory is altered for the dream and within the dream. Unless the dreamer wakes up, most dreams are lost forever. Upon awakening, memory for the dream often vanishes rapidly unless written down or recorded, even for intense emotional dreams. It is not clear why this is the case given that, from a neuroimaging perspective, limbic circuits in the medial temporal lobe that are implicated in memory processes, are highly active during REM sleep [15–18] (Figure 1). Perhaps the hypoactivity of the prefrontal cortex, also implicated in mnemonic processes, has an important role in dream amnesia. Contemporary theories of dreaming (Table 1) offer different accounts of dream amnesia. For example, according to psychodynamic models, dream amnesia is due to processes of active repression [5]. According to Hobson's Activation-Input-Mode [AIM] model, dream amnesia is related to a state-change involving inactivity of monoaminergic systems ('aminergic de-modulation') and deactivation of dorsolateral prefrontal cortex [11]. The neurocognitive model claims that dreams are usually forgotten because they are internal narratives; unless internal experiences are tied to external cues, such as times and places, they are bound to be forgotten [13].

Episodic memory is also impaired within the dream. Indeed, a dream is not like an episode of life being 'replayed'. In one example in which subjects had intensively played the computer game Tetris, there was no episodic memory in subsequent dreams that subjects had indeed played Tetris. In fact, dreams of healthy subjects were indistinguishable from those of profoundly amnesic subjects, who could not remember having played Tetris at all. By contrast, both normal and amnesic subjects often reported perceptual fragments, such as falling blocks on a computer screen, at sleep onset [38]. Whereas 'residues' from waking experience are incorporated in ~50% of dreams [39–41], they do so in new and unrelated contexts, and verified memories for episodes of recent life are only found in ~1.5% of dreams [42]. Such residual recollections have been interpreted by some to suggest that dreaming has an active role in forgetting [5,43]. Finally, many have the impression that the network of associations stored in one's memory might become looser than in wake [44,45], perhaps favoring creativity, divergent thinking and problem resolution [4,46].

In summary, dream consciousness is similar to waking consciousness, although there are several intriguing differences. These include reduced attention and voluntary control, lack in self-awareness, altered reflective thought, occasional hyperemotionality and impaired memory. Traditionally, dream phenomenology has often been compared to madness or psychosis [3,11,47], but in fact the hallucinations, disorientation and subsequent amnesia of some bizarre dreams might be more akin to the acute confusional state (also known as delirium) that occurs after withdrawal from alcohol and drugs [48]. However, most dreams are less bizarre, perhaps more similar to mind wandering or stimulus-independent

thoughts [14,49,50]. Waking thoughts jump around and drift into bizarre daydreaming, rumination and worrying far more than stereotypes of rational linear thinking suggest [51]. Importantly, individual dreams are variable in their phenomenology, and only some conform to the typical monolithic template that is often portrayed. Thus, just like diverse waking experiences, 'Not all dreams are created equal', and future studies should consider different kinds of dreams and their neural correlates separately.

What mechanisms are responsible for regional differences in brain activity between waking and REM sleep, and thus presumably for some of the cognitive differences between waking and dreaming? Single-unit physiology indicates that generally, cortical activity in REM sleep reaches similar levels as found in active wake (Figure 2), but variability between brain areas remains poorly explored. Regional differences probably stem from changes in the activity of neuromodulatory systems (Figure 2). During REM sleep, acetylcholine is alone in maintaining brain activation, whereas monoaminergic systems are silent, an observation that could explain many features of dreams [11]. For example, consistent with imaging results, cholinergic innervation is stronger in limbic and paralimbic areas than in dorsolateral prefrontal cortex [52], which could explain why limbic regions are active in REM sleep whereas the dorsolateral prefrontal cortex is deactivated (Figure 1). Dopaminergic modulation might also have a role [23], because dreaming is decreased by prefrontal leucotomies that cut dopaminergic fibers [53] and is increased by dopaminergic agonists [23] (Table 1; Figure 2).

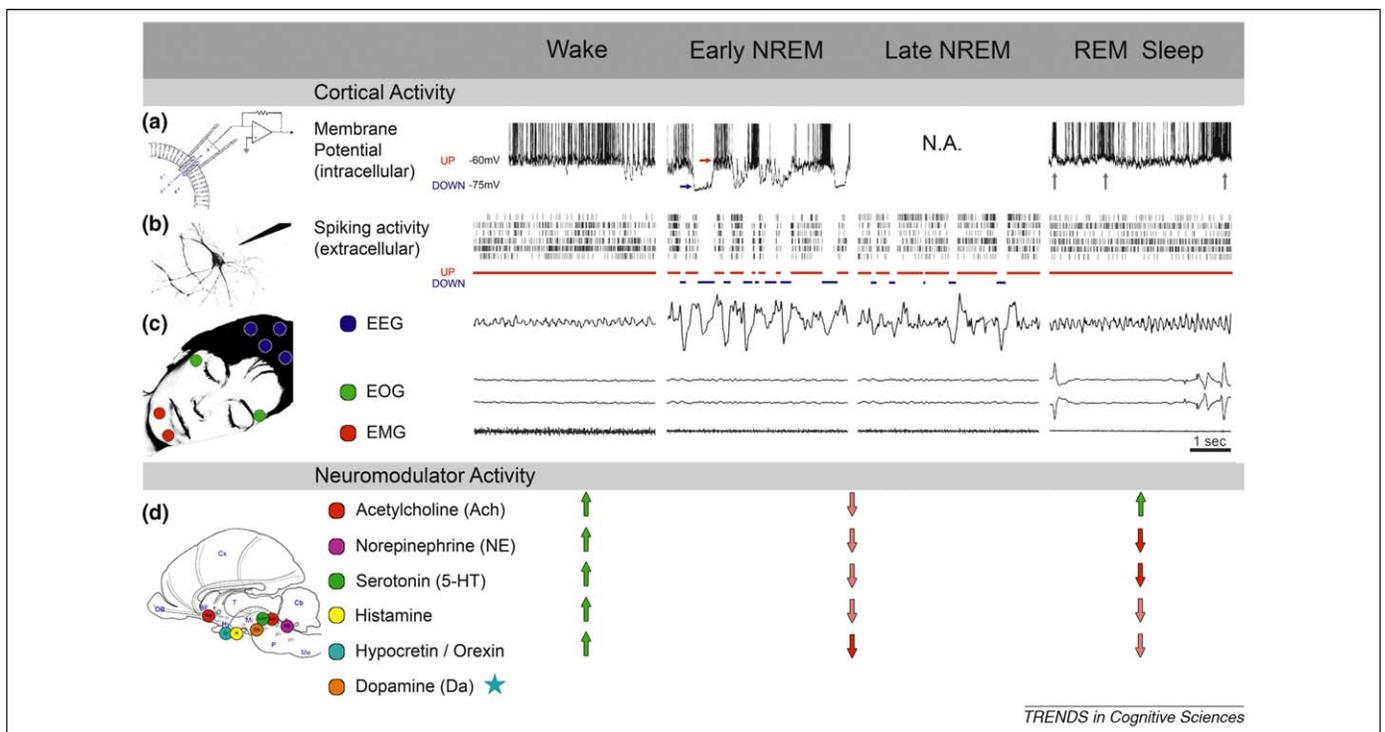
On the whole, relating typical dreams to the neurophysiology of REM sleep has proven to be a useful starting point for revealing the neural basis of dreaming. However, dream consciousness can not be reduced to brain activity in REM sleep. Indeed, some fundamental questions concerning the relationship between the brain and dreaming linger on. We discuss three in turn: (i) what determines the level of consciousness during sleep; (ii) why the dreamer is disconnected from the environment; and (iii) whether dreams are more akin to perception or to imagination.

#### **What determines the level of consciousness during sleep?**

In principle, studying mental experiences during sleep offers a unique opportunity to explain how changes in brain activity relate to changes in consciousness [3,54]. In fact, if it were not for sleep, when consciousness fades in and out on a regular basis, it might be hard to imagine that consciousness is not a given, but depends on the way in which the brain is functioning. Traditionally, studies have focused on differences among reports obtained after awakenings from different sleep stages or at different times of night. When REM sleep was initially distinguished from NREM sleep [55], it was reported that 74–80% of REM sleep awakenings produced vivid dream recall, compared to only 7–9% of awakenings from NREM sleep [56,57]. It was only natural to conclude that, compared with NREM sleep, the distinct physiology of REM sleep, especially its fast, low-voltage EEG resembling that of wakefulness, was

Table 1. Contemporary theories of dreaming

Psychodynamic (Freud, Solms)	Activation-input-modulation (AIM) model (Hobson)	Neurocognitive (Foulkes, Domhoff)
<b>General</b> Dreams represent fulfillment of unconscious wishes related to egoistic (often infantile sexual) impulses [5]. Latent unconscious content is disguised via censorship creating the bizarre manifest dream content [5]. More recently, the drive for dreaming has been associated with dopaminergic systems and 'appetitive interests' [130]	The conscious state is determined by three factors: (i) Activation: total and regional brain activity levels; (ii) Input: activation generated internally or externally; and (iii) Modulation: the ratio of aminergic to cholinergic neuromodulators; REM sleep and dreaming are characterized by high levels of activation, internal input and cholinergic modulation [11]	Dreaming is what occurs when the mature brain is adequately activated, disconnected from external stimuli and without self-reflection. Once instigated, dreaming actively draws on memory schemas, general knowledge and episodic information to produce simulations of the world [13,14]
<b>Dream amnesia</b> Given that unconscious wishes are noxious to our consciousness, they are actively repressed via censorship processes [5]. Dream amnesia is anything but arbitrary: 'our memory reproduces the dream not only incompletely but also untruthfully, in a falsifying manner' [5]	Dream amnesia largely stems from a state change. Aminergic de-modulation and deactivation of dorsolateral prefrontal cortex in REM sleep create a brain state that is not favorable for subsequent memory [11]. This also explains why humans forget moments of brief awakenings during sleep	Dream amnesia is primarily related to a cognitive state and lack of context. To remember, one needs an external narrative to which internal events can be tied [14,21]. Dream amnesia cannot be explained by a state change because dreaming can occur at any state (NREM sleep and wake)
<b>Signal propagation in dreaming</b> 'Top-down': dreams originate from psychic motives that are later instantiated as sensory percepts: 'a thought... is objectified in the dream, and represented as a scene' [5]	'Bottom-up': dreams originate from activation of sensory cortex by the brainstem (e.g. PGO waves), later to be interpreted and synthesized by mnemonic and high-order modules [11,47]	'Top-down': dreams originate in abstract knowledge and figurative thought, which are processed back into 'imaginal copies' of perceptual phenomena [14]
<b>Is REM sleep a good model for dreaming?</b> No. REM sleep and dreaming can occur one without the other [23,152]; e.g. in neurological patients. Dream-like experiences are related to forebrain mechanisms rather than to REM sleep generators in brainstem [22,23]	Yes. Because REM sleep provides the most favorable brain conditions for dreaming, researchers can focus on its neurophysiology in attempts to model the neuronal basis of dreaming [4,47]	No. Dream-like experiences can also occur in NREM sleep, sleep onset and wakefulness [13,153]. Studies of children show that REM sleep is an important condition for dreaming but not sufficient [13,21]
<b>Is dreaming largely similar to waking consciousness?</b> No. The apparent (manifest) aspect of dreams is bizarre and includes nonsensical changes in time and place, as well as incongruities of plot, character and action [5]. This is because the true (latent) dream content is disguised by the censor [5]. Dreaming might be closely akin to mental illness [5,154]	No. Dreaming is altogether comparable to delirium (acute confusional state) that can occur upon alcohol withdrawal [3]; REM sleep shares its physiological substrate with psychopathological conditions, such as schizophrenia (limbic hyper-activation and frontal hypo-activation) [155,156]	Yes. Dreams are 'a remarkably faithful replica of waking life' [157]. They are largely coherent and internally plausible narrative sequences rather than the stereotypical illogical sequences of bizarre images. Content analysis indicates a strong continuity between dream content and waking life [13]. Evidence linking dreams to psychosis is limited [153]: REM sleep deprivation does not alter schizophrenic pathology and aminergic agonists suppress REM sleep with no psychopathological effects
<b>Neurochemistry of dreaming</b> Dreaming is driven by the 'wanting' dopaminergic system: evidence from prefrontal leucotomies and effects of L-DOPA on dreaming [23,154]	Primarily, a cholinergic role for REM sleep and dreaming [4,11]. Administration of cholinergic agonists (e.g. pilocarpine) can induce an artificial REM sleep period associated with dream reports [158]	Dreaming is unlikely to be driven by a specific chemical or brain region. It is probably related to a complex neurochemical mixture where serotonin, norepinephrine and histamine are absent whereas acetylcholine and dopamine are both present [13,153]
<b>The function of dreaming</b> According to Freud, dreams preserve sleep in the face of unconscious needs for excitement [5]. More recently (Solms): 'the biological function of dreaming remains unknown' [23]	Dreams might serve a creative function by providing a virtual reality model (protoconsciousness). The brain is preparing itself for integrative functions, including learning and secondary consciousness [4]	Dreams probably have no function, but they do have coherence and meaning, which is often conflated with function [13]: 'dreaming is a spandrel of the mind, a by-product of the evolution of sleep and consciousness.' [13]
<b>What is the psychological meaning of dreams?</b> This theory emphasizes dream content: individual dreams carry meaningful information about the dreamer. This theory lacks in power with regards to explaining dreams shared by all people [5] (e.g. flying or teeth falling out)	Dreaming is an attempt to best interpret activating signals in a coherent manner, and contents of individual dreams are nearly random. Nevertheless, the process of interpretation might carry some psychological meaning [11]	This theory emphasizes dream form: dreams are based on stored memory representations and therefore reflect individual ways of abstracting knowledge, but specific dreams are not traceable back to particular episodes in one's life [14]
<b>Are dreams directly related to previous experience?</b> Yes. Dream content is related to daytime experience ('Day's residue') that triggers the emergence of related memories. 'All the material making up the content of a dream is in some way derived from experience' [5]	No. Dream content is largely unrelated to the experiences from the preceding day [45] and, in general, does not accurately represent episodic memories that are available during wakefulness [42,45]	No. Familiar settings and people are sometimes incorporated into dreams but dreams are not a recollection of everyday life [14]



**Figure 2.** Neurophysiology of wake and sleep states. A comparison of cortical activity (a–c) and neuromodulator activity (d) in wake, early NREM (when sleep pressure is high and dream reports are rare), late NREM (when sleep pressure dissipates, and dream reports are more frequent), and REM sleep (when dreams are most common). (a) Intracellular studies. The membrane potential of cortical neurons in both wake and REM sleep is depolarized and fluctuates around  $-63$  mV and  $-61$  mV, respectively [76]. In REM sleep, whenever phasic events such as rapid eye movements and PGO waves occur (gray arrows, events not shown), neurons increase their firing rates to levels that surpass those found in wake [76,144]. In early NREM sleep, neurons alternate between two distinct states, each lasting tens to hundreds of milliseconds: UP states (red arrow) are associated with depolarization and increased firing, whereas in DOWN states (blue arrow) the membrane potential is hyperpolarized around  $-75$  mV, and neuronal firing fades [77,145]. Intracellular studies focusing specifically on late NREM sleep are not available (N.A.). (b) Extracellular studies. Spiking of individual neurons in wake and REM sleep can be viewed as a continuous UP state [77] (red bars). In early NREM sleep, UP states are short and synchronous across neuronal populations, and are frequently interrupted by long DOWN states (blue bars). In late NREM sleep, UP states are longer and less synchronized [78]. (c) Polysomnography. Waking is characterized by low-amplitude, high-frequency EEG activity ( $>7$  Hz), occasional saccadic eye movements, and elevated muscle tone. In early NREM sleep, high-amplitude slow waves ( $<4$  Hz) dominate the EEG. Neuronal UP (red) and DOWN (blue) states correspond to positive and negative peaks in the surface EEG, respectively [78]. Eye movements are largely absent and muscle tone is decreased. In late NREM sleep, slow waves are less frequent, whereas spindles (related to UP states and surface EEG positivity) become more common. Eye movements and muscle tone are largely similar to early NREM sleep [150]. In REM sleep, theta activity (4–7 Hz) prevails, rapid eye movements occur and muscle tone is reduced. (d) Neuromodulator activity. Subcortical cholinergic modulation is active in wake and REM sleep (green arrows) and leads to sustained depolarization in cortical neurons and EEG activation [76]. Wake is further maintained by activity of monoamines, histamine and hypocretin/orexin (green arrows). In sleep, monoaminergic systems, including norepinephrine and serotonin, reduce their activity (pink arrows), and are silent in REM sleep (red arrows). Whereas dopamine levels do not change dramatically across the sleep–wake cycle (asterisks), phasic events and regional profiles can differ [151]. Data are pooled across different species for illustration purposes. Intracellular cat data adapted, with permission, from Ref. [76]; extracellular and EEG rat data obtained from V. Vyazovskiy (pers. commun.).

the reason why humans are conscious and dream in REM sleep, and not in NREM sleep [29]. Indeed, for some time, reports of mental activity upon awakenings from NREM sleep were assumed to be recalls of earlier REM sleep dreams, or considered analogous to sleep talking [3], or treated as confabulations made up by subjects confused upon awakening [9] (Box 1). However, when changing the question from ‘tell me if you had a dream’ to ‘tell me anything that was going through your mind just before you woke up,’ reports of conscious experiences in NREM sleep ranged between 23% and 74% [9]. Subsequent studies unequivocally demonstrated that NREM sleep awakenings yielded reports of mental activity [58,59].

Specifically, reports from sleep stage N1 are frequent (80–90% of the time), although they are short [60]. Usually, people report vivid hallucinatory experiences, so-called ‘hypnagogic hallucinations’. In contrast to typical dreams, hypnagogic hallucinations are often static, similar to single snapshots [11,47], and usually do not include a self character [14]. Some activities performed before sleep (e.g. video games) might influence the content of hypnagogic

dreams [38,61]. Awakenings from NREM sleep stages N2 and N3 yield reports of some experienced content 50–70% of the time [59], although there is variability throughout the night and between subjects. Early during the night, when stage N3 is prevalent and many large slow waves dominate the EEG, awakenings yield few reports [62]. Moreover, these reports are often qualitatively different from typical REM sleep reports, being usually short, thought-like, less vivid, less visual and more conceptual, less motorically animated, under greater volitional control, more plausible, more concerned with current issues, less emotional and less pleasant [9,11,63]. Also, the average length of REM sleep reports increases with the duration of the REM sleep episode, whereas this is not true for NREM sleep reports [62]. However, late during the night, NREM sleep reports are longer and more hallucinatory. Indeed, 10–30% of all NREM sleep reports are indistinguishable by any criteria from those obtained from REM sleep [64,65]. Given that NREM sleep accounts for 75% of total sleep time, this means that full-fledged NREM sleep dreams account for a significant portion of all typical dreams.

Thus, the initial equation of a physiological state (REM sleep) with a mental state (dreaming) was incorrect, or at best, an oversimplification. Moreover, neuropsychological evidence indicates that dreaming and REM sleep can be dissociated: forebrain lesions can abolish dreaming and spare REM sleep, whereas brainstem lesions can almost eliminate overt features of REM sleep without abolishing dreams [23] (Box 3). But if dream reports can be elicited during any stage of sleep [11,47,59,66,67] and, conversely, some awakenings can yield no report, no matter in which sleep stage they were obtained [59], where do researchers now stand with respect to the relationship between brain activity and consciousness during sleep?

The one thing that is clear is that researchers need to move beyond the REM–NREM sleep dichotomy and beyond traditional sleep staging. Although staging is useful, it treats brain activity as uniform in space (only a few electrodes are used) and in time (for 30-s epochs). Inevitably, subtler features of brain activity, which could well influence the presence, degree and reportability of consciousness, are missed both in space and time.

In the spatial domain, increasing evidence suggests that different brain regions are in different states at the same time. For example, preliminary findings suggest that during sleepwalking, thalamocingulate pathways are as active as when in wake, whereas the rest of the cerebral cortex is in NREM sleep [68]. A related notion of dissociated states is derived from the study of parasomnias, where wake-like behaviors occur during sleep [69]. For instance, the study of REM sleep behavior disorder suggests that, contrary to common assumptions, wakefulness, REM sleep and NREM sleep are not mutually exclusive states [69]. In the current context, it has been suggested that dreaming in NREM sleep is related to ‘covert’ REM processes that occur locally [59]. Thus, refined spatial analysis using fMRI or high-density EEG (hd-EEG) could identify regionally specific predictors of dreaming, and indicate, in real time, whether dream reports will be obtained.

In the temporal domain, some attempts have been made to relate transient, phasic activities [70] to dreaming. For example, various studies have tried to link dream recall to eye movements [71,72], PGO waves [73] and EEG power bouts in specific frequency bands [74] but with limited success, and little has been done for NREM sleep [11,75]. It is now known that slow waves in NREM sleep reflect a slow oscillation of cortical neurons between UP and DOWN states (Figure 2) [76,77]. Perhaps long UP states are necessary for dreaming to occur. This is normally the case in REM sleep because slow waves are absent. As for NREM sleep, we believe that higher occurrence of recalls, especially of typical dreams in the morning hours, would reflect longer UP periods upon dissipation of sleep pressure (Figure 2) [78]. In general, focusing on (rather than avoiding) ‘gray zones’, where it is more difficult to predict whether a dream report will be obtained, for example in early REM sleep or late NREM sleep, might be a promising strategy for identifying psychophysiological correlates that go beyond traditional staging.

Finally, theoretical considerations suggest that the level of consciousness depends on the ability of the brain to

integrate information [79]. Indeed, during wakefulness, external perturbations such as transcranial magnetic stimulation (TMS) pulses cause changing patterns of activation across distant interconnected brain regions [10]. In REM sleep, evoked activity propagates much like it does in wakefulness [80]. By contrast, in deep SWS early during the night, when consciousness is most likely to fade, the response evoked by TMS remains either local (loss of integration), or spreads nonspecifically (loss of information). Apparently, the capacity of the brain for information integration is reduced whenever neurons become bistable between UP and DOWN states. Intriguingly, the response of the brain to a TMS pulse could offer a more sensitive measure of the inner state than does spontaneous EEG. For example, such perturbations can uncover inherent bistability in short stretches of NREM sleep even when the EEG shows a wake-like low-voltage pattern [81].

### Why is the dreamer disconnected from the environment?

The most obvious difference between dreaming and waking consciousness is the profound disconnection of the dreamer from their current environment. Such disconnection is a key feature of sleep: by definition, a sleeping person shows no meaningful responses to external stimuli, unless they are strong enough to cause an awakening. This feature is known as ‘high arousal threshold’, and it persists in REM sleep despite its wake-like low-voltage EEG [82]. Moreover, stimuli fail not only to elicit a behavioral response, but also to be incorporated in the content of the dream [8,83–85] (although some stimuli, such as a spray of water, pressure on the limbs and meaningful words have more of a chance of incorporation [83,84]). This striking disconnection occurs even when subjects sleep with their eyes taped open and objects are illuminated in front of them [8]. Surely just before awakening, stimuli such as the sound of an alarm clock can enter one’s dreams, but when sleep is preserved, such relations are usually surprisingly weak and dream consciousness is disconnected from the external environment.

The disconnection of the dreamer poses an intriguing paradox, especially if one considers that dreams involve vivid sensory experiences, and that they can occur upon a state of strong cortical activation. Several possibilities come to mind. For example, it has been suggested that, during sleep, a thalamic ‘gate’ closes and sensory inputs do not reach the cortex effectively [86]. However, evoked responses in primary sensory cortices are largely preserved during REM sleep [87,88]. Also, olfactory stimuli are not directly incorporated in dreams [89], although they are not routed through the thalamus (their emotional valence, however, might affect dreams). A related notion is that of a cortical ‘gate’ leading to diminished intercortical propagation [90], as seems to be the case in the dissociation of primary visual cortex (V1) from high-order visual cortex in REM sleep [18]. It would be interesting to establish whether direct activation of cortical areas can overcome the disconnection from the environment. For example, can TMS over V1 or area MT bypass thalamic or cortical ‘gates’ and produce sensations of phosphenes or movement in dream consciousness?

An intriguing possibility concerns the putative antagonism between externally oriented cortical networks and internally oriented, default-mode networks [91,92]. Perhaps in dreams, intrinsic activity dominates, as it does during stimulus-independent thoughts in wake [50]. This might occur at the expense of the processing of external stimuli, leading to disconnection from the environment. Indeed, both PET and magnetoencephalography (MEG) suggest that medial prefrontal cortex, a part of the default network, is highly active in REM sleep [16,17,93] as it is during wakeful rest (Figure 1). Conversely, other components of the default network, including the posterior cingulate and inferior parietal cortices, are deactivated in REM sleep [15,16], as in highly engaging waking tasks (Figure 1). The exact cognitive task associated with the default-mode network is still not well understood [94] and it might be driven primarily by self-related introspective processes rather than by general mind wandering [31,95,96]. Indeed, because most nodes of this network are deactivated in REM dreaming and mental imagery [97], cognitive states that are oriented internally but away from the self do not seem sufficient to elicit activity in this network.

Another possibility is that dreams are analogous to altered states of consciousness in which attention is profoundly altered, as might be the case in extreme absorption, hypnosis, neglect [98] and Balint's syndrome, when visual experience can persist for single but unlocalizable objects (simultanagnosia) [99,100]. The reticular thalamic nucleus has been implicated in redirecting attention across modalities [101,102] and its activity in sleep might underlie some aspects of disconnection. It would also be interesting to determine whether neuronal correlates of

momentary lapses of attention [103] occur regularly while dreaming.

Finally, as we have discussed, the neuromodulatory milieu changes drastically in sleep (Figure 2). Specifically, the levels of norepinephrine, serotonin, histamine and hypocretin are reduced in REM sleep compared to wake, so the presence of one or more of these neuromodulators might be necessary for external stimuli to be incorporated into one's stream of consciousness. This search can be narrowed down by considering cataplexy, which affects people with narcolepsy [104]. Cataplexy is a transient episode of muscle tone loss in which humans report that awareness of external stimuli is preserved, and presumably animals are likewise aware of their environment during cataplectic attacks. Neuromodulatory activity in cataplectic dogs is similar to that in REM sleep, except that levels of histamine are high, much like during wakefulness [104]. It thus seems that levels of histamine are correlated with one's ability to incorporate sensory stimuli into conscious experience. It would be important to establish whether histamine is necessary for such incorporation, and how it might do so. For instance, could it be that, in wakefulness, histaminergic tone facilitates transmission of feed-forward sensory inputs in cortical layer 4, at the expense of backward signal propagation?

#### Are dreams more like perception or imagination?

Whether dreams are generated in a 'bottom-up' or a 'top-down' manner is a question that has been asked since at least Aristotle [105]. To put the question in a modern context, do dreams start from activity in low-level sensory areas, which is then interpreted and synthesized by higher-order areas, as is presumably the case in waking

### Box 4. Future directions

#### Signal propagation in dreams

During wakefulness, sensory responses precede responses in higher-order areas by  $>100$  ms [132,133]. Does neural activity during dreaming sleep show a similar feed-forward progression as in perception? Or does neural activity propagate backwards, from higher to lower areas, as it is thought to do during imagery? This issue, which is crucial to our understanding of dream generation, could be resolved by examining unit and field potential recordings from the same neuronal populations in wake and REM (or late NREM) sleep in both animals and humans [133]. One can also apply directional measures of signal propagation (e.g. Granger causality) to hd-EEG data, and check whether the main direction of signal flow inverts between wake and sleep. Finally, one could use TMS with concurrent hd-EEG during both wake and REM sleep, and examine whether there is a preferential direction of the response of the brain to perturbations depending on behavioral state [10].

#### Functional networks underlying dreaming

So far, most regional studies of brain activity during sleep have used PET. Although this enables quantification of cerebral blood flow and comparison across vigilance states, functional MRI (fMRI) offers superior spatial and temporal resolutions. Event-related fMRI has been already used to map brain activity associated with phasic events, such as slow waves [134] and eye movements [135,136]. Studies of functional and effective connectivity [137] might be especially well suited to map the functional networks underlying dreaming. Notably, perceptual awareness is associated with specific functional connectivity patterns within sensory modalities [138], between modalities [139] and with a striking segregation between

sensory systems and the default-mode/intrinsic system [31,92,103]. Are such connectivity patterns also a hallmark of activity in the dreaming brain? What regional brain activity underlies dreaming in NREM sleep? How do functional networks of mental imagery and dreaming compare in the same subjects? Finally, hd-EEG might be particularly suited for sleep imaging because it (i) enables relatively undisturbed sleep; (ii) upon source modeling, can provide a spatial resolution roughly comparable to PET; (iii) offers high temporal resolution suitable for evaluating signal propagation; and (iv) can be combined with TMS during sleep.

#### Initial steps towards studying dream content

Progress in signal decoding might ultimately enable researchers to investigate the neural correlates not only of dream form (what is common to all dreams) but also of dream content (what is specific to a particular dream). This can be done, for instance, by using classification techniques applied to fMRI or hd-EEG data [140]. At least initially, it might be worthwhile considering some coarse properties of individual dreams, such as the frequency of occurrence of faces or places in a dream report, the amount of movement, or the dominant affective valence. In principle, it should be possible to predict not only the likelihood of a report upon awakening, but also the likelihood of specific features based on preceding brain activity. An important step would be to identify the contents of internally generated mental imagery using the same approach [141]. Furthermore, some patients with epilepsy or post-traumatic stress disorder who experience recurring dream contents [142,143] could provide a unique opportunity to relate specific dream content to its neural basis.

perception? Or do they begin as wishes, abstract thoughts and memories deep in the brain, which are then enriched with perceptual and sensory aspects, as in imagination? Of course, it is possible that such a dichotomy is misguided, and dreams might be best conceptualized as global attractors that emerge simultaneously over many brain areas. However, as we shall show, the available data suggest that there is a privileged direction of dream generation.

During the 19th century, sensory experience was often regarded as the source of dreams, which were considered to be an attempt of the mind to interpret somatic nerve-stimuli (Online Supplementary Material Figure S1). A similar notion was later adopted by Henri Beaunis, and recently championed by Allan Hobson (Table 1) [4,11,47]. According to Hobson's AIM model, internally generated signals originating in the brainstem during REM sleep, such as PGO waves, excite the visual cortex and are later processed and synthesized by higher-order areas. High levels of acetylcholine in the absence of aminergic neuromodulation might enhance feed-forward transmission and suppress back-propagation [3,106]. By contrast, Freud and some of his followers asserted that dreams originate from psychic motives that are later instantiated as sensory percepts, similar to mental imagery [5].

Deciding between these alternative views will probably require experiments in which the direction of signal flow during dreaming sleep is evaluated and compared to that during waking perception and imagery [107] (Box 4). However, various lines of evidence suggest that dreaming is more closely related to imagination than it is to perception. From lesion studies (Box 3), it is known that dreaming requires an intact temporo-parieto-occipital junction [22,23] and that lesions in this region also affect mental imagery in wakefulness [108]. Cognitive studies indicate that the skill that maximally correlates with dream recall in adults is visuo-spatial imagery [109]. In children, dream recall develops hand-in-hand with visuo-spatial imagery (Box 2). In epileptic patients, direct electrical stimulation in high-order regions, such as the medial temporal lobe, rather than the visual cortex, can elicit 'dream-like' experiences [110], although such patients are simultaneously aware of their surroundings. Other evidence comes from lucid dreamers [25], who report that it is impossible to focus on fine-grain details of visual objects, as is the case in mental imagery [111]. Perhaps top-down connections lack the anatomical specificity to support detailed representations. The rare occurrences of smells or pain in dreams might also be related to the difficulty in imagining them vividly when awake. However, one important difference between dreaming and mental imagery is that while imagining, one is aware that the images are internally generated (preserved reflective thought).

If the flow of brain activity during dreaming were shown to be largely backwards, as one would expect in imagery, rather than forwards, as in perception, many of the seemingly bizarre properties of dreams, such as blended characters and scene switches, would be easier to explain, as they are standard features of one's imagination. Such a top-down mode might disrupt the encoding of new memories, and thus underlie dream amnesia. In addition, top-down mental imagery could obstruct the processing of

incoming stimuli and disconnect one from the environment. If this view is correct, waking consciousness is more like watching the news in real time, whereas dreaming is more like watching a movie created by an imaginative director [80]. As in some B-movies, the director is not particularly choosy and any actor, dress, means of transportation, or object that is readily available will do. Albert Einstein said that 'imagination points to all we might yet discover and create', and indeed, dreaming might turn out to be the purest form of imagination.

### Concluding remarks

In summary, dream consciousness is remarkably similar to waking consciousness, although there are several intriguing differences in volition, self-awareness and reflection, affect and memory, and there is considerable variability between individual dreams. The neurophysiology of REM sleep, and in particular recent insights into its regional activity patterns, offers a useful starting point for relating dream phenomenology to underlying brain activity. However, the initial equation of REM sleep with dreaming has been shown to be inaccurate. Thus, it is time that researchers moved beyond sleep stages when trying to link dream consciousness to neuronal events, and focused on more subtle features of brain activity in space and time.

One's disconnection from the external environment when dreaming poses a central unsolved paradox, the answer to which might be instrumental for understanding dreams. Converging evidence from multiple fields of study, including phenomenology, development, neuropsychology, functional imaging and neurophysiology, support the notion that dreaming might be closely related to imagination, where brain activity presumably flows in a 'top-down' manner. Viewing dreams as a powerful form of imagination can help explain many of their unique features, such as sudden transitions, uncertainty about people and places, poor subsequent recall and disconnection from the environment, and offers testable predictions for future studies.

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### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.tics.2009.12.001](https://doi.org/10.1016/j.tics.2009.12.001).

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