

Exploring the neural correlates of dream phenomenology and altered states of consciousness during sleep

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Abstract

The science of dreaming constitutes a relevant topic in modern-day neuroscientific research and provides major insights into the study of human consciousness. Linking specific, universal, and regularly occurring stages of sleep with dreaming encourages the direct and systematic investigation of a topic that has fascinated humankind for centuries. In this review, we explore to what extent individuals dream during periods of rapid eye movement and non-rapid eye movement sleep, and we introduce research on lucid dreaming. We then discuss how dreaming during different stages of sleep varies in terms of phenomenological characteristics, and to what extent individuals are conscious throughout the sleep cycle. Finally, we provide a synopsis of the previous literature on brain activity during sleep, and we aim to clarify how the neurofunctional changes observed throughout sleep may lead to changes in phenomenological aspects of dreams, and in the domain of consciousness.

Key words: sleep and dreaming; consciousness; phenomenology; neuroscience; psychosis

Introduction

Sleep deceives by the ingenuity of its illusions, that there are no certain indications by which we may clearly distinguish wakefulness from sleep. From death, even.

—Philip Kerr, *A Philosophical Investigation*, 1992

Dreaming may be defined as a mental state, an altered state of consciousness, which occurs during sleep. Dreams usually involve fictive events that are organized in a story-like manner, characterized by a range of internally generated sensory, perceptual, and emotional experiences (Desseilles *et al.* 2011). The world of dreams constitutes a major aspect of human experience and has both fascinated and mystified mankind since time immemorial. Much has been speculated about the origin, meaning, and purpose of dreaming, while the private nature of dreams has made an objective analysis extremely difficult

(Horikawa *et al.* 2013). Early accounts of dream interpretation suggested that dreams predict the future (Artemidorus 1975) or reflect the current state of one's mental health (Bond 1753). The scientific investigation of dreaming only emerged during the late 19th century and primarily focused on factors that influence dream content (e.g. odours) (Hervey de Saint-Denys 1867).

Throughout the past few decades, several biological and psychological theories about the purpose of dreaming have been put forward (Lavie and Hobson 1986; Barbera 2008). Whereas earlier theories by psychoanalytic scholars suggested that dreams constitute a meaningful reflection of unconscious processes 'whose psychic importance is equal to that of the conscious mind itself' (Jung 1934, 139), others have argued that dreams are not inherently meaningful. According to one of the most prominent theories of the origin of dreams, the activation-synthesis hypothesis, dreaming results from rapid eye

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movement (REM) sleep physiology (Hobson and McCarley 1977). More recent theories suggest that dreams fulfil an adaptive function related to emotion-regulation, learning, and memory consolidation (e.g. Eiser 2005; Desseilles et al. 2011). Dreaming may play an important role in reactivating and further consolidating novel and individually relevant experiences that occurred during waking hours (Cipolli et al. 2004; Schwartz 2010). It might also constitute a biological defence mechanism, which has evolved as a capacity to repeatedly simulate threatening situations (Revonsuo 2000).

In the present review, we provide an overview of the extent to which dreaming occurs during different stages of sleep and discuss how dreams vary in terms of phenomenological characteristics and consciousness. To this end, one way of studying a mechanism—such as consciousness—is to examine it in different states of functionality. This is a necessary endeavour to gather a comprehensive understanding of the overall functionality of the mechanism or process in question. We provide a synopsis of the literature that explored the neural correlates of dreaming and highlight some methodological issues in dream research. Our aim is to clarify how the neural correlates of dreams relate to changes in phenomenological characteristics and features of consciousness throughout sleep.

Dreaming in Different Phases of Sleep

Every night individuals undergo several cycles of REM and non-rapid eye movement (NREM) sleep (further described below) that are on average 90–100 min long. Dreaming often goes unnoticed, and people tend to underestimate how often and how much they dream (Nir and Tononi 2010). This is due to our tendency to forget dreams, also known as dream amnesia (Roth et al. 1988).

REM sleep

During the early 1950s, Aserinsky and Kleitman (1953) discovered REM sleep, which is characterized by REMs, global high-frequency and low amplitude electroencephalogram (EEG) activity (similar to the waking state), as well as increased heart rate, respiratory activity, and muscle atonia (i.e. temporary muscular paralysis; Jouvet 1994). In the early days of dream research, dream physiology was equated with REM sleep physiology (Aserinsky and Kleitman 1953; Dement and Kleitman 1957; Eiser 2005) because individuals are most likely to report dreams after awaking from this phase of sleep (Maquet et al. 1996, 2000; Nofzinger et al. 1997; Maquet 2000; Fox et al. 2013). However, it is important to note that REM sleep and dreaming can be dissociated: lesions in the forebrain can leave REM sleep intact while dreaming ceases, whereas brain stem lesions can prevent REM sleep from occurring while individuals continue to report dreams after awakening (Solms 2000).

NREM sleep

Even though dream research has in the past mostly focused on the study of REM sleep, awakenings from NREM sleep yielded reports of dreaming as well (Foulkes 1962; Nielsen 2000; Nir and Tononi 2010; Limosani et al. 2011). NREM sleep is now commonly divided into three different stages (N1, N2, and N3; Iber et al. 2007) [N3 sleep, also known as deep sleep or slow-wave sleep, was referred to as NREM sleep stages III and IV in earlier terminology (Foulkes 1962).] and is in several ways physiologically distinct from REM sleep. NREM sleep is characterized by a global low frequency and high amplitude EEG signal, slow and regular breathing and heart rate, as well as low blood pressure.

Sleep stage N1 reports frequently contain accounts of dreaming (80–90% of the time), but these reports tend to be shorter than those following periods of REM sleep (Foulkes 1966). Reports after awakenings from NREM sleep N3 contained accounts of dreaming 50–70% of the time (Nielsen 2000); only few reports contained elements of dreaming after awakenings from N3 sleep early during the night, when large slow waves are most prevalent in the EEG signal (Stickgold et al. 2001). Sleep inertia (i.e. the subjective feeling of grogginess following abrupt awakening) after awakening from deep sleep (NREM sleep stage N3) makes the evaluation of reports following these stages very difficult, and it is unclear to what extent individuals are conscious during this phase (Chugh et al. 1996).

Dreams that were reported after awakenings from NREM sleep were frequently attributed to confounding factors such as recall of dreams from REM sleep periods or waking confabulations (i.e. the unintentional production of false, distorted, or misinterpreted memories). However, it is important to note that reports of dreams after awakenings from NREM sleep are not merely a recall of dreams that occurred during the REM sleep phase (Nielsen 2000), because (1) dreaming has been reported after awakenings from the first period of NREM sleep before the occurrence of REM sleep (Nielsen 2000; Cavallero et al. 1992) and (2) individuals reported dreams after awaking from short naps that consisted of NREM sleep only (Suzuki et al. 2004; Carr and Nielsen 2015). As such, it has been suggested that dreaming during NREM sleep relates to “covert REM” brain activation processes, which occur outside polysomnographically scored REM sleep (Nielsen 2000). In line with this view, it is important to realize that wakefulness, REM, and NREM sleep are not necessarily mutually exclusive phenomena (Mahowald and Schenck 2005); sleep is far from being homogenous in terms of mental experiences. Hence, dreaming might be described along a continuum, ranging from thought-like mentation that is typical of the early stages of NREM sleep to very vivid dreams that are more typical of REM sleep (Desseilles et al. 2011).

Lucid dreaming

Lucid dreaming is a rare state of sleep in which individuals achieve awareness of their own state of consciousness. According to the most frequently used sleep scoring criteria, lucid dreaming is considered being a part of REM sleep (Rechtschaffen and Kales 1968; Iber et al. 2007) and typically occurs during late night REM sleep periods (Voss et al. 2009). However, recent preliminary evidence suggests that lucid dreaming may also occur during periods of NREM sleep (Stumbrys and Erlacher 2012). Lucid dreaming has a special status compared with non-lucid REM and NREM dreaming because it is a skill that needs to be trained and occurs only rarely in untrained individuals. Dream lucidity can be achieved through metacognitive training, developing autosuggestions, external sensory stimulation, and through frequently contemplating about one’s own state of consciousness (LaBerge 1980; Hearne 1983; Purcell et al. 1986; Stumbrys et al. 2012). Lucid dreaming itself might occur in different degrees, ranging from pre-lucid reflections (i.e. a minimal awareness that one is dreaming) to deliberately controlling the dream narrative (Hearne 1982; Tyson et al. 1984; Barrett 1992; Kahan and LaBerge 1994). Since dream lucidity can be trained and signaled in experimental settings by means of the eye-signalling technique (LaBerge et al. 1981), it constitutes a promising endeavour for dream and consciousness research.

Phenomenological Characteristics of Different Sleep Phases

Many of the typical qualities of dreaming are similar to our waking experience. Such similarities include the full range of multimodal sensory qualities, colourful visual imagery, occasionally realistic pain perception, as well as almost identical spatial organization (i.e. the experience of a real world with the dreamer being at its centre) (Windt and Noreika 2011). However, Swiss psychiatrist and founder of Analytical Psychology Carl Jung already recognized in his famous work *On the Nature of Dreams* that dreams could be distinguished from wakefulness 'by many "bad qualities" such as lack of logic, questionable morality, uncouth form, and apparent absurdity or nonsense' (Jung 1945, 364). Interestingly, the phenomenological characteristics of dreams in the various phases of the sleep cycle differ in several ways.

REM sleep

Narrative. Particularly rich, emotional, and perceptually vivid dream experiences have been reported after awakenings from REM sleep (e.g. Foulkes 1962; Dresler et al. 2015). Dreaming during REM sleep typically follows loose, fanciful, and often very bizarre narratives; relates to current concerns; reflects interests, personality, and mood; draws on long-term memory; and involves social interactions (Hall and Van de Castle 1966; Domhoff 2003; Fox et al. 2013; Underwood 2013; Foulkes 2014). The dreamer is often uncertain about time, space, and personal identities and typically has the subjective experience of being awake (Schwartz and Maquet 2002). Reports of dreaming tend to be most elaborate and bizarre after waking up from the last period of REM sleep (Hobson 2009).

Sensation and perception. Dreams share similarities with experiences during wakefulness, since the perceptual modalities that are utilized most during waking hours also dominate during dreaming (Hobson 1989). Dream experiences are typically characterized by a range of visual and auditory sensations, physical activities such as self-motion or interaction with objects in the environment, and involve written and spoken language (Desseilles et al. 2011). Reports of awakenings from REM sleep contain significantly more accounts of sensory experiences than do reports following NREM sleep (Carr and Nielsen 2015). Tactile percepts, odours, tastes, as well as pleasure and pain are not as commonly reported following REM sleep awakenings (Hall and Van de Castle 1966; Domhoff 2003; Hobson 2009; Foulkes 2014). Oftentimes the sensational and perceptual experiences of the dream world are unlike those which occur in the world of wakefulness. Alterations from waking life experiences include sensory distortions, misidentifications of characters and places, changes in spatio-temporal integration (e.g. the integration of time and location of an event), misbinding of objects' features, dissociation, and transpositions (e.g. frequent and abrupt changes in the dream narrative) (Desseilles et al. 2011).

Emotion. Reports following REM sleep awakenings consistently contain more emotional content than those following NREM sleep (Wamsley et al. 2007). Dreamers tend to report elevated levels of joy, surprise, anger, fear, and anxiety (Foulkes et al. 1988; Strauch and Meier 1996; Fosse et al. 2001), whereas sadness, guilt, and depressed affect tend to be less common. A possible explanation for this finding might be less critical self-reflection during dreams (Hobson et al. 2000). Since REM dream reports frequently contain fear- and anxiety-related

elements (Valli and Revonsuo 2009), it has been suggested that the realistic representation of fear in dreams and nightmares serves as a threat simulation in a harmless environment in order to prepare individuals for dangerous situations in real life (Revonsuo 2000; Valli et al. 2005). It has also been shown that several periods of dreaming during one night may be related to the same emotional conflict (Offenkrantz and Rechtschaffen 1963).

NREM sleep

During the sleep-onset phase, individuals frequently experience hypnagogic hallucinations while being unaware that they have already fallen asleep (Underwood 2013). These experiences share some similarities with dreams during REM sleep in terms of dream bizarreness but are typically characterized by emotional flatness (Foulkes and Vogel 1965; Vogel et al. 1972). They are often static (Hobson et al. 2000; Hobson and Pace-Schott 2002) and usually involve no self-character (Foulkes 2014). Activities that were performed before sleeping might influence the content of such hallucinations (Stickgold et al. 2000; Wamsley et al. 2010).

After the sleep-onset, NREM dreams are typically more thought-like, fragmentary, and related to current concerns, unlike the vivid, hallucinatory, and mainly visual content of REM dreams (Eiser 2005). After awakenings from sleep stage N3 early during the night, reports tend to be short, thought-like, less vivid, less visual, less motorically animated, less emotional, and less emotionally pleasant than REM reports, while being more conceptual, more plausible, more concerned with current issues, and typically involve greater volitional control (Rechtschaffen 1973; Hobson et al. 2000). Late night NREM sleep reports are usually longer and more hallucinatory, often indistinguishable from REM sleep reports (Monroe et al. 1965; Antrobus et al. 1995).

Similarities with psychosis

Interestingly, dream phenomenology has often been compared with psychosis because dreams share large similarities with many of the typical characteristics of psychosis and particularly with the positive symptoms of schizophrenia (e.g. false beliefs due to incorrect inferences about reality or distorted sensory perceptions that have no apparent external source) (Hobson 1989; Hobson et al. 2000; Hobson and Pace-Schott 2002; Limosani et al. 2011; Windt and Noreika 2011; D'Agostino et al. 2013). These similarities range from internally generated, vivid imagery to intensified and often inappropriate affect as well as diminished ego functions (i.e. the capacity to distinguish what is occurring in one's mind and what is occurring in the outside world). Most pronounced are elevated levels and uncritical acceptance of cognitive bizarreness, decreased reality testing, and the delusional belief of being awake while dreaming (Limosani et al. 2011). Furthermore, the dreamer lacks control of dream events and often shows blunted distinction between first- and third-person perspectives (Hobson et al. 1998; Schwartz and Maquet 2002; Maquet et al. 2005). These observations are supported by functional magnetic resonance imagining data of psychotic patients, which suggest that dream bizarreness (i.e. improbability, incongruity, and vagueness) largely overlaps with patients' incongruous and bizarre waking experience (for review, see Limosani et al. 2011). In fact, there are remarkable similarities in terms of cognitive bizarreness between the waking thoughts of individuals with psychosis, their dream

reports, and the dream reports of healthy individuals (e.g. Scarone et al. 2008). Interestingly though, the psychotic patients differ from the healthy individuals in that they tend to judge their dream reports as less bizarre (Lusignan et al. 2009); they fail to distinguish self-generated and non-self-generated percepts and perceive cognitive bizarreness as being real without any critical reflection (D'Agostino et al. 2013).

Contrasting the state of lucid dreaming with psychosis, Dresler et al. (2015) suggested that understanding lucidity during dreams may shed light on the mechanisms underlying the lack of insight into the delusional nature of one's current state of consciousness that patients with psychosis often suffer from. Taken together, these findings indicate that there might be a shared mechanism responsible for some of the features of dreaming and psychosis (Limosani et al. 2011). However, a recent paper by Mota et al. (2016) challenges this notion: psychotic lucid dreamers reported more frequent control of their dreams than non-psychotic lucid dreamers. As such, psychosis could potentially amplify the experience of internal stimuli at the expenses of external ones, enabling psychotic patients to better control their internal reality than healthy individuals.

Changes in Level and Quality of Consciousness during Sleep

'Just as the psyche has a diurnal side which we call consciousness, so also it has a nocturnal side: the unconscious psychic activity which we apprehend as dreamlike fantasy' (Jung 1934, 147). In line with this notion, Jung (1945, 364) suggested that dreams are 'fragment[s] of involuntary psychic activity, just conscious enough to be reproducible in the waking state.' Even though this illustrates that dreaming and wakefulness likely differ with regards to conscious experience, advances in cognitive neuroscience and dream research reveal that these differences are not as clear-cut as originally assumed but can—in a simplified model—be placed along a continuum (more complex models assume a space of multiple dimensions; Voss and Voss 2014; Bayne et al. 2016). These range from no consciousness to simple awareness of perception and emotion (i.e. primary consciousness) to self-reflective awareness, abstract thinking, volition, and metacognition (i.e. secondary consciousness, also referred to as higher-order consciousness or self-consciousness) (Morin 2006). [It should be noted that a number of different models concerning the idea of levels of consciousness have been proposed: for instance, the four-level structural model of cognition by Brown (1976), Neisser's (1997) five-level model of consciousness, a three-level model by Schooler (2002), or Block's (1995) notion of phenomenal and access consciousness. In the present review, we use the concepts of primary and secondary consciousness to represent the general notions of sensory awareness and higher level of awareness such as reflection, respectively. These concepts fit the purpose of our distinction between different states of consciousness during sleep (Edelman 1992); they have been frequently used in the sleep and dream research literature (Edelman 2003; Hobson and Voss 2011; Kahan and LaBerge 2011; D'Agostino et al. 2013; Voss et al. 2014; Zink and Pietrowsky 2015).]

One can generally differentiate between consciousness during wakefulness, consciousness during dreaming, and non-consciousness, with the possibility of intermediate states being present (Limosani et al. 2011). Consciousness during waking hours is characterized by the awareness of the external world, our bodies, and our selves. When people are dreaming, they are

to some extent consciously aware of their internal world, have sensory, perceptual, and emotional experiences but typically fail to recognize their own condition, the bizarre features of the dream world, their poor memory access, and their limited thought capabilities (Hobson 2009). Dream consciousness and waking consciousness may differ in terms of their origin (i.e. their respective causal pathway), with the former partly representing an offline, internally generated simulation of the latter. In line with this notion, it has been suggested that dreams may be seen as a purer form of consciousness, which is free of the constraints imposed by the perception of, and interaction with, physical environments (Revonsuo 2006).

Early reports suggested a single-mindedness and isolation during dreaming, which refers to the dreamer being absorbed in the dream world without being aware of an alternative reality (Rechtschaffen 1978). However, the nature, level, and quality of conscious experience during sleep show large variability (Nir and Tononi 2010). To some extent, this might be comparable to the multiplicity of conscious substates that occur during wakefulness (e.g. task vs. default modes of the brain) (Singer and Antrobus 1965; Raichle and Mintun 2006). Consciousness is clearly not an all-or-nothing phenomenon but a multifaceted concept with aspects varying across species, vigilance states (i.e. the degree of responsiveness to stimuli), and health conditions.

Although there is likely a consensus that consciousness exists while individuals are dreaming, there is an ongoing debate as to whether consciousness exists during dreamless sleep as well (Windt et al. 2016). Some authors argue that consciousness continues throughout dreamless sleep, provided that one remains aware of having slept. The topic of dreamless sleep is beyond the scope of this paper (for further discussions on this issue, please see Thompson 2015; see also Windt 2015).

REM sleep

Dreams that occur during REM sleep show mostly aspects of primary but not of secondary consciousness. During REM sleep, the dreamer tends to have less metacognitive activity (i.e. the processes by which individuals monitor and control their own cognitive processes), reflective thought, and volitional capabilities (Kahan et al. 1997; Kahan and LaBerge 2011; Dresler et al. 2014). The dreamer has only limited access to information about the past and anticipated future, and typically concerns him or herself exclusively with the present content of the dream narrative (Fox et al. 2013). However, some reports of REM dreams involve reflective thought, such as puzzlement about improbable or impossible events, contemplative alternatives in decision-making, and reflection during social interactions (Wolman and Kozmová 2007), as well as theory of mind processes (i.e. the ability to attribute mental states to oneself and others) (Kahn and Hobson 2005).

NREM sleep

Reports of conscious experience across NREM sleep phases vary to a great extent (Rechtschaffen 1973). Although the frequency of reporting dreams after NREM awakenings is sparse and generally less elaborate than after periods of REM sleep, which might be due to the brain's inability to encode memories of the dreams (Massimini et al. 2005), the very existence of NREM dream reports provides evidence for the idea that consciousness does not fully cease during NREM sleep (e.g. Goodenough et al. 1965; Suzuki et al. 2004).

Lucid dreaming

Lucid dreaming is a hybrid state of consciousness with features of both waking and dreaming (e.g. hallucinatory dream activity combined with aspects of primary and secondary consciousness such as self-reflective thought, abstract thinking, metacognition, and agentive control) (Voss et al. 2009). Dresler et al. (2014) recently investigated how volitional aspects of consciousness vary across wakefulness, non-lucid, and lucid dreaming. They found that levels of self-determination (i.e. the subjective experience of acting freely according to one's will) were similar for lucid dreaming and wakefulness while being reduced in periods of non-lucid dreaming. Furthermore, planning ability (i.e. how well organized one pursues plans and intentions) seemed to be impaired during both non-lucid and lucid dreaming. However, this may be because it is not necessary to plan during dreams and spontaneous execution of intentions is simply more common. Intention enactment (i.e. how promptly and determined intentions are executed) was most pronounced during lucid dreaming and did not differ between wakefulness and non-lucid dreaming. This seems plausible because the lucid dreamer is aware that obstacles in dreams are not real and can easily be overcome (Dresler et al. 2014). In line with this, it has been suggested that restored access to metacognitive abilities and memory functions during lucid dreaming enable the dreamer to execute his or her intentions (Metzinger 2004; Windt and Metzinger 2007). Contrasting lucid dreaming and non-lucid dreaming mirrors contrasting primary and secondary consciousness (Dresler et al. 2009). Non-lucid REM sleep dreams lack those very features of secondary consciousness, which are the defining characteristic of dream lucidity. These include insight, control over thought and actions, as well as logical thought (Voss et al. 2013). Interestingly, lucid dreaming may be the only phenomenon that can be utilized to examine changes in primary and secondary consciousness in the same vigilance level (Spoomaker et al. 2010) and therefore constitutes an important topic of research.

Brain Activity during Sleep

Establishing a link between dreaming and its underlying neurofunctional changes constitutes a major challenge for researchers (Limosani et al. 2011) because dreaming arises from brain activity that is largely independent of interactions with external stimuli (Revonsuo 2006). Dream research typically aims to retrospectively correlate neural activity with the dream characteristics that are common to all dreams (e.g. dream bizarreness—although varying tremendously depending on the sleep stage) rather than the content of individual dreams (Nir and Tononi 2010; but see Siclari et al. 2017). Periods of REM sleep, NREM sleep, and lucid dreaming are characterized by patterns of regional brain activity that are both similar and distinct from those observed during wakefulness. In what follows, we review studies on brain activity during REM and NREM sleep rather than brain activity during REM and NREM 'dreaming' per se. As such, it is important to note that the interpretations of these findings are to some extent speculative, given that the methods used in the majority of these studies do not allow for a separation of the duration of REM/NREM sleep and dreaming.

REM sleep

The REM sleep phase has most clearly been defined in terms of neurofunctional activation (Fig. 1), which corresponds to some

of the key characteristics of the subjective experience of dreaming (e.g. vivid imagery as well as articulate and incongruous storylines) (Limosani et al. 2011).

Similarities with wakefulness. The EEG signal during REM sleep shares large similarities with that of wakefulness, and positron emission tomography (PET) studies have shown that global brain metabolism tends to be very similar as well (Hobson et al. 2000; Maquet 2000).

Hyperactivity. Several brain regions become particularly active during REM sleep. There is strong metabolic activity in higher-order occipito-temporal visual association areas, which might be responsible for the often very vivid visual dream imagery during REM sleep (Braun et al. 1997; Nofzinger et al. 1997; Maquet et al. 2000). Hyperactivity in motor regions such as the primary motor and premotor cortices, the cerebellum, and the basal ganglia may account for the frequently reported motor content of dreams (Braun et al. 1997; Maquet et al. 2000). Furthermore, increased levels of activity have been observed in the pontine tegmentum, the thalamus, the basal forebrain, as well as in limbic and paralimbic structures (e.g. amygdaloid complexes, hippocampal formation, and anterior cingulate cortex) (Maquet et al. 1996; Braun et al. 1997; Nofzinger et al. 1997). These brain regions are associated with emotional processing and might be responsible for the often very intense emotional aspects of REM sleep dreaming (Maquet and Phillips 1998; Hobson et al. 2000). There is also increased activity in other regions such as the medial prefrontal cortex, circuits of the medial temporal lobe region, and the posterior cingulate cortex (Maquet et al. 1996; Braun et al. 1997, 1998; Nofzinger et al. 1997; Fox et al. 2013), which are implicated in memory and self-referential processing (Nofzinger et al. 1997; Ioannides et al. 2009). In fact, there is striking overlap between the default mode network (i.e. the network of brain regions that are active when an individual is awake and not currently engaged in a task), which is associated with self-referential processing, and areas that become increasingly active during REM sleep (Fox et al. 2013). This network may play a key role in both mind-wandering and dreaming and possibly represents a shared neural substrate of the two phenomena (Domhoff and Fox 2015).

Hypoactivity. Even though several brain regions become hyperactive during REM sleep, a number of structures show decreased levels of activity. Among these structures is the right inferior parietal cortex, which is involved in waking volition (Goldberg et al. 2008; Desmurget et al. 2009) and which contributes to a unified representation of self and self versus other perspectives (Farrer et al. 2003). Decreased activity of the right inferior parietal cortex (Maquet et al. 1996; Braun et al. 1997) might allow the dreamer to participate in both first- and third-person perspectives (Maquet et al. 2005). Moreover, there is deactivation of executive regions of the prefrontal cortex such as the dorsolateral prefrontal cortex (DLPFC) and the orbitofrontal cortex, but also in regions including the posterior cingulate gyrus, the precuneus, and the inferior parietal cortex. These areas are typically involved in cognitive control, metacognition, and ego functions (e.g. orientation in time and space, reality testing, and self-monitoring) and may underlie the lack of insight, restricted volitional capacities, and impaired metacognition during dreaming (Maquet et al. 1996; Braun et al. 1997; Nofzinger et al. 1997; Maquet 2000, 2005; Hobson and Pace-Schott 2002; Schwartz and Maquet 2002; Fox et al. 2013). Hypoactivation of the prefrontal cortex may also be a contributing factor for dream amnesia (Fox et al. 2013).

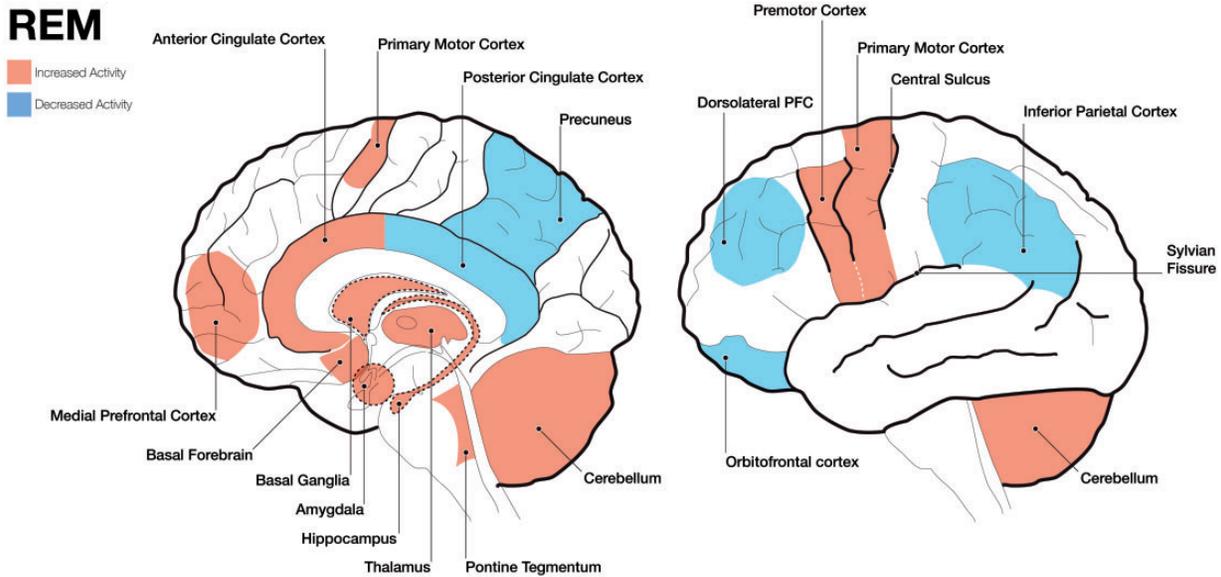


Figure 1. Schematic brain images showing increased and decreased activity of different brain areas during rapid eye movement (REM) sleep. The left panel shows a mid-line incision looking at the right hemisphere and the right panel shows a lateral surface of the brain. Areas highlighted with dashed borders are deeper structures.

NREM sleep

The neuroscientific study of NREM dreaming (Fig. 2) only emerged more recently, but findings tend to be more informative with regards to exploring the neural correlates of dreaming because of methodological and data-analytical advances including the use of computational learning algorithms. A recent study by Horikawa et al. (2013) which utilized machine learning techniques showed that visual imagery during sleep onset is represented by brain regions including the early visual pathway, fusiform face area, and parahippocampal place area. Brain activity underlying these hypnagogic hallucinations may differ from that underlying dreams occurring during REM sleep though (Underwood 2013). Utilizing high-density EEG recordings and performing serial awakenings, Siclari et al. (2017) showed that dream reports following awakenings from the N2 stage were preceded by ‘decreased’ low-frequency and ‘increased’ high-frequency power in bilateral parieto-occipital areas including the medial and lateral occipital lobes as well as the precuneus and posterior cingulate gyrus (for high-frequency power, the lateral frontal and temporal cortices showed increased activity as well). Furthermore, the authors confirmed these findings for sleep stages N2 and N3 in an independent sample and irrespective of the dreamer’s ability to remember specific dream contents.

Lucid dreaming

Periods of lucid dreaming show increased activity in areas such as the DLPFC, bilateral frontopolar prefrontal cortex, and parietal areas including the precuneus, the inferior parietal lobules, and the supramarginal gyrus (Fig. 3). It has been suggested that the fronto-parietal activity during lucid dreaming corresponds to the reinstatement of reflective capabilities (Dresler et al. 2015), thereby mediating features of secondary consciousness (Dresler et al. 2012) such as metacognitive evaluation (Stuss et al. 2001; Schmitz et al. 2004; Fleming et al. 2012) and self-referential processing (Cavanna and Trimble 2006). In fact, research on the neural correlates of lucid dreaming might be key in

understanding the neural substrates of secondary consciousness (Hobson and Voss 2010; Dresler et al. 2014). So far, the study of lucid dreaming is limited to periods of REM sleep because the classical method to investigate lucid dreaming, the eye-signalling technique, is not applicable to NREM sleep (Dresler et al. 2015). Furthermore, research on lucid dreaming mostly pertains to case studies, and conclusions about the neural correlates of lucid dreaming should be regarded as preliminary.

Neural Correlates of Dream Phenomenology and Changes in Consciousness

The heterogeneous brain activity during sleep may explain some of the typical features of, and variation across, dreams during different stages of sleep (Desseilles et al. 2011). This is in line with Pace-Schott (2010) who described dreaming as ‘an imprecise experiential simulacrum [i.e. a representation or imitation] of waking resulting from neurobiological processes that must differ from those that generate waking consciousness.’

Consciousness

Decreased metabolic activity in the DLPFC during periods of REM sleep might be responsible for reduced features of secondary consciousness, which return during periods of lucid dreaming when the DLPFC becomes more active again (Voss et al. 2009; Hobson and Voss 2010; Dresler et al. 2012). During REM sleep dreaming, the dreamer thinks that he or she is awake, which is a delusion that might be due to persistent inactivation of frontal and parietal circuits necessary for waking memory, self-reflective awareness, and insight. The global deactivation of the pontine tegmentum, the amygdala, the anterior commissure, the parietal operculum, deep frontal white matter, and the mid-line thalamus during NREM sleep compared with waking, and their subsequent reactivation during REM sleep might explain why some aspects of consciousness during REM sleep might be more readily available than during NREM sleep (Maquet et al. 1996; Braun et al. 1997; Nofzinger et al. 1997).

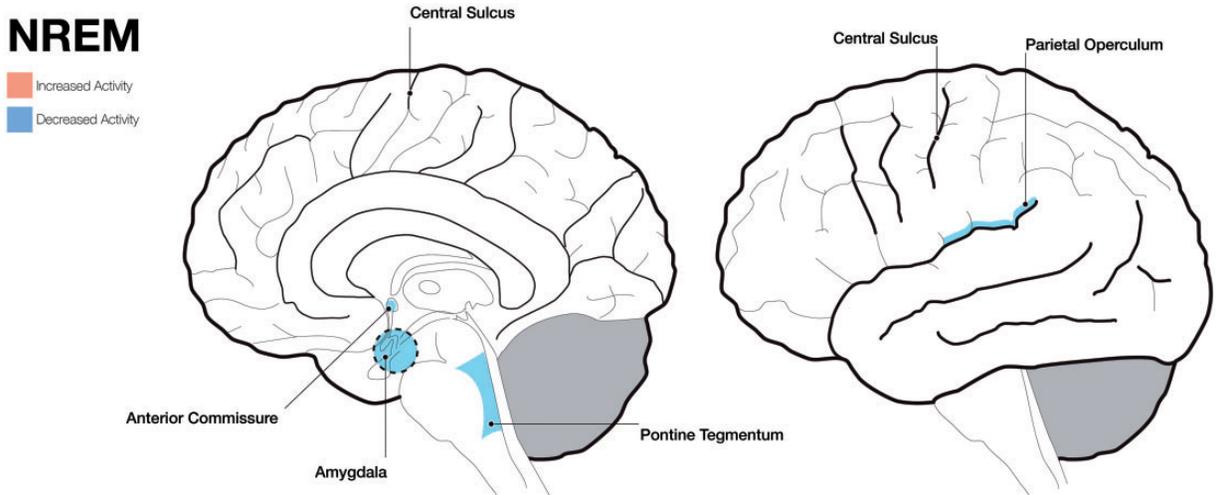


Figure 2. Schematic brain images showing increased and decreased activity of different brain areas during non-rapid eye movement (NREM) sleep. The left panel shows a mid-line incision looking at the right hemisphere and the right panel shows a lateral surface of the brain. Areas highlighted with dashed borders are deeper structures.

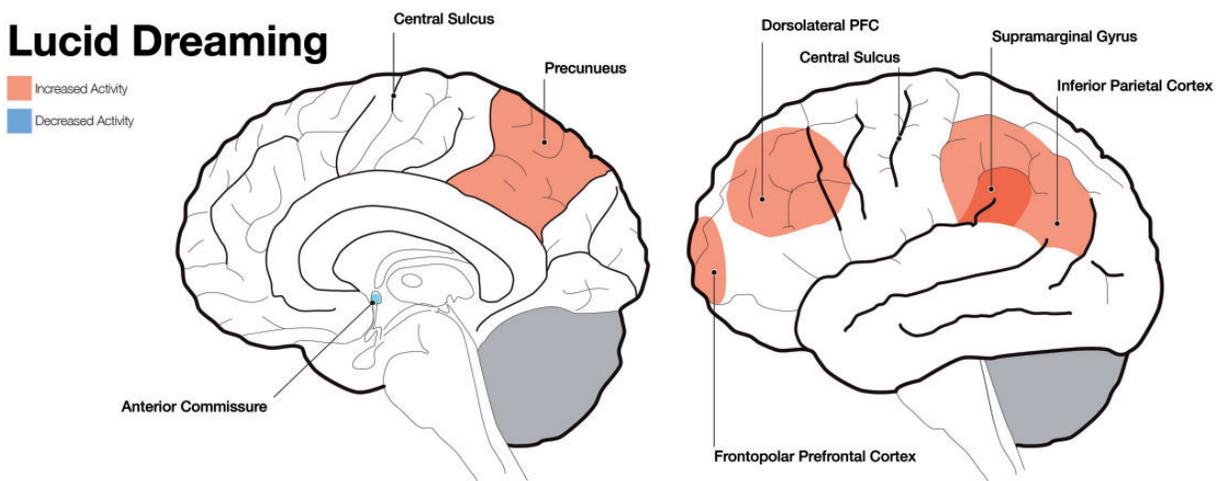


Figure 3. Schematic brain images showing increased and decreased activity of different brain areas during lucid dreaming. The left panel shows a mid-line incision looking at the right hemisphere and the right panel shows a lateral surface of the brain.

However, preliminary findings suggest that localized activity changes in the parieto-occipital region, irrespective of global activity in the rest of the cortex, may constitute a marker of conscious experience during sleep (Siclari et al. 2017). The neural correlates of lucid dreaming largely overlap with brain areas that are involved in self-reflective thought and subserve volitional capabilities (Voss et al. 2009; Hobson and Voss 2010; Dresler et al. 2014).

Phenomenology

According to the principle of perceptual equivalence (Finke 1989), there are common neural substrates for perception and imagery. Some of the visual experiences during the sleep onset phase are represented by brain activity patterns that are similar to the ones observed during stimulus perception (Horikawa et al. 2013), and activation in visual-occipital and auditory-temporal cortices during REM sleep may underlie the visual and

auditory elements that are frequently reported after awakenings from REM sleep (Braun et al. 1997). In line with this, patients with extrastriate occipito-temporal lesions report cessation of visual dream imagery (Solms 1997). Several other behaviours share similar neural correlates during wakefulness and dreaming (Erlacher and Schredl 2008; Siclari et al. 2017). For instance, dream hand movements activate the same areas of the motor cortex that are active when actually executing hand movements during wakefulness (Dresler et al. 2011). Since a range of subcortical and neocortical structures that are active during waking are also active during REM sleep, but inactive during NREM sleep, this might explain why the phenomenological experience of dreaming during REM sleep is much more diverse than during NREM sleep (Hobson 2009). For instance, waking emotional processes that are active during REM sleep are inhibited during NREM sleep, and mechanisms governing sensory vividness of imagery are enhanced in REM sleep while being inhibited during periods of NREM sleep (Carr and Nielsen 2015).

Conclusion and Future Directions

In what follows we will highlight some important shortcomings that have emerged from reviewing the current literature on the neural correlates of dreaming and we will suggest potential ways to address these in future research.

1. Given that most research has focused on the study of REM sleep, much remains to be learned about the mechanisms underlying dreaming during NREM sleep. Future investigations should more systematically contrast the different phases of NREM sleep with wakefulness, REM sleep, and periods of lucid dreaming. Recent efforts in dream research have investigated whether daytime naps are suitable for sampling and comparing dreaming during REM and NREM sleep. It was shown that recall rates for REM and NREM naps were slightly elevated to normal night-time recall rates (Carr and Nielsen 2015), making it perhaps an even more efficient tool to study dreams.
2. Causal links have—until recently—not received much attention in the literature on dreaming. Novel brain stimulation methods including transcranial alternating current stimulation (tACS) and transcranial magnetic stimulation can be used to make causal inferences on the relationship between brain activity and behaviour (e.g. Nieminen et al. 2016). For example, tACS has recently been utilized to experimentally induce lucid dreaming (Noreika et al. 2010; Stumbrys et al. 2013; Voss et al. 2014), and might hence be a valuable tool for a more systematic study of the neural substrates of dreaming.
3. No objective assessment (or verification) of dreams is currently possible and researchers rely exclusively on the collection of subjective dream reports. These are being obtained only after a change in vigilance state has occurred, which might alter the quality and content of the report (Kussé et al. 2010). Novel brain imaging methods, in terms of both hardware (e.g. functional near-infrared spectroscopy, fNIR or fNIRS; Dresler et al. 2011), and software (statistical learning or machine learning algorithms; Huth et al. 2016; Wen et al. 2016, preprint; Zurawel et al. 2016) may enable a more objective readout of the dream. This is particularly important considering that (i) memory is reconstructive and there is a time lag between the actual dream and its report, (ii) the original dream content may be distorted due to interfering material of the waking environment, (iii) there are limitations inherent to verbal reports, and (iv) moral censorship (Hobson et al. 2000; Windt 2013). Moreover, the absence of dream reports does not necessarily imply an absence of dreaming, since these are easily and quickly forgotten.
4. At present, most researchers are working in highly specialized fields (e.g. research on sleep and lucid dreaming), potentially overlooking knowledge in other relevant areas (e.g. coma and vegetative state) that could benefit their own discipline. To gain a more comprehensive understanding of the mechanisms underlying consciousness, cross-fertilization between multiple fields is necessary.
5. Some evidence suggests that dream lucidity training can be applied in clinical settings as a form of nightmare therapy (Spoormaker et al. 2003; Spoormaker and Van Den Bout 2006). Although the mechanism of action of lucid dreaming is not fully understood, examining the characteristics of patients for whom this type of therapy seems

effective may shed light on the nature of lucid dreaming itself.

6. Understanding the mechanisms underlying consciousness in the healthy human brain might enable us to identify processes that are dysfunctional in pathologies, thereby enabling us to develop better treatments. For instance, lucid dreaming might be of therapeutic value in sleep disorders and for individuals experiencing frequent nightmares. At the same time, studies on the neural correlates of dreaming in clinical populations are informative: for example, a recent study by Dodet et al. (2015) has shown that comparing individuals with and without narcolepsy can elucidate the nature of lucid dreaming.

Due to limited space, only a small number of studies on pathological states were included in the present review. Moreover, research on altered states of consciousness that occur during meditation (Lutz et al. 2007), hypnosis (Rainville and Price 2003), vegetative states (Owen et al. 2006), coma (Laureys and Schiff 2012), or drug use (Carhart-Harris et al. 2014) could not be discussed here.

The study of dreaming is of major importance insofar as it helps to more fully understand consciousness. It offers a unique opportunity to gain insight into the processes and mechanisms involved in waking consciousness through studying the similarities with, and differences from, dream consciousness. However, we have only just started to understand the neural correlates of dreaming.

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Author contributions

A.-H.J. conceived the initial project idea; J.M. further developed the focus and structure of the review under the supervision of A.-H.J.; J.M. wrote the initial draft of the paper; J.M. and A.-H.J. critically revised the paper.

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