



REM sleep and dreaming: towards a theory of protoconsciousness

J. Allan Hobson

Abstract | Dreaming has fascinated and mystified humankind for ages: the bizarre and evanescent qualities of dreams have invited boundless speculation about their origin, meaning and purpose. For most of the twentieth century, scientific dream theories were mainly psychological. Since the discovery of rapid eye movement (REM) sleep, the neural underpinnings of dreaming have become increasingly well understood, and it is now possible to complement the details of these brain mechanisms with a theory of consciousness that is derived from the study of dreaming. The theory advanced here emphasizes data that suggest that REM sleep may constitute a protoconscious state, providing a virtual reality model of the world that is of functional use to the development and maintenance of waking consciousness.

Perception

Detailed visuomotor and other sense modality information that constitutes the representational structure of awareness. Such awareness must involve the interaction and integration of emotion.

Secondary consciousness

Subjective awareness including perception and emotion that is enriched by abstract analysis (thinking) and metacognitive components of consciousness (awareness of awareness).

Rapid eye movement (REM) sleep

Sleep with electroencephalographic evidence of brain activation (similar to that of waking) but with inhibition of muscle tone (as measured by electromyography) and involuntary saccadic eye movements (the REMs).

Division of Sleep Medicine,
Harvard Medical School,
Boston, Massachusetts,
02215, USA.

e-mail: allan_hobson@hms.harvard.edu

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Primary consciousness can be defined as simple awareness that includes perception and emotion. As such, it is ascribed to most mammals. By contrast, secondary consciousness depends on language and includes such features as self-reflective awareness, abstract thinking, volition and metacognition¹. In adult humans, dreams that occur during rapid eye movement (REM) sleep have features of primary consciousness but, as shown in FIG. 1 and [Supplementary information S1](#) (table), dreams do not strongly evince the characteristics of secondary consciousness.

In humans, consciousness varies dramatically in intensity and quality during the sleep–wake cycle. Whether we are awake (and alert with the full panoply of secondary aspects of consciousness), asleep (with greatly diminished awareness) or dreaming (with the internally generated perceptions and emotions of primary consciousness) depends on the three objectively identifiable states of the brain: waking, non-rapid eye movement (NREM) sleep and REM sleep (BOX 1). The strategies by which those states are investigated are outlined in [Supplementary information S2](#) (box).

Waking consciousness can be defined as the awareness of the external world, our bodies and our selves (including the awareness of our awareness) that humans experience when awake. When dreaming we are also consciously aware; we have perception and emotion, which are organized in a scenario-like structure, but we erroneously consider ourselves to be awake despite abundant cognitive evidence that this cannot be true. Another difference between waking and dreaming is the striking

multiplicity of conscious substates during waking and the contrasting single-mindedness of dreaming².

Waking consciousness is richer than dream consciousness in allowing the measurable distinction between task and default modes of the brain³ and the related difference between background and foreground processing⁴. Dream consciousness is richer than waking consciousness in its ability to create a remarkably reliable simulacrum of the world and the notable capacity to integrate highly disparate images and themes into a seamless scenario, as shown in FIG. 1.

Dreaming abounds in features of primary consciousness, especially perceptions and emotions, which are produced by the brain without external stimulation. But, compared with waking, dreaming is deficient in its failure to recognize its own true condition, its incoherence (or bizarreness), its severe limitation of thought and its impoverishment of memory (see [Supplementary information S1](#) (table), which illustrates the scientific utility of subjective experience). In consideration of these data, we might expect that some brain processes are enhanced during REM sleep (during which humans dream), others are suppressed and still others remain the same as they are during waking⁵. As will be discussed below, that is exactly what we find.

In this Review, I first describe the differences between primary and secondary consciousness in relation to waking and sleep. I then consider evolutionary and developmental aspects of REM sleep, the sleep stage that correlates highest with dreaming. This is followed by an overview of theories of the function of REM sleep,

including the new hypothesis that primary consciousness is an important building block on which secondary consciousness is constructed. Last, I describe the AIM

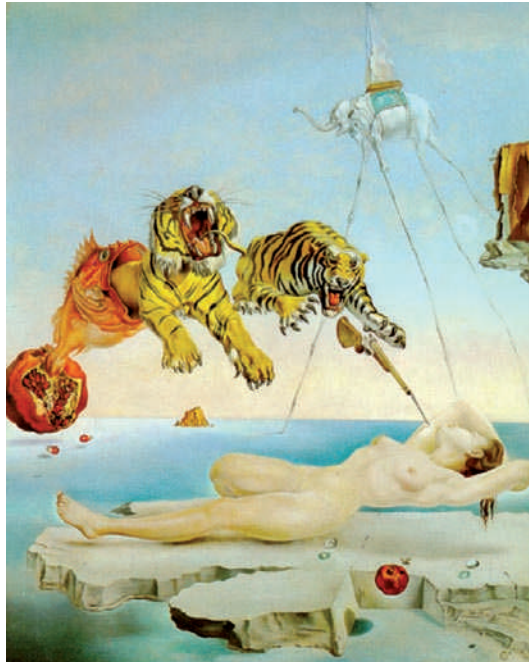


Figure 1 | Dream Caused by the Flight of a Bee around a Pomegranate a Second Before Awakening (Salvador Dalí). In this painting, Salvador Dalí depicts a loosely connected set of dream images in the space above the sleeping body of his wife, Gala. Dalí's surrealist vision of dreaming anticipates modern dream science findings in several ways. First and foremost is the representation of intense and vivid visual imagery, which arises within the head of the inert sleeper. Second is the implicit abrogation of perceptions of external stimuli by the dream hallucinations and the implied takeover of critical judgement that deludes the dreamer into believing that she is awake. Third is the loosely associated linkage of the bizarrely discordant images: an exploding pomegranate emits a fish that belches out a ferocious tiger which is in turn transformed into a bayonet pointed aggressively at Gala's head. An incongruously long-legged elephant roams behind this image sequence. Fourth is the emotional salience of the bizarre sequence, which helps to bind the images together in a coherent but probably fleetingly remembered narrative of Gala's experience. Given the intensity of dream experiences such as this, it is surprising how few are remembered. Gala may have remembered such a dream but many others were almost certainly lost to her after waking. It was Dalí's idea that this dream was caused by the sting of the bee shown buzzing behind Gala's left ear. Thus, Dalí himself was probably not aware that dreams with this intensity may occur with no external stimulation whatever. With the help of modern neuroscience, many of Gala's dream features can begin to be explained naturalistically without recourse to questionable psychological speculation. The emerging picture suggests that Gala's dream consciousness state may have helped her subsequent waking consciousness to be more accurately perceptive, more orderly in thought, more temperate emotionally and better able to remember her experience. Figure © Salvador Dalí, Gala-Salvador Dalí Foundation, DACS, London, 2009.

Primary consciousness
Subjective awareness of perception and emotion.

Consciousness
Subjective awareness of the world, the body and the self, including awareness of awareness.

Waking
A brain state associated with electroencephalographic activation (similar to that of REM) but with the muscle tone enhancement (as measured by electromyography) that is necessary for posture and movement.

Non-rapid eye movement (NREM) sleep
Sleep with electroencephalographic evidence of brain deactivation; spindles and slow waves characterize this brain state.

Lucid dreaming
The subjective awareness that one is dreaming and not awake (as is usually incorrectly assumed).

model for control of the conscious state, which explains the psychological features of dreaming and waking at the mechanistic (neuronal and molecular) level, and I use the AIM model to show that lucid dreaming is an intermediate position between REM sleep and waking.

An important caveat is that although the distinctive features of dream consciousness (see Supplementary information S1 (table)) are maximally correlated with REM sleep, they are also found — to a limited degree — in NREM sleep, especially in stage I, at sleep onset, and in stage II, late in the night^{6–8}. Because of sleep inertia, it is difficult to evaluate the reports of mental content when subjects attempt to awaken from the deeper stages III and IV of NREM sleep⁹, so it is unclear whether some features of dream consciousness also occur during these stages. For these reasons, I focus here on the comparison between waking and REM sleep because the similarities and differences are reliable and informative with respect to theories of consciousness. Importantly, all the variables under discussion in this Review, be they psychological or physiological, can be differentiated quantitatively rather than qualitatively⁶.

Developmental and evolutionary considerations

REM sleep is an evolutionarily recent behaviour¹⁰ (FIG. 2). It is regulated by the pontine brainstem, a phylogenetically ancient brain structure¹¹ — a trenchant example of a new physiological function depending on old brain parts¹².

REM sleep has evolved separately in mammals and birds. In both, there is a preponderance of REM sleep in early life. In humans the amount of REM sleep peaks in the third trimester of gestation¹³ (FIG. 2a) and plummets after birth, as waking time and cognitive capability increase. Thus, primary consciousness declines and secondary consciousness grows with the development of the brain and the capacity for prolonged waking (FIG. 2).

Although REM sleep occurs early in human development, it is likely that adult-type dream consciousness becomes associated with REM only when brain development has advanced sufficiently that the narrative organization of subjective experience becomes possible⁶. Although the exact timing of the emergence of adult-type dream consciousness is debated, it is not before age 5 years and may be as late as age 8 years (REFS 14, 15). This dissociation raises the question of what REM sleep does to advance the brain's capacity for cognition before the emergence of dream consciousness as we know it as adults. Could REM sleep have a role in brain development?

Language acquisition, dreaming itself, dream reporting and other cognitive skills increase gradually during childhood. Learning continues over the lifespan as memory is updated and expanded. These facts are consistent with the persistence of REM sleep in mature individuals, whose dreams are evidence of the ongoing importance of REM for brain–mind maintenance and reconstruction^{14,16–19}.

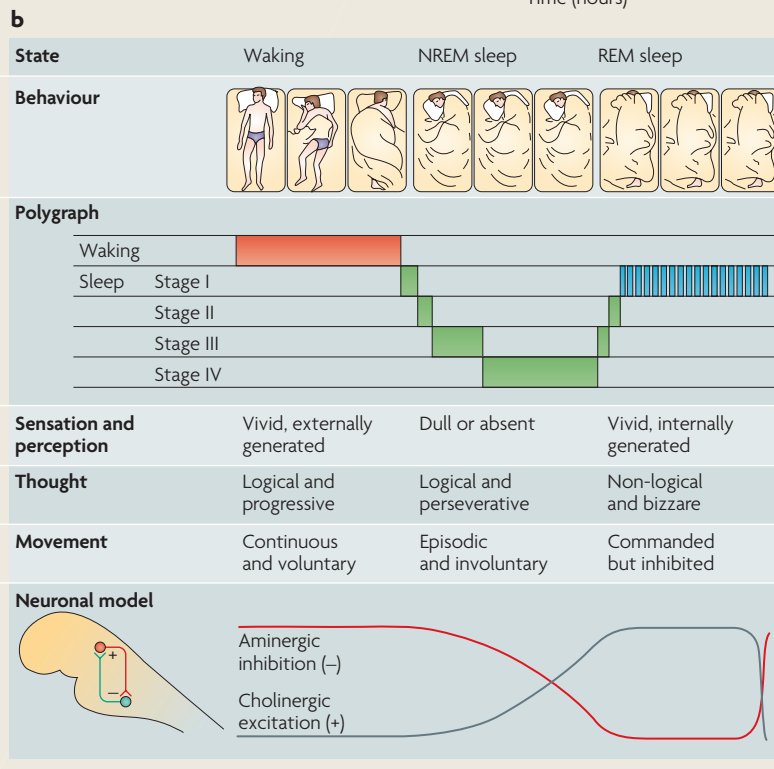
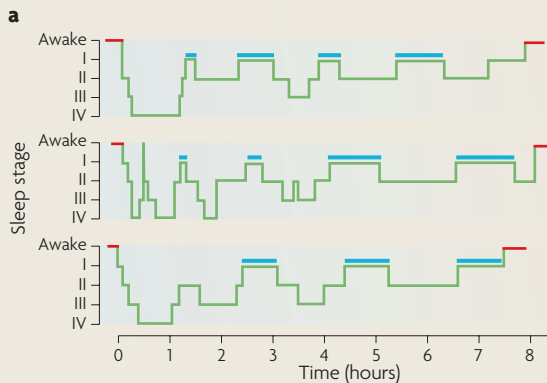
Developmental neurobiology has shown that a neuron's location and chemical signature are under genetic control²⁰, but the construction of neuronal circuits, including oscillators and clocks, requires use-dependent interactions between neuron groups²¹. Such

Box 1 | Sleep science basics

Standard sleep laboratory measurements reveal 90–100 minute cycles of rapid eye movement (REM) and non-rapid eye movement (NREM) sleep (see the figure, part a, which shows cycles for three subjects; the blue lines indicate periods of REM sleep). Reports of dreaming are most common from sleep onset stage I (when dreams tend to be fragmentary and unsustained), late-night stage II (when dreams tend to be thought-like) and stage I REM (when they tend to be long, vividly hallucinatory and bizarre). All of the deep phases of sleep (III and IV) occur in the first half of the night, whereas lighter stages of sleep (stages I and II) predominate in the second half of the night. Regardless of time of night, reports of dreaming are longest and most bizarre following awakenings from stage I REM.

The states of waking and sleep have behavioural, polygraphic and psychological manifestations (see the figure, part b), which seem to be orchestrated by a control system in the pontine brainstem. In the figure, the neuronal model of the clock that programs these states is depicted as the reciprocal interconnection between aminergic inhibitory neurons and cholinergic excitatory neurons. The activity levels of these two groups of neurons are also reciprocal: the activity of aminergic cells is highest during waking, declines during NREM sleep and is lowest during REM sleep, whereas the activity of cholinergic cells shows the reverse pattern. Changes in state and phase take place whenever the two activity curves cross; these are also the times when major postural shifts occur. The motor immobility during sleep depends on two different mechanisms: disfacilitation during stages I–IV of NREM sleep and inhibition of motor systems during REM sleep.

The motor inhibition during REM sleep prevents motor commands from being carried out, so that we do not act out our dreams. Part b of the figure is reproduced, with permission, from REF. 117 © (1983) J. Allan Hobson.



excitatory–inhibitory interaction is under genetic control, but without use-dependent exercise function cannot be achieved²². It seems that use-dependent exercise ‘fine-tunes’ neuronal connections. Another example of this rule is provided by the visual system, which must be stimulated to develop properly^{23,24}. Such excitation-driven inhibition is maximal during waking. By contrast, REM sleep is marked by minimal levels of inhibition throughout the brain; thus, the brain activity that is detected during REM sleep (see below) is a function of disinhibition. (In this paper, I emphasize activation of the forebrain during REM sleep, but the cerebellum, brainstem and spinal cord are also activated during this stage. I assume that the corticothalamic and limbic systems, which are active in waking and REM sleep, are directly responsible for conscious experience.)

The emerging control of alternating states of activation (REM sleep), inactivation (NREM sleep) and, later in development, waking could therefore be a function of the developing interaction between pontine brainstem neurons, some of which are inhibitory and some of which are excitatory (FIG. 3). In human fetuses, a REM-like state alternates with periods of brain deactivation. The precedence, in time, of REM sleep autoexcitation may set the stage for the increased inhibition that is necessary for waking. In other words, the developing brain might self-activate in a way that anticipates its later, wake-state operation^{13,25}.

The idea that REM sleep is developmentally important because it allows a necessarily limited set of genetic instructions to be converted into an automatic and self-organizing activation program for the brain–mind is not new. More than 35 years ago, Michel Jouvet proposed that REM sleep promoted the rehearsal of instinctual behaviour²⁶. It was also suggested that REM sleep stimulates the development of the visual system²⁷; indeed, REM sleep declines sharply in kittens after their eyes open²⁸. It has recently been argued that dreaming itself is useful in the practice of escape from threat²⁹. All of these theories support the idea that sleep is as much a preparatory as it is a recovery process. This theory is, in fact, a scientific recasting of Kant’s model, in which innate ideas interact with perceptual experience in the genesis of consciousness³⁰.

Functional theories

Dreaming has invited as many speculations about its function as it has triggered theories about its mechanistic source. There is an important distinction to be made between dreaming, which is a subjective, psychological state, and REM sleep, the brain state with which it is most highly correlated, especially when discussing function. Many of the functional theories for dreaming that have been advanced have assumed a single identity for the two domains of discourse, despite the fact that we can speak only of a correlation^{6,31}. Here I focus on the function of REM sleep and assume that dreaming is an indispensable — if sometimes misleading — subjective informant about what the brain does during REM sleep. Indeed, we may be bound to admit that dreaming itself could be an epiphenomenon without any direct effect on normal or abnormal cognition³².

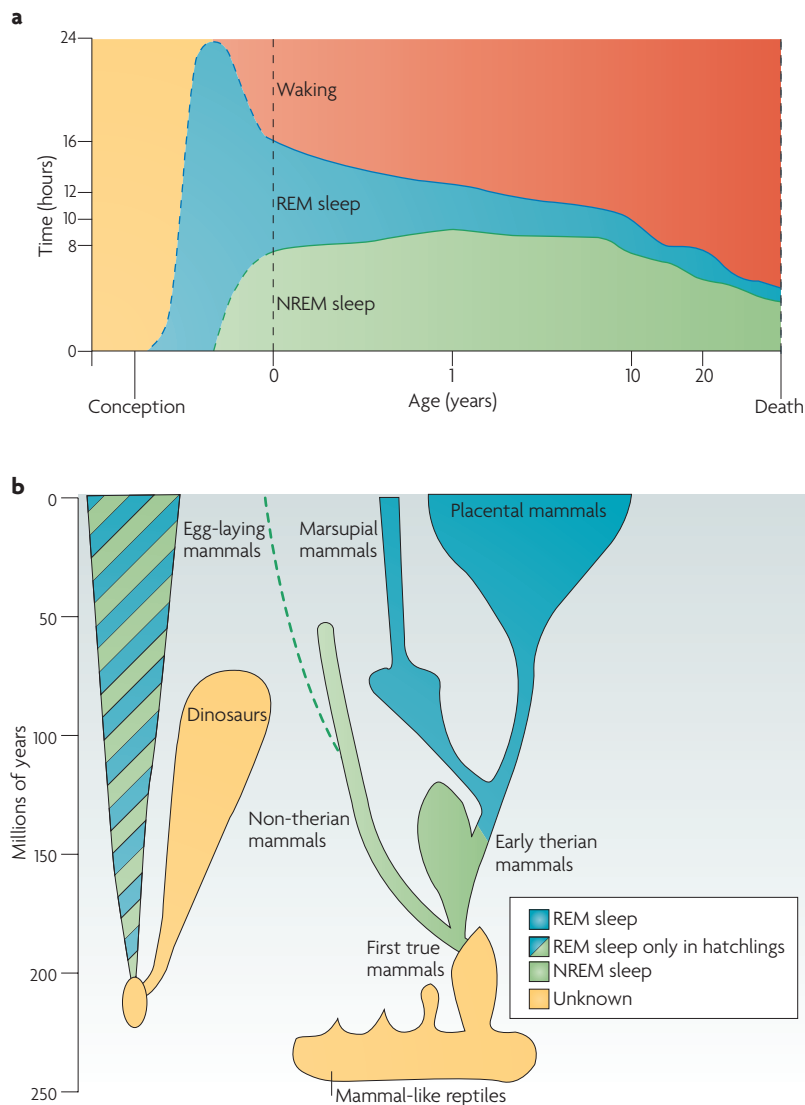


Figure 2 | Developmental and evolutionary considerations. a | Human sleep and age. The marked preponderance of rapid eye movement (REM) sleep in the last trimester of pregnancy and the first year of life decreases progressively as waking time increases. Note that non-rapid eye movement (NREM) sleep time, like waking time, increases after birth. Despite its early decline, REM sleep continues to occupy approximately 1.5 hours per day throughout life. This suggests that its strongest developmental contribution is to early brain–mind development but that it subsequently plays an equally indispensable part in brain–mind maintenance. **b** | The evolution of REM sleep. Birds and mammals evolved separately after branching off from the ancestral tree many millions of years ago. Both birds and mammals are homeothermic, and both classes of animal have appreciable cognitive competence. Restoration of thermoregulatory capacity is a strongly evidenced function of REM sleep. With respect to the possible enhancement of cognitive skills by REM, it is significant that both birds and mammals are capable of problem solving and both can generate forms of verbal communication (‘primitive language’). Part **a** is modified, with permission, from REF. 27 © (1966) American Academy for the Advancement of Science. Part **b** is reproduced, with permission, from REF. 10 © (1970) American Museum of Natural History.

Sleep and energy regulation. The most convincing evidence of sleep function comes from the experiments of Allan Rechtschaffen and colleagues³³. Rats that were subjected to total sleep or selective REM sleep deprivation all died with a stereotyped syndrome of caloric and thermal dyscontrol. *En route* to their demise, the

sleep-deprived rats lost weight (despite eating more) and evinced heat-seeking behaviour (in an environment in which they were comfortable before the initiation of sleep deprivation).

These results indicate that homeothermic animals might require sleep to maintain body weight and body temperature. Importantly, only mammals and birds are homeothermic, and they are also the only animals to evince REM sleep^{10,34} (FIG. 2b). Moreover, REM sleep is the only state of which deprivation is associated with a loss of central body temperature regulation in experimental animals³⁵.

Temperature control not only confers a behavioural advantage by allowing an animal to act in a range of ambient hot and cold climates but also contributes to brain function, especially consciousness and its component skills³⁵, which are crucial to higher cognitive states. The fact that humans can cognize effectively only in a narrow range of brain temperature suggests that our consciousness depends on homeothermy and that homeothermy, in turn, depends on sleep.

Sleep deprivation and psychological equilibrium.

Wishing to test Freud’s hypothesis that dreaming is a psychic escape valve for the unconscious mind, William Dement deprived human subjects of REM sleep and reported that 3–5 days of this procedure triggered cognitive deterioration^{36,37}. On the first night sleep was interrupted only 5 times to prevent REM sleep, but on the fifth night 50 arousals were needed, indicating that the body was attempting a homeostatic ‘catch up’ on lost REM sleep. The conclusion — that it was dreaming, not sleep, that was essential to mental health — was challenged by Anthony Kales, who showed that equivalent amounts of NREM sleep deprivation were equally deleterious³⁸. Although the relative benefits of REM and NREM sleep to mental health are still being investigated, it should be noted that both stages of sleep are almost certainly useful. In any case, it is clear that both stages are exquisitely regulated and conserved^{39,40}.

The significance of these early studies in humans is clear: sleep is essential to mental health. Needless to say, psychologists generally adhere to the theory of psychological benefit^{41,42}. The fact that sleep deprivation invariably causes psychological dysfunction supports the functional theory that the integrity of waking consciousness depends on the integrity of dream consciousness and that of the brain mechanisms of REM sleep.

A paradoxical improvement in mood is observed in depressed patients after one night of REM sleep deprivation^{43,44}. Equally paradoxical is the complete suppression of REM by the monoamine oxidase-inhibiting (MAOI) drugs that are used to treat depression. These facts invite speculation and further study. For now, we can say only that the monoamines serotonin, noradrenaline, histamine and dopamine, as explained below, are important in the regulation of sleep, mood, learning and temperature control. The balance between these biogenic amines and acetylcholine is central to our concepts of the regulation of cognition and mentation.

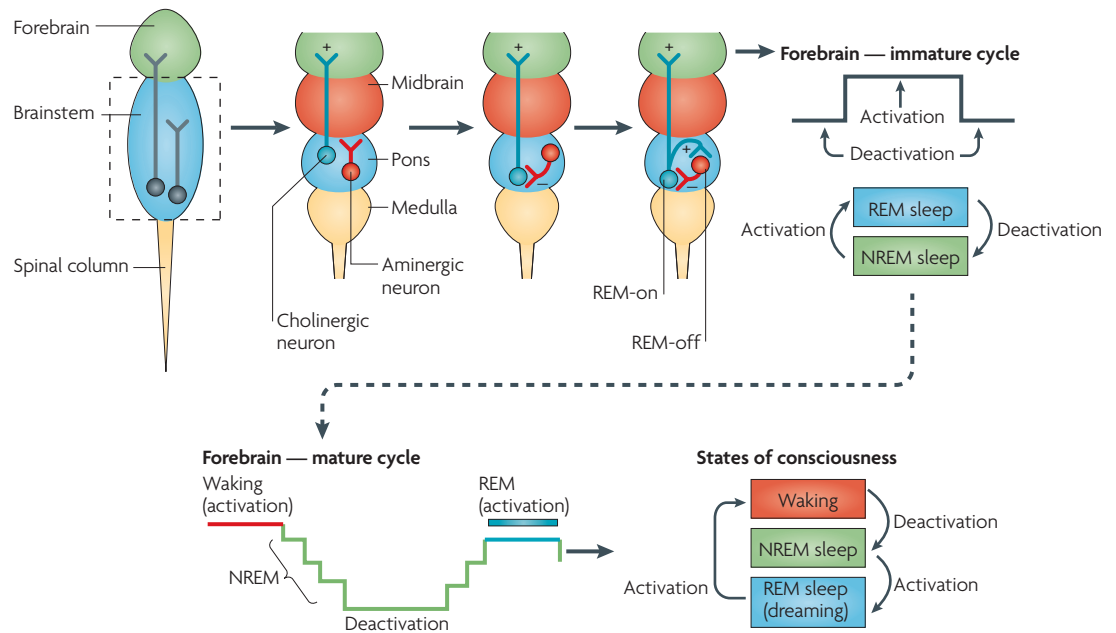


Figure 3 | Proposed steps in brain development leading to the emergence of the NREM-REM sleep cycle and its alternation with waking. Following fertilization, blastulation, gastrulation and neural crest formation (not shown) the developing brain takes on a recognizable form in a tripartite structure (forebrain, brainstem and spinal cord) and then through a second tripartite division of the brainstem (to form the midbrain, pons and medulla). The processes described in this Review develop in these parts. Based on inferences derived from adult neurobiology, the figure schematizes how the establishment of neuronal location (in the brainstem) and chemical signature (aminergic or cholinergic) might parallel the development of, first, activation and inactivation and, later, of rapid eye movement (REM) sleep, non-rapid eye movement (NREM) sleep and waking. For example, initial activity of cholinergic brainstem neurons probably leads to forebrain activation; subsequent activity of aminergic brainstem neurons and their interaction with cholinergic neurons result in a primitive cycle of brain activation and deactivation. As a differentiated neuronal circuitry is formed in the forebrain, a complex set of features comes to characterize the REM-NREM sleep cycle. The protoconsciousness that I intuit in this Review would begin here and continue as REM sleep dreaming throughout life. During the third trimester of pregnancy in humans REM-like brain activation predominates, but in the first years of life the time that the brain is in the REM sleep state declines, whereas the time it is in the NREM sleep state and the waking state increases (see also FIG. 2). These are the building blocks of adult conscious states, although many of the details of the transition to adult states of consciousness remain to be established.

Sleep and learning. Giuseppe Moruzzi was the first to suggest that sleep mediates plastic processes in the brain⁴⁵. Numerous studies subsequently showed that REM sleep duration is augmented when animals learn a new task and that REM sleep deprivation interferes with such learning^{18,19,46-49}. These effects — if they were found at all — are small, prompting some critics to deny that there is any significant benefit to learning from sleep⁵⁰⁻⁵². Whether or not such a conclusion is justified, it must be admitted that learning cannot be the only or even the prime function of sleep. A more overarching and compelling theory is needed, but any such theory should be compatible with and take account of scientific findings, which support the hypothesis that the brain changes the status of its information as it sleeps⁵³.

If sleep is essential to memory, we must wonder why semantic memory does not seem to be strongly enhanced by sleep, why the enhancement of procedural learning by sleep, although statistically significant, is so weak, why neither selective REM nor selective slow-wave sleep (SWS) deprivation impairs memory consolidation and why the suppression of REM sleep with selective serotonin reuptake inhibitors (SSRIs) and

serotonin-norepinephrine reuptake inhibitors (SNRIs) actually enhances learning⁵⁴⁻⁵⁷. Could it be that updating memory with newly learned material is only a small part of the learning maintenance task of the sleeping brain? Could it be that we must relearn all that we already know, as well as integrate new experiences into that vast storehouse of data? Or do we simply need to rerun our built-in virtual reality simulation circuits to prevent disuse-induced memory loss?

The hyperassociative and synthetic properties of dreaming suggest tentative answers to these important questions. The fact that no more than 20% of dream material is in any way related to what the dreamer recollects of events in his or her life history⁵⁸ indicates that dreaming could represent a set of foreordained scripts or scenarios for the organization of our waking experience. According to this hypothesis, our brains are as much creative artists as they are copy editors. What we may need to navigate our waking world is an infinite set of charts from which we may draw the one best suited to an equally infinite set of real-life possibilities. To this end, it makes sense to tie even remotely connected scraps of experience together to give our library of plots enough

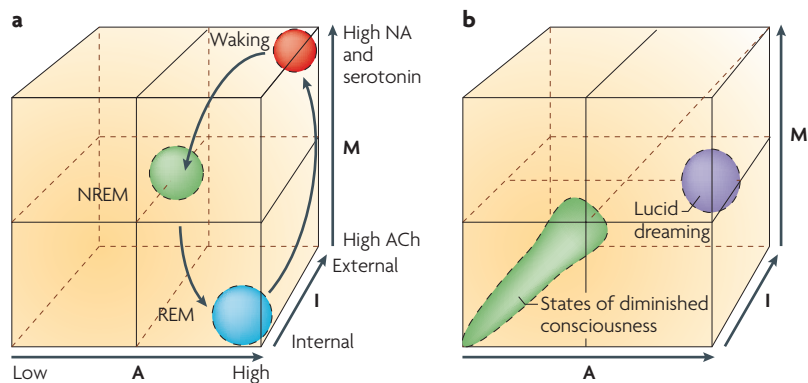


Figure 4 | AIM model of brain–mind state control. a | The three-dimensional AIM state-space model showing normal transitions within the AIM state space from waking to non-rapid eye movement (NREM) and then to rapid eye movement (REM) sleep. The x axis represents A (for activation), the y axis represents M (for modulation) and the z axis represents I (for input–output gating). The values of A, I and M can be derived from the neuronal data of animal experiments; factors A and I can also be estimated in human sleep laboratory data but, as yet, there is no way of measuring factor M in humans. Waking, NREM sleep and REM sleep occupy distinct loci of this space. Waking and REM sleep are both in the right-hand segment of the space, owing to their high activation levels, but they have different I and M values. Thus, the activated, REM-sleeping brain–mind is both off-line and chemically differentiated compared with the waking brain–mind. NREM sleep is positioned in the centre of the space because it is intermediate in all quantitative respects between waking and REM sleep. The values of A, I and M change constantly, but the changes are constrained. Sleep and waking states alternate owing to circadian influences (not shown). During sleep, AIM values tend to follow elliptical trajectories through the space. As sleep advances in time, AIM values go less deeply into the NREM sleep domain and more deeply into the REM sleep domain. The normal, cardinal domains of waking, NREM and REM sleep occupy relatively limited zones of the space. **b** | Diseases, such as those neurological conditions that produce coma and minimally conscious states, are arrayed in the left-hand segment of the space, owing to their low activation values¹³⁵. Lucid dreaming, which is a hybrid state with features of both waking and dreaming, is situated in the middle of the extreme right-hand side of the AIM state space between waking and REM, towards either of which lucid dreamers are drawn. Sleep and psychiatric disorders can also be placed in the schema¹³⁶. ACh, acetylcholine; NA, noradrenaline.

verisimilitude to be useful. This turning on its head of the habitually reductive approach to dream interpretation sets the stage for a view of dreaming as an autocreative process.

A new theory: dream consciousness and protoconsciousness. If REM sleep precedes dreaming during human development, what happens in the brain–mind during REM sleep before dreaming appears? One possible answer is that the brain is preparing itself for its many integrative functions, including consciousness. The development of consciousness is thus seen as a gradual, time-consuming and lifelong process that builds on, and constantly uses, a more primitive innate virtual reality generator, the properties of which are defined for us in our dreams.

The activation of the forebrain in the absence of external input during sleep, both before and after birth, could have several important functions. These include the provision of an automatic, built-in, self-organizing process that offers a spontaneous solution to the so-called binding problem⁵⁹. Indeed, there is abundant evidence that REM sleep enhances sensorimotor

integration^{60,61}. To act as a unified system, neurons need to be connected to one another and activated in temporal and chemical unison. REM sleep does just that through its activation and neuromodulatory functions (see below), on which the differentiation of dreaming and waking consciousness depends. During waking, the brain has access to information about external space and time. These external inputs are not available in sleep and must therefore be simulated in dreaming. I propose that the developing REM-sleeping brain has built-in predictions of external space and time. These intrinsic predictions are then adjusted on the basis of experiences of the outside world.

As the intrinsic activation of the forebrain during REM sleep arises early in development, it does not seem far-fetched to propose that a ‘protoself’ is instantiated, at first to account for and later (after the development of secondary consciousness) to take responsibility for what begin as entirely automatic acts. These acts are fixed and result from the excitation of motor pattern generators, of which the gait control centres of the pontine brainstem are a prime example⁶². When we dream, we suppose that it is we who command our dreamed motor acts, but a moment’s reflection shows this sense of volitional agency to be as much an illusion as our wake-state sense of conscious will^{63,64}.

Originally dreamless, protoconscious REM sleep could therefore provide a virtual world model, complete with an emergent imaginary agent (the protoself) that moves (via fixed action patterns) through a fictive space (the internally engendered environment) and experiences strong emotion as it does so. This state is at first not associated with awareness⁶⁵. I propose that only during childhood do we become able to integrate this experience and become aware of it. The consciousness that we come to enjoy in our dreams is predominantly primary in the sense that it emphasizes perception and emotions at the expense of reason. Although our dreams seem to be agent driven, they are not volitional nor do they contain the self-reflection, insight, judgment or abstract thought that constitute secondary consciousness. For those attributes of secondary consciousness to be present, activity in the requisite cortical structures must be modulated appropriately as we wake up or as we become aware that we are dreaming while we are still asleep (lucid dreaming, see below).

The neurobiology of conscious state control

The control of the waking, REM sleep and NREM sleep states lies in the brainstem, which orchestrates events in the forebrain above it and in the spinal cord below it^{11,66}. This system of consciousness states has been described in terms of three factors, the levels of which vary between states: activation (A), input–output gating (I) and modulation (M) (FIG. 4). Here I give a preliminary account of how these three factors may be engineered and coordinated⁶⁶.

Activation (A). Large parts of the brain, including many subcortical and neocortical areas, that are active during waking are inactive during NREM sleep and are

Binding problem

A science of consciousness must explain how so many aspects of our experience are integrated. The ‘binding’ of perception, emotion, thought and memory requires a physical explanation at the level of brain function.

Protoconsciousness

A primordial state of brain organization that is a building block for consciousness. In humans, protoconsciousness is proposed to develop as brain development proceeds in REM sleep *in utero* and in early life.

Box 2 | Historical background

The idea that the brain can be internally activated in sleep began with the discovery of rapid eye movement (REM) sleep¹¹⁸, which was shown to be associated with dreaming in adult humans¹¹⁹. REM sleep was also found in cats¹²⁰, and it was shown in that species to be mediated by the pontine brainstem¹¹. By 1960, it was clear that the brain produced two activation states, waking and REM sleep. It was subsequently established that each has its own distinctive state of consciousness.

These discoveries were made possible by the development of the electroencephalogram (EEG)¹²¹ and its application to the study of sleep¹²², which evolved into the polygraphic description of the substates of non-REM and REM sleep¹²³. The sleep and dream laboratory was thus born, and a profusion of studies attempted to link the objective findings with conscious-state variables. The claims of many of these studies were controversial, in part because of theoretical confusion and in part for methodological reasons^{124,125}.

Meanwhile, the parallel development of basic neurophysiology focused on sleep itself and ignored consciousness^{126–131}. This line of work was informed by the idea of neuronal clocks — first suggested by Thomas Graham-Brown, a pupil of Sherrington¹³² — and famously evidenced by the studies of circadian rhythms¹³³, which were found to be controlled in the suprachiasmatic nucleus of the hypothalamic brainstem¹³⁴. It was the recognition that dreaming could be analysed formally that allowed psychophysiological integration to proceed.

reactivated during REM sleep. The concept that the brain is not only a collection of passive reflex circuits^{67,68}, but that it actually possesses the means of regulating its own activation, developed slowly based on two events: first, the observation that sleepiness developed after destruction of the dopamine neurons of the substantia nigra in the midbrain of patients with encephalitis lethargica⁶⁹; and second, the discovery of the reticular activating system⁷⁰, on which, it was suggested, waking consciousness depends.

It gradually became clear that behavioural rest and activity, as well as the level and quality of conscious experience, were functions of intrinsic brain activation and deactivation, which were controlled by the neurons of the brainstem (BOX 2). Thus, the stage was set for an attempt to decipher the brainstem mechanisms of conscious state control using microelectrodes to determine the activation and deactivation patterns of neuronal populations during waking, REM sleep and NREM sleep⁶⁶. This approach led to a theory of dreaming⁷¹, which has evolved into the theory of primary and secondary consciousness that is described in this Review.

Input–output gating (I). If the brain is activated during REM sleep, why is dreaming, not waking, the result? One answer is that during REM sleep the internal activation of the brain (factor A) is associated with the active suppression of both external sensory input⁷² and motor output^{73–76}. The brain is thus actively kept ‘off-line’ during REM sleep. The input–output gate control (factor I) is mediated by the brainstem⁷², which thus guarantees the coordination of factors A and I. The inhibition of spinal motor neurons during REM sleep^{75,77} causes a motor paralysis that is often noticed by us as the annoying flaccidity of our legs as we try to run faster and faster to elude imaginary dream assailants. It should be noted that this paralysis can be dissociated from muscle atonia and can even occur when muscle activity is present^{78–80}.

An important feature of REM sleep is the occurrence of phasic activation signals. These signals have been recorded, in cats and humans^{81,82}, in the pontine brainstem (P), the lateral geniculate body of the thalamus (G) and the occipital cortex (O) and are therefore called PGO waves^{11,83–85}. Although they are prominent in the visual system, they also occur in sensorimotor systems in the forebrain⁶¹. PGO waves may therefore constitute endogenously generated signals that not only occlude external sensory input, enabling the brain to remain asleep⁶⁶, but also constitute informational building blocks for perception and motor control. During dreaming our sensation and movement are entirely fictive, but the simulation of real, wake-state sensation and movement is impressive. The brain, isolated from the outside world, treats this endogenous stimulation as if it were exogenous.

The nature of the internally generated signals that arise as PGO waves during REM sleep suggests how the PGO system might foster sensorimotor integration. The spontaneous activation of this system in sleep supports the hypothesis that the brain simulates its interaction with the external world. In the visual system, PGO waves encode saccadic eye movement directions that are commanded by the oculomotor brainstem network; the visual system is thus informed of impending shifts in the visual field before they occur⁸⁶. It has been proposed that, during dreaming, PGO signals are used in the construction of the hallucinoid visual imagery of dreams⁷¹. The robust evidence for the generation of feedforward information, the excitability and functional significance of which varies systematically with brain state⁸⁷, is an important element of dream consciousness theory. In dreams, we see — in the absence of light — by activating the visual system of the brain from the motor side up.

Modulation (M). Among the most strongly state-dependent neurons of the brainstem are the aminergic neurons⁸⁸. The neuromodulators they release exert a widespread chemical influence on the brain; for example, they instruct other neurons and circuits to keep or discard a record of the information they have processed⁸⁹. This instruction is relevant to the difference between waking consciousness, which remembers well, and dream consciousness, which does not.

What determines the shift from predominantly external input, during waking, to predominantly internal input, during dreaming? It has been proposed that this is due to a shift in the activity of two neuromodulatory cell populations in the brainstem as animals move from waking through NREM sleep to REM sleep, the so-called REM-off cells (which are active during waking and inactive during REM sleep^{90,91}) and REM-on cells (which are active during REM sleep and inactive during waking) — these could just as well have been called waking-on and waking-off cells, respectively^{92,93}. The pharmacological implications of this hypothesis have been confirmed experimentally^{94–97}. It is now widely accepted that REM sleep is cholinergically potentiated and aminergically suppressed. More recently, using molecular techniques and selective manipulation of REM sleep, it has been

Activation

(A). In behavioural neurobiology and cognitive science, the term activation is used to express the level of energy of the brain and its constituent circuits. The analogy to a power supply with an on–off switch conveys the essence of this idea.

Input–output gating

(I). The process that facilitates or inhibits, as the brain changes state, access to the brain of sensory information (input) from the outside world and the transmittal of motor commands from the brain (output) to the musculature.

Modulation

(M). The chemical microclimate of the brain is determined largely by neurons in the brainstem, which send their axons widely to the forebrain, spinal cord and cerebellum. Among the chemicals released by these cells are dopamine, noradrenaline, serotonin, histamine and acetylcholine.

confirmed that the cholinergic pedunculopontine tegmental neurons are REM-on cells and serotonergic dorsal raphe nucleus and noradrenergic locus coeruleus neurons are REM-off cells⁹⁸. It has also become clear that GABA (γ -aminobutyric acid) and glutamate participate in this process⁶⁶.

Waking consciousness is associated with the activation of all modulatory brainstem neurons — that is, the neurons that manufacture and release the neuromodulators acetylcholine, dopamine, histamine, noradrenaline and serotonin^{90,92,99,100}. Dopamine- and acetylcholine-releasing neurons are also active during REM sleep, but noradrenaline-, serotonin- and histamine-releasing neurons shut off completely during that state^{92,101}. NREM sleep is intermediate in that all modulatory neurons slow down relative to the waking state, but they do not shut off (as some of them do during REM sleep).

Owing to the inactivation of the REM-off cells, the activated but off-line brain is said to be aminergically demodulated and, reciprocally, cholinergically hypermodulated¹⁰⁰. The absence of three wake-state modulators and the persistence of dopamine release could explain some of the cognitive characteristics of dreaming, such as the visual hallucinations, the bizarreness, the lack of self-reflective awareness and the amnesia. Interestingly, dopamine has been proposed to mediate the psychosis of mental illness, especially *schizophrenia*¹⁰², and it might have a similar role in the psychosis of dreams. The importance of chemical balance is illustrated by these considerations. Whether a brain generates a state of external awareness (waking) or simulates that state (dreaming) may be a function of its neuromodulatory ratio.

The AIM model. When the differences in brainstem neuronal activity during waking and REM sleep were first noted, we proposed that the wake–NREM–REM sleep cycle was the result of interactions between the aminergic REM-off cells and the cholinergic REM-on cells⁹³. We advanced the ‘activation-synthesis’ hypothesis of dreaming⁷¹, which posits that brain activation during REM sleep results in the synthesis of dream mentation. Since that time, we have tested, modified and extended these two hypotheses in the light of new experimental data^{66,100,103}. Recent work has revealed additional mechanistic details regarding neuronal control^{104,105} during REM sleep. For example, the triggering mechanism for PGO waves in the lateral pons has been shown to interact with glutamergic neurons in the pontine reticular formation.

The claim that waking and dreaming are at once similar and different has been developed into the AIM model and dream consciousness theory. A three-dimensional AIM model (FIG. 4) describes different states of the brain and shows how they vary over the course of a day and night in adult humans. The model cannot yet explain the regional differences in brain activity that distinguish REM sleep from waking. It remains to be seen whether the blood flow changes measured with positron emission tomography and functional MRI reduce to the changes of value M in the AIM model. Because M is the composite ratio of aminergic and cholinergic influences, it

is likely that at least some regional activation patterns are caused by these autonomic control systems as, in the periphery, blood flow control is mediated by similar autonomic mechanisms. Thus, time is a fourth dimension of the AIM model. Waking has high values of A, I and M, whereas REM has a high value of A but low values of I and M (FIG. 4). The brain is activated in both states, but only in waking are the input–output gates open and is aminergic modulation strong.

The ‘state space’ approach also enables the mapping of exceptional mental states such as lucid dreaming¹⁰⁶ and abnormal conditions such as coma and minimally conscious states¹⁰⁷. Sleep disorders such as narcolepsy¹⁰⁸ and many psychiatric syndromes (such as depression^{43,44}) also find their place in the AIM state space⁶⁶.

Imaging, lesion and EEG studies

The advent of brain imaging technology (positron emission tomography, single-photon emission computed tomography and MRI) has revolutionized sleep and dream research^{109–112}. These techniques have revealed a global deactivation of the brain during NREM sleep compared with waking and a subsequent reactivation during REM sleep — to levels above those seen in waking — of the pontine tegmentum, the amygdala and its projections to the parahippocampal cortex, the anterior commissure, the parietal operculum, the deep frontal white matter and the midline thalamus^{109–111} (FIG. 5a). These findings fit well with the subjective experience of the abeyance of consciousness during NREM sleep and the reinstatement of consciousness (but now with an accentuation of such internally generated primary features as perception and emotion) during REM sleep.

The findings are also in agreement with reports by patients that dreaming ceases after stroke damage to the parietal operculum and deep frontal white matter¹¹³, two of the brain areas shown by imaging methods to be hyperactivated in REM sleep. Patients with therapeutic interruptions of deep frontal white matter (lobotomy) also reported cessation of dreaming. By contrast, patients with temporal lobe epilepsy experienced their seizures as “dreamy states”¹¹⁴; these patients also reported intensification of nocturnal dreams, suggesting that the temporal lobe and its connections to other brain regions are involved in the generation of primary consciousness and dreaming¹¹³. As these structures are highly evolved in lower mammals, it is possible that the limbic brain has an important role in mediating primary consciousness and dreaming.

Lucid dreaming. How can primary and secondary aspects of consciousness be investigated neurobiologically? A unique opportunity to advance the science of consciousness in relation to sleep is the study of an unusual state called lucid dreaming, in which subjects regain many aspects of waking while continuing to dream¹¹⁵. New evidence from quantitative electroencephalographic (EEG) studies¹⁰⁶ suggests that lucid dreaming is the subjective experience of a waking dream in a hybrid brain state, with the rare but instructive coactivation of both primary and secondary consciousness circuits.

When subjects shift from non-lucid to lucid REM sleep, they show an increase in the high-frequency (40 Hz) band of their frontal EEG¹⁰⁶ (FIG. 5b). This sort of high-frequency EEG activity could represent the

synchronization of cortical neuronal activity that is necessary to effect the temporal binding that is believed to be essential to waking consciousness⁵⁹. In addition, during lucid dreaming there is an increased coherence of frontal activation with activation in the posterior cortex¹⁰⁶ (FIG. 5c). This means that the cortex is not only more activated but also more synchronized when subjects become aware that they are dreaming.

Functional MRI results complement and extend these observations by revealing that dream lucidity is correlated with increased activation of the cortical areas that are thought to mediate the features of secondary consciousness, including the precuneus, frontopolar and dorsolateral prefrontal cortex, temporal cortex and inferior parietal lobules (M. Czisch, R. Wehrle and M. Dresler, personal communication).

Conclusions and future directions

The REM sleep–dream protoconsciousness hypothesis proposed here suggests that the development and maintenance of waking consciousness and other high-order brain functions depends on brain activation during sleep. The hypothesis places an emphasis on the primary aspects of consciousness, the basis for which — it is posited — arises late in evolution and earlier in brain development than do the brain substrates that support the secondary aspects of waking consciousness. Waking consciousness, with its impressive secondary features, might be present only in humans, who have the highly evolved and extensive cortical structures that are probably necessary to mediate the abstract aspects of conscious awareness.

From this hypothesis flows a new theory of consciousness that suggests that the brain states underlying waking and dreaming cooperate and that their functional interplay is crucial to the optimal functioning of both. The hypothesis is grounded in neuroscience, through which its developmental and cognitive implications can be further explored. The new theory brings consciousness research into register with the burgeoning field of sleep science.

Dreaming is proposed to be the subjective experience of a brain state with phenomenological similarities to — and differences from — waking consciousness, which is itself associated with a distinctive brain state. A three-dimensional model can be constructed to represent the temporal changes in the brain — and its cardinal subjective states. How these changes in activation, input–output gating and modulation are correlated with, or perhaps even determine, the regional changes in brain activation during REM sleep compared with waking, as revealed by recent quantitative EEG and MRI experiments, can now be explored.

The concepts advanced in this Review are directly related to one of the greatest challenges faced by modern science: what is the mind and how can it be described in terms of brain function? The new field of cognitive neuroscience focuses on details that are pertinent to this question but has, until now, tended to ignore the global and comprehensive aspects that tie the details together¹¹⁶. The field of psychiatry has long sought, and may find here, a solid bridge between mental disorders

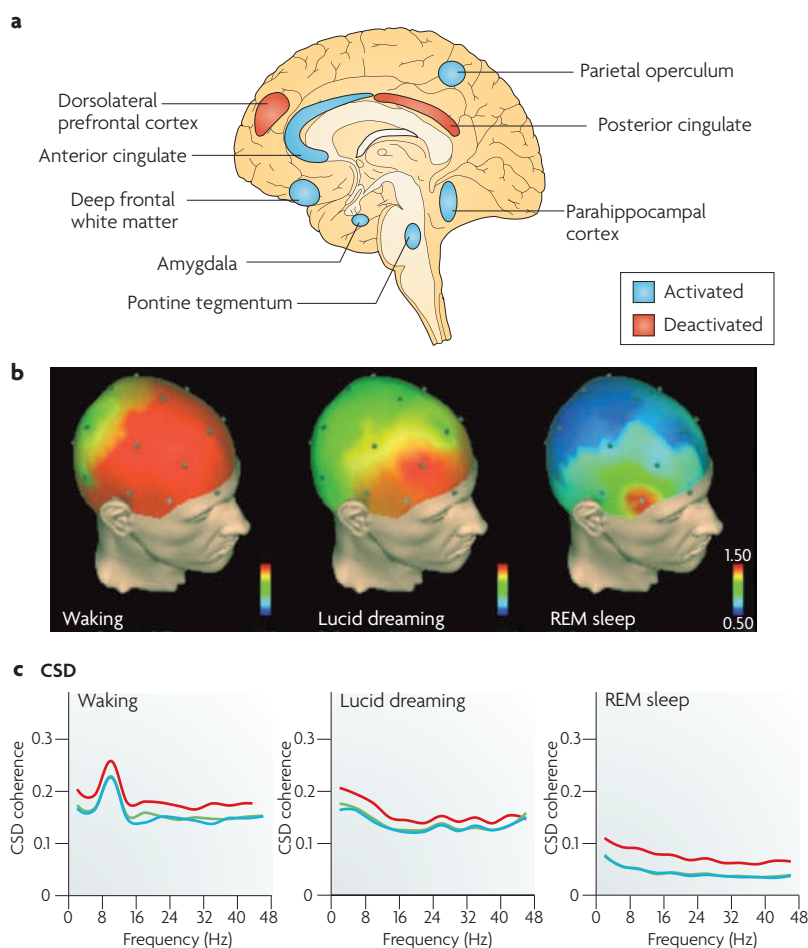


Figure 5 | Normal and lucid dreaming: differential regional activation patterns. **a** | Positron emission tomography studies^{109–111} have measured activation in brain areas during rapid eye movement (REM) sleep in healthy controls and after stroke. Blue and red areas indicate regions showing hyperactivation and deactivation, respectively, during REM (compared with waking) in normal controls. Lesions in two of the activated zones, the parietal operculum and the deep frontal white matter, are associated with reports of cessation of dreaming in subjects following stroke or prefrontal lobotomy. The activation state of the primary visual cortex during REM sleep that is detected in imaging studies is controversial but, contrary to what one might expect, this area is clearly not hyperactivated. **b** | Quantitative electroencephalographic (EEG) studies comparing brain activity during waking, lucid dreaming and REM sleep. Frontal areas are highly activated during waking but show deactivation during REM sleep. During lucid dreaming there is an increase in 40 Hz power and coherence in frontal areas compared with non-lucid REM sleep. In lucid dreaming, additional electrical activation of the brain is needed to activate the dreamer's forebrain enough to recognize the true state without causing waking and thus terminating the dream. Differentiated regional activation may underlie the phenomenological distinction between the states of REM sleep, lucid dreaming and waking. Scale bars indicate standardized power based on scale potentials (0.50% to 1.50% power). **c** | In addition to the increased 40 Hz EEG power in frontal EEG leads, EEG coherence (that is, the degree to which the brain waves are synchronized across regions) is much higher during lucid dreaming than during non-lucid REM sleep. In fact, the EEG coherence during lucid REM sleep is roughly equal to that during waking (left panel), except for the 8–12 Hz alpha range, which shows a peak during waking. CSD, cross-spectral density. Parts **b** and **c** are reproduced, with permission, from REF. 106 © (2009) Associated Professional Sleep Societies, LLC.

and the brain states that underlie them¹⁰⁰. Without such a bridge, there is no safe passage between the genetic and the phenotypic banks of the mind–brain chasm that still divides that field. To the humanities in general, and to psychology and philosophy in particular,

the new neuroscience of dream consciousness sends an appeal for more detailed attention to phenomenology that could help those disciplines advance without loss of their traditional and important adherence to meaning and to moral values.

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DATABASES

OMIM: <http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=OMIM>
schizophrenia

FURTHER INFORMATION

Allan Hobson's homepage: <http://allanhobson.net>

SUPPLEMENTARY INFORMATION

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Biography

Allan Hobson directed the Laboratory of Neurophysiology at the Massachusetts Mental Health Center (Boston, Massachusetts, USA) from 1968 to 2003. He has published more than 200 original peer-reviewed articles and 10 books on sleep and dreaming. He is the recipient of the Distinguished Investigator Award of the Sleep Research Society and the Farrell Prize of the division of Sleep Medicine at Harvard Medical School. In 2005 he moved to Sicily, where he now lives with his family. He has taught his course on the basic science of sleep and dreaming to graduate students throughout Europe and Asia.

Online At a Glance

- We know how, but not why, the brain is activated in sleep. I suggest that brain activation in sleep allows the development and maintenance of circuits necessary for higher brain functions, including consciousness.
- Brain activation and sleep occurs early in the development of mammals and birds. It may therefore be a state of protoconsciousness in those animals that evince rapid eye movement (REM) sleep.
- Our dreams are reminders that we too were (and still are) proto-conscious. We are always ourselves in our dreams; we sense, we act and we feel vividly in an entirely fictive world of the brain's devising.
- The protoconscious state of REM sleep dreaming is as much a preparation for waking consciousness as a reaction to it. We are as much getting ready to behave as we are getting over the effects of our behaviour.
- Dreams have more in common than not across individuals. As a species, we need REM sleep dreaming to accomplish shared goals, such as being capable of consciousness when awake.
- REM sleep dreaming can be viewed as a virtual reality pattern generator used by the brain to instantiate and maintain its readiness for adaptive interaction with the world.

TOC blurb

000 REM sleep and dreaming: towards a theory of protoconsciousness

J. Allan Hobson

Brain activation during REM sleep and dreaming resembles that during waking, but what is the meaning of this activity? Allan Hobson discusses the emergence of REM sleep states during evolution and development and proposes that the activity constitutes a protoconscious state.