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Cognitive and emotional processes during dreaming: A neuroimaging view [☆]

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ABSTRACT

Dream is a state of consciousness characterized by internally-generated sensory, cognitive and emotional experiences occurring during sleep. Dream reports tend to be particularly abundant, with complex, emotional, and perceptually vivid experiences after awakenings from rapid eye movement (REM) sleep. This is why our current knowledge of the cerebral correlates of dreaming, mainly derives from studies of REM sleep. Neuroimaging results show that REM sleep is characterized by a specific pattern of regional brain activity. We demonstrate that this heterogeneous distribution of brain activity during sleep explains many typical features in dreams. Reciprocally, specific dream characteristics suggest the activation of selective brain regions during sleep. Such an integration of neuroimaging data of human sleep, mental imagery, and the content of dreams is critical for current models of dreaming; it also provides neurobiological support for an implication of sleep and dreaming in some important functions such as emotional regulation.

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1. Introduction

Dreaming represents a major facet of human experience. Yet, the nature of the dream-state is highly subjective and a genuinely personal experience making a scientific analysis of dreaming somewhat prohibitive. Dreaming is a state of consciousness characterized by internally-generated sensory-motor, verbal, cognitive and emotional experiences, which may unfold in actions and events forming imaginary plots. Sensory content predominantly involves visual and auditory modalities. Dreamed motor behaviors are frequent and diverse, including physical activities like self-motion (walking, running, jumping) and interacting with objects. Verbal content might include written and spoken language (heard or produced by the dreamer). Cognitive content also encompasses several aspects of executive functions (planning, reasoning, thinking, etc.), memory (elements in dreams involve retrieval from recent or more remote memory), as well as spatial navigation abilities, among others. Emotional experiences in dreams are frequent, intense, and possibly biased toward negative emotions. Yet, probably all the categories of dream experience described above are also subject to many alterations and distortions that are unlikely to occur in real waking life (Hobson, Stickgold, & Pace-Schott, 1998; Schwartz & Maquet, 2002). Despite the implausibility of many dream elements with respect to the real world, the dreamer usually remains unaware of being in

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a dream and experiences the dream as a world analog (Johnson, Kahan, & Raye, 1984). Because of these distinctive properties, the study of dreaming offers a fascinating opportunity to better understand the varieties of conscious experiences across common, daily but dramatic changes in brain states.

Below, we first provide some historical background for a neuroscience approach to dreaming. We then review the available functional neuroimaging data that describe regional cerebral activity during normal human REM sleep, as well as the likely neurophysiological source for such spontaneous patterns of activity. We also review brain imaging of mental imagery and sensory imagery. We also discuss how brain activity during sleep might be interpreted in neurocognitive terms based on common dream features. In sum, this integrated view on the neural correlates of dreaming provides fundamental elements for the understanding of the organization and functions of dreaming.

1.1. Modern history of dream research

In the modern occidental era, pioneering scientific experimentations on dreaming emerged during the second half of the 19th century (Delboeuf, 1885/1993; Macario, 1857/1978; Maury, 1862; Saint-Denys, 1867/1977; Schwartz, 2000). In those days (as nowadays), introspective dream reports were considered as a valuable material for scientific enquiry, yielding unique information about what was perceived, felt, or thought in a dream. Very ingenious experiments were designed to determine what factors might influence the dream content and what rules may determine the dream scenario. For example, the French sinologist and man of letters Hervey de Saint-Denys designed the following experiment to test the influence of memory associations on the formation of dreams (Hervey de Saint-Denys, 1867/1977). During a trip that lasted a few weeks, he used a new perfume and hermetically closed the bottle of perfume before traveling back home. A few months later, he asked one of his servants to put a few drops of the perfume on his pillow, but he also asked his servant not to tell him what night that would be. Ten days later, Hervey de Saint-Denys suddenly dreamt that he was back in the same place that he visited during his trip – on that night the servant had put some of the perfume on his master's pillow. The same experiment was successfully repeated for different perfumes, different places, and different time lags, thus corroborating Hervey de Saint-Denys' hypothesis that the stream of dreams is guided by associations or what he called "psychological affinities". A similar use of odors as cues for memory replay during sleep was recently reported in an elegant brain imaging study (Rasch, Buchel, Gais, & Born, 2007).

These early and promising developments for a scientific approach to dreaming were considerably slowed down at the beginning of the 20th century, because of two major events in the history of psychology. On the one hand, after the publication of Freud's psychoanalytic masterpiece, "The Interpretation of Dreams", studies relying exclusively on the manifest content of dreams were discredited on behalf of a quest for the "true" dream, i.e., the latent content hidden beneath the apparent dream (Freud, 1955/1900). On the other hand, the advent of behaviorism was detrimental to the study of dreaming because of its refutation of the existence of mental experiences such as dreams. Hence, both the emphasis on dream phenomenology and the use of introspective dream reports initiated in the late 19th century were rapidly challenged, the former by psychoanalysis and the latter by behaviorism.

A next turning point for the history of the science of dreaming was in the late 1950s, when (i) an objective indicator of the dreaming state was discovered and (ii) a new cognitive approach to the phenomenology of dreams was developed (for a review, Foulkes, 1996).

Between 1953 and 1957, in a laboratory at the University of Chicago, Nathaniel Kleitman and his two students, Eugene Aserinsky and William Dement made a revolutionary discovery. They observed that dreaming occurred during specific periods of sleep when cortical activity is high (i.e., high-frequency/low-amplitude electroencephalographic [EEG] activity, analogous to resting wake state) and accompanied by rapid eye movements (REM), increased heart rate, and respiratory activity (Aserinsky & Kleitman, 1953; Dement & Kleitman, 1957). These REM periods were also found to be associated with muscle atonia (Jouvet, 1994), thus preventing the dreams from being acted out. Compared to non-REM periods, REM awakenings yielded longer dream reports, which appeared to also be more emotional and perceptually vivid, and contained more bizarre features (Aserinsky & Kleitman, 1953; Hobson, Pace-Schott, & Stickgold, 2000). Thus, REM sleep was considered as a state of high cerebral and low physical activation that would provide a neurophysiological marker of dreaming. Not surprisingly, this discovery was extremely influential because it opened new perspectives for the scientific study of dreaming. Critically, the discovery of REM sleep also demonstrated that sleep is not a homogenous state of mental and cerebral quiescence, but that some sustained periods of elevated neurophysiological activity underlying the production of dream experiences were distributed across the sleep night (Aserinsky & Kleitman, 1953). While the equation "REM sleep = dreaming" effectively reduces the characterization of the neural correlates of dreaming to a comparison between REM sleep and waking or NREM sleep, it is important to keep in mind that neither dreaming nor REM sleep are stable, homogeneous and unique states. Indeed, dreaming might best be described along a continuum, from thought-like mentations typical of early NREM sleep to florid and vivid dreamlike experiences typical of REM sleep (Cavallero, Cicogna, Natale, Occhionero, et al., 1992; Stickgold, Malia, Fosse, Propper, & Hobson, 2001). In addition, some studies suggested the presence of a shift toward more dreamlike hallucinations and fewer directed thoughts both by REM and by time spent in sleep (Fosse, Stickgold, & Hobson, 2001, 2004; Nielsen, 2004; Stickgold, Malia, et al., 2001). These findings suggest that REM sleep might reasonably be considered as a facilitating neurophysiological state for dreaming to occur, even though dreams are not exclusively experienced during this sleep stage.

About the same time as Aserinsky and Kleitman wrote their inaugural article on REM sleep, Hall (1953/1966) published "The Meaning of Dreams" in which he described and classified the phenomenological characteristics of thousands of dreams

from college students. Based on this first investigation, Hall and Van De Castle (1966) later developed a detailed coding system for quantifying the manifest content of dreams (e.g., characters, settings, objects, emotions, social interactions), which was updated in recent investigations (e.g. Schneider & Domhoff, 2009). From then on, the phenomenological content of the dreams was again considered as useful descriptions of cognitive processes at play during sleep.

1.2. Functions of dreaming

The conception of dreaming has considerably changed through history, which led to many different hypothesized functions of dreaming (Barbera, 2008; Lavie & Hobson, 1986). Below we non-exhaustively review some of the main models of dreaming that have been proposed over the past 50 years or so, and which may have implications for the assessment of the neural bases of dreaming. For instance, several theories encompass the mind-brain reductionism claim that dreaming is a random by-product of REM physiology (Hobson & McCarley, 1977), which could be related to some “unlearning” mechanisms in an otherwise overloaded brain (Crick & Mitchison, 1983, 1995). More recent models involve that dreams echo dynamic functions like reactivation and further consolidation of novel and individually-relevant features encountered during previous waking experience (e.g. Cipolli, Fagioli, Mazzetti, & Tuozzi, 2004; Schwartz, 2010; Wamsley & Antrobus, 2009; Wamsley, Perry, Djonlagic, Reaven, & Stickgold, 2010). Such models of dreaming might be consistent with accumulating evidence showing the potential benefit of reprocessing freshly encoded information for long-term storage (Diekelmann & Born, 2010; Stickgold, Hobson, Fosse, & Fosse, 2001).

Extending this view to affective processes, Revonsuo and Valli recently proposed that the realistic representation of fear in dreams and nightmares might serve an evolutionary sound and adaptive function of “threat simulation”, by affording the rehearsal of threat perception and avoidance in an entirely harmless situation and without any detrimental consequences (Revonsuo, 2000; Valli et al., 2005). This proposal is compatible with psychological models suggesting that dreaming is a process of internal activation, arising from a person’s affective and emotional history and serving an emotion-regulation function (e.g. Cartwright, Lloyd, Knight, & Trenholme, 1984; Cartwright, Luten, Young, Mercer, & Bears, 1998; e.g. Mancia, 2005; Nielsen & Levin, 2007). In particular, since the 1970s several authors (among which Cartwright and Greenberg have been particularly influential) have shown that dreaming may promote the resolution of emotional conflict and reduce next-day negative mood (Cartwright, Agargun, Kirkby, & Friedman, 2006; Cartwright, Kravitz, Eastman, & Wood, 1991; Cartwright et al., 1998; Greenberg, Pearlman, Fingar, Kantrowitz, & Kawliche, 1970; Trenholme, Cartwright, & Greenberg, 1984). Along the same lines as Revonsuo’s evolutionary hypothesis, Franklin and Zyphur (Franklin & Zyphur, 2005) suggested that REM sleep may act as a general “virtual rehearsal mechanism”, which would play an important function in the early brain development, congruent with the prominent presence of REM sleep in new-born baby and infants. According to these authors, the optimization of brain development and connectivity in young organisms would benefit from adaptively experiencing rich and vivid environments during dreams. Thus, dreaming might have an adaptive function by facilitating the consolidation of relevant, new information into preexisting knowledge and neural networks, and by promoting the reorganization of cortical networks to maintain a psychological well-being and individuality despite potentially unfavorable influences arising during waking experiences (see Jouvet, 1998).

We will close this section with a brief practical note about challenges that the study of dreaming imposes to scientific enquiry. One first main constraint is that the dreamer is the unique observer and reporter of his/her own dream experiences, and dream content is obtained introspectively through memory recall. Consequently, several confounding factors may influence the accuracy of dream reports including forgetting, reconstruction mechanisms, verbal description difficulties, and censorship. The researchers must be well aware of these limitations and should minimize them by using suitable strategies when collecting or analyzing dream data (Schwartz & Maquet, 2002).

2. Neuroimaging of REM sleep

Since the 1990s, human brain imaging became a key player in the field of sleep research. Based on the hypothesis that dreaming mechanisms are most powerfully engaged during REM sleep (see above), neuroimaging studies have shown that the distribution of brain activity during REM sleep is not homogeneous, thus providing important insights into the putative cerebral underpinnings of dreaming. Sustained (tonic) versus transient (phasic) activations have been highlighted in REM (and non-REM) sleep. The neuroimaging methods that have been most widely used include positron emission tomography (PET) and more recently functional magnetic resonance imaging (fMRI). Unlike PET, fMRI allows repeated, non-invasive and high-resolution measurements of functional changes in the human brain. However, fMRI is associated with some constraints that make this method relatively complicated to use for sleep studies (e.g. strict head immobilization, loud auditory noise). As we discuss below, both these imaging techniques had a major influence on our understanding of the neural mechanisms at play during dreaming, and ultimately on our models of dreaming.

2.1. Distribution of brain activity during REM sleep

Early neuroimaging data first confirmed the sustained neuronal activity observed with EEG (Jones, 1991; Steriade & McCarley, 1990) by showing a high-level of cerebral energy requirements (Maquet et al., 1990) and a widespread increase

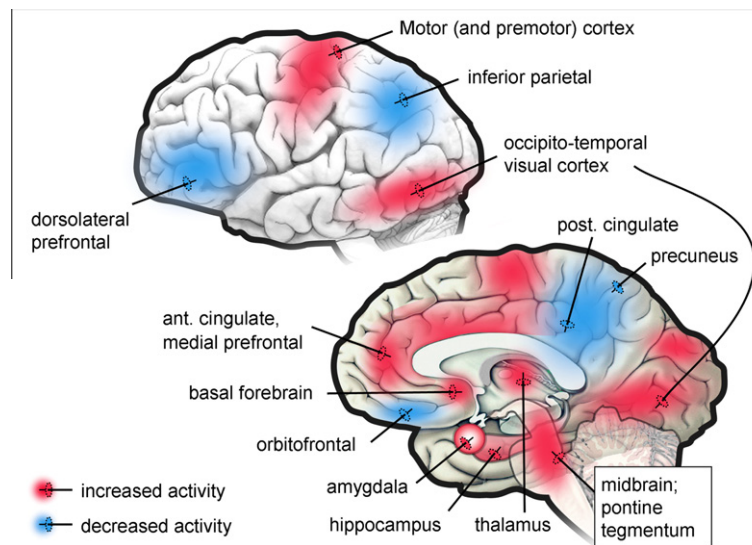


Fig. 1. Functional neuroanatomy of human REM sleep. Regions showing increased or decreased brain activity in the PET studies reported in the main text (Section 2) (For interpretation of the references to color in this figure, the reader is referred to the web version of this article).

of cerebral blood flow (Madsen, Holm, et al., 1991; Madsen, Schmidt, et al., 1991; Madsen & Vorstrup, 1991) during REM sleep. As compared to wakefulness and/or non-REM sleep, REM sleep is characterized by a specific “landscape” or pattern of brain activation (Fig. 1).

During REM sleep in humans, significant increase in regional brain activity has been found in the pontine tegmentum, thalamus, basal forebrain, as well as in limbic and paralimbic structures, including amygdaloid complexes, hippocampal formation, and anterior cingulate cortex (ACC) (Braun et al., 1997; Maquet et al., 1996; Nofzinger, Mintun, Wiseman, Kupfer, & Moore, 1997). Activation in these regions suggest that memory consolidation processes, in particular emotional memories, may occur during REM sleep (Hu, Stylos-Allan, & Walker, 2006; Nishida, Pearsall, Buckner, & Walker, 2009; Sterpenich et al., 2009; Wagner, Gais, & Born, 2001; Wagner, Hallschmid, Rasch, & Born, 2006; Walker, 2009). While a large body of data support the involvement of sleep in memory (for review, see Dang-Vu, Desseilles, Peigneux, & Maquet, 2006), the relationship between processes related to memory consolidation and those underlying dream experience is still poorly understood (e.g. Cipolli et al., 2004; Frank & Benington, 2006; Schwartz, 2003; e.g. Wamsley & Antrobus, 2009; Wamsley, Perry, et al., 2010; Wamsley, Tucker, Payne, Benavides, & Stickgold, 2010).

Several motor regions are activated during REM sleep including primary motor and premotor cortices, as well as the cerebellum and basal ganglia (Braun et al., 1997; Maquet et al., 2000). These results are in line with the motor content of dreams, and also with the observation that patients with REM sleep behavior disorder typically exhibit a large range of motor behaviors while enacting their dreams (Oudiette et al., 2009; Schenck, Bundlie, Ettinger, & Mahowald, 1986).

Braun and colleagues (1998) found that, during REM sleep, activation within the temporo-occipital regions showed some functional dissociation: extrastriate cortex (visual association areas) activation significantly correlated with striate cortex (primary visual cortex) deactivation during REM sleep, whereas activity in both regions are usually found to positively correlate during wakefulness (Braun et al., 1997). For these authors, opposite interactions between low- and high-level visual areas during REM sleep might indicate that internal visual information is processed within a closed system (extrastriate areas and paralimbic projections, among others) dissociated from interactions with the environment (via striate cortex and prefrontal cortex, both deactivated during REM sleep; Braun et al., 1998). These early PET results are also consistent with the observation that patients with cortical blindness (after primary visual cortex or perichiasmatic lesions) report that they still dream with visual images (Solms, 1997a). Yet, some recent fMRI studies suggest that rapid eye movements during REM sleep might be associated with increased fMRI activity in V1 (Miyauchi, Misaki, Kan, Fukunaga, & Koike, 2009). On the other hand, because several studies found that auditory stimuli may be processed to some extent during sleep (Atienza, Cantero, & Escera, 2001; Czisch et al., 2002; Perrin, Garcia-Larrea, Mauguire, & Bastuji, 1999; Portas et al., 2000; Wehrle et al., 2007), we would predict that external auditory stimulation during sleep may effectively coordinate activation within primary and associative auditory cortices.

Several regions are significantly hypoactive during REM sleep when compared to wakefulness, in particular in the dorsolateral prefrontal cortex (DLPFC), orbitofrontal cortex, posterior cingulate gyrus, precuneus, and the inferior parietal cortex (Braun et al., 1997; Maquet, 2000, 2005; Maquet et al., 1996; Nofzinger et al., 1997) (Fig. 1). Deactivations in regions that subserve important executive and attentional functions during wakefulness suggest that both cognition and the functional neuroanatomy of REM sleep significantly differ from those observed during wakefulness.

2.2. Transient activations and functional connectivity

In animals (Datta, 1995; Marini, Gritti, & Mancina, 1992) as well as in humans (Braun et al., 1997; Maquet et al., 1996), REM sleep is believed to be generated by cholinergic processes arising from brainstem structures (pedunculopontine tegmentum and laterodorsal tegmentum) that mediate some widespread cortical activation via a ventral pathway innervating the basal forebrain and a dorsal pathway innervating the thalamus (Steriade & McCarley, 2005). In animals, rapid eye movements during REM sleep co-occur with “ponto-geniculo-occipital” (PGO) waves (Fig. 2A). These PGO waves are observed in many regions of the animal brain, but are most easily recorded in the pons, the lateral geniculate bodies of the thalamus and the occipital cortex. PGO waves are bioelectrical phasic potentials occurring during the transition from non-REM sleep to REM sleep or during REM sleep itself (Callaway, Lydic, Baghdoyan, & Hobson, 1987). Potentially important functional roles have been attributed to these waves, including the promotion of brain development and the facilitation of brain plasticity (Datta, 1999). Several lines of evidence suggest the existence of PGO waves in humans: direct intracranial recordings in epileptic patients (Salzarule et al., 1975), surface EEG (Salzarule et al., 1975), magnetoencephalography (MEG) (Inoue, Saha, & Musha, 1999). Neuroimaging studies using PET and fMRI also found correlations during REM sleep, but not during wakefulness, between spontaneous eye movements and regional cerebral blood flow (rCBF) in the occipital cortex and the lateral geniculate of the thalamus (Peigneux et al., 2001; Wehrle et al., 2005; Miyauchi et al., 2009).

In addition to changes in regional brain activity, changes in functional connectivity – i.e. in the way brain regions communicate to each other – have been reported during sleep. For instance, PGO waves (see above) provide an important source for coordinated brain activation during sleep. PGO waves are frequent during REM sleep and may represent the main mechanism for internally-generated neural activity subtending dreaming (Hobson & McCarley, 1977). EEG recordings also revealed that both wakefulness and REM sleep states are characterized by widespread, coherent 40-Hz oscillation and it was proposed that these oscillations can induce large functional states that bring about cognition (Llinas & Ribary, 1993). Conversely, transcranial magnetic stimulation (TMS) studies revealed a breakdown of functional connectivity during non-REM sleep as evidenced by a reduced propagation of neural activity triggered by a TMS pulse during non-REM sleep (Massimini et al., 2005), as well as a reduction of interhemispheric connectivity after awakenings from REM sleep (Bertini et al., 2004). Intracranial EEG recordings in epilepsy patients have also started to provide important information about brain connectivity during sleep. For example, the quantity of dream recall was found to correlate with functional coupling between rhinal and hippocampal cortices (Fell et al., 2006). Because the processing of declarative memories (i.e. consciously accessible events and facts) relies on these structures of the medial temporal lobe, increased interaction between those

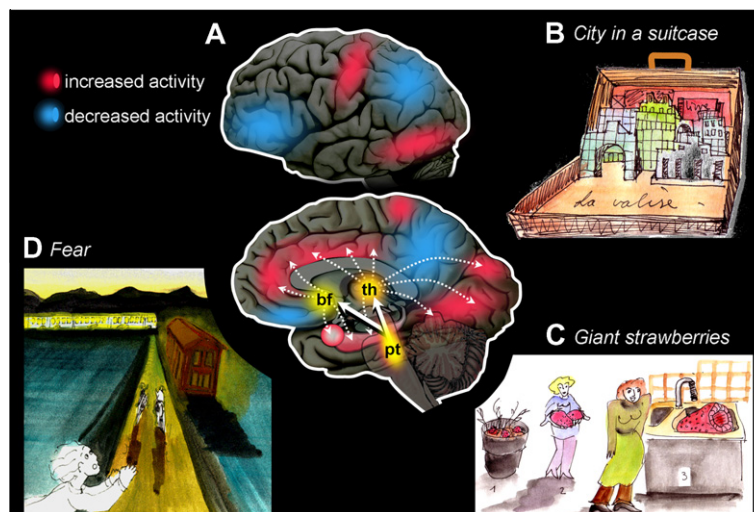


Fig. 2. Correspondence between the distribution of activity in REM sleep and typical dream features. (A) Ponto-geniculo-occipital waves (PGO) originating from the pontine tegmentum (pt) mediate some widespread cortical activation via a ventral pathway innervating the basal forebrain (bf) and a dorsal pathway innervating the thalamus (th). (B) Dreaming of “a city in a suitcase” corresponds to contextual dissociation, and (C) dreaming of “strawberries becoming enormous within minutes” is a visual scaling distortion. Both these examples illustrate the highly visual content of the dreams, consistent with the widespread activity along occipital–temporal visual regions, as well as some bizarre but typical features in the dreams. Contextual transpositions and scaling anomalies are common in dream reports and might partly imply a deactivation in the posterior cingulate and inferior parietal cortices, which are involved in the binding of object features and contexts, among other functions. The absence of supervisory control functions normally exerted by the frontal lobe (markedly hypoactive during REM sleep) would then prevent the detection of these elements in the dream as somehow incompatible with our knowledge about the world. (D) Illustration of a dream involving fear-related emotions: the dreamer runs away from a terrifying danger, hoping to catch the yellow train at the end of the road. Such frightening experiences in dreams are evocative of increased amygdala activation during REM sleep, which was reported in several PET studies (see main text). Note that this dream report also contains an important motor component, which is consistent with activation in motor regions during REM sleep. The drawings come from a dream diary extensively analyzed elsewhere (S. Schwartz, Doctoral thesis). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

structures might be a key factor in determining declarative memory formation during REM sleep and thus increase dream recall.

Taken together, the studies reviewed above suggest that REM (and non-REM) sleep is characterized by a specific landscape of activation, with regional increases and decreases of brain activity, associated with changes in functional neural connectivity. The observation that brain activity during sleep involves the regular engagement of distinct specialized brain subsystems also suggest that the modular architecture of brain functions may be expressed and consolidated during sleep (Schwartz, 2004). As we discuss in more detail below, such functional characteristics of human sleep may also underlie some distinctive features in dream experiences.

3. Neuroimaging of illusion and sensory imagery

In addition to dreams during sleep, our awake brains can also generate illusions or perceptual objects that are not present in the actual physical environment. Thus, neuroimaging data of illusions and mental imagery may be relevant for our understanding of the neural underpinnings of our dreams.

Illusory motion induced by a display called “Enigma” based on contrasting black and white spokes elicited increased of rCBF in the motion area V5, overlapping with the area activated by the perception of a physically moving checkerboard (Zeki, Watson, & Frackowiak, 1993). Similarly, brain activity related to the perception of illusory contours using Kanizsa triangle elicited significant activation in early visual areas (Ffytche & Zeki, 1996; Hirsch et al., 1995) and imagining a visual detail with high resolution causes early visual cortex activation (Kosslyn & Thompson, 2003). During dreams subjects do not often report perceiving objects with a very high degree of detail, which is congruent with the relative quiescence of early visual cortices during REM sleep (e.g. Maquet et al., 1996) (see above Section 2.1). Yet, what these and other more recent studies on mental imagery suggest is that brain regions that are involved in the processing of real sensory stimuli are also active for their imaginary equivalent (Daselaar, Porat, Huijbers, & Pennartz, 2010).

Besides sensory brain regions, other modality-independent regions such as the precuneus have been found to be activated during mental imagery (Roland & Gulyas, 1995), during episodic memory retrieval and self-processing operations (Cavanna & Trimble, 2006), as well as during awake resting state (Raichle & Snyder, 2007; Raichle et al., 2001). It has recently been proposed that regions of the default mode network (DMN; regions showing increased activity and connectivity during resting state) form a modality-independent “core” imagery network (Daselaar et al., 2010). It thus suggests that high-level cognitive processes in the DMN support all types of mental imagery and that the same processes could occur during dreams. While the potential role of the DMN in dreaming is appealing, early neuroimaging studies suggest that average activity in the precuneus, a key region of the DMN, might be low during REM sleep (see above Section 2.1). A recent EEG study found a characteristic positive brain potential, which is time-locked to the onset of rapid eye movements during REM sleep, and whose neural generators are located in motor, parietal, and occipital regions, encompassing bilateral precuneus (Ogawa, Abe, Nittono, Yamazaki, & Hori, 2010). Such phasic brain activity might thus underlie motor and visual processing, including mental imagery during REM sleep. These findings also further indicate that imaging techniques with good temporal and spatial resolution, such as functional MRI or advanced brain topography approaches using EEG, might uncover important aspects of the functional neuroanatomy of the dreaming brain.

4. Integration of brain imaging and dream data

In this section, we show that the specific distribution of sustained brain activity during REM sleep may relate to specific dream features, such as sensory, cognitive and emotional experiences in the dreams.

Dream reports contain a variety of sensations across different modalities. The most prevalent sensory modality is vision (nearly 100% of the dream contain at least one visual element) and audition (40–60%), while movements and tactile sensations (15–30%) or smell and taste (less than 1%) are less frequent (Calkins, 1893; Strauch, Meier, & Foulkes, 1996). Activation in visual occipital and auditory temporal cortices during REM sleep might thus provide a neural substrate for visual and auditory elements in dreams (Braun et al., 1997) (see Fig. 2 for examples of visual imagery in dreams). Consistent with this hypothesis, patients with extrastriate occipito-temporal lesions report cessation of visual dream imagery (Solms, 1997b).

Dreams are also characterized by bizarre features including a large range of sensory distortions, frequent misidentifications of characters and places in the dream, alterations in spatio-temporal integration, misbinding of objects' features, contextual dissociations and transpositions. Examples of such visual anomalies in dreams (when compared to waking life experiences) are shown on Fig. 2B and C. Several years ago, Revonsuo and Salmivalli proposed that “the possible patterns of the breakdown of the binding of consciousness—the patterns of incoherent phenomenology in dreams—form an important source of information for theories of consciousness” (Revonsuo & Salmivalli, 1995, p. 185). Moreover, consistent with evidence that insightful behavior and problem solving can benefit from one night of sleep (Wagner, Gais, Haider, Verleger, & Born, 2004), the spontaneous restructuring of mental features observed in the dreams also appear to stimulate creative processes (Schredl & Erlacher, 2007) and are often used as a source of inspiration for artists and other creative minds.

Such perceptual and cognitive anomalies in dreams are usually associated with the delusional belief of being awake during dreams, the uncritical acceptance of bizarreness, the relative lack of control over the dream events, and the blunted distinction between first- and third-person perspectives (Hobson et al., 1998; Maquet et al., 2005; Schwartz & Maquet, 2002).

Regional deactivation of the prefrontal and parietal cortex might account for most of these cognitive characteristics (Maquet et al., 2005). In particular, the DLPFC is involved in the selection of stimulus–response associations according to contextual signals, past events, and internal goals (Brass, Derrfuss, Forstmann, & von Cramon, 2005; Nee, Wager, & Jonides, 2007). The deactivation of this area during REM sleep might be consistent with the fact that the dreamers usually only exert a poor control over the dream actions and events, while uncritically accepting many bizarre and incongruous elements in the dream. In addition, the DLPFC and the inferior parietal lobule, which are deactivated during REM sleep, are known to subserve important attentional functions. Particularly, during wakefulness, this network is involved in a bottom-up attentional control aiming at reorienting the focus of attention toward salient stimuli, most often behaviorally relevant (Corbetta & Shulman, 2002). During REM sleep, a relative quiescence of this attentional network might also explain why external stimuli delivered during REM sleep are either ignored or automatically incorporated into the dream narrative, instead of interrupting the dream storyline (Burton, Harsh, & Badia, 1988; Foulkes, 1966), thus suggesting that the dream might be the guardian of (REM) sleep (Freud, 1955/1900).

However, highly emotionally-loaded dreams, in particular nightmares and internally-generated stimuli associated with memories of traumatic events as seen in Post-Traumatic Stress Disorder (PTSD) can disrupt the maintenance of REM sleep (Nielsen & Levin, 2007). Patients with PTSD also suffer from insomnia due to a cognitive hyperarousal at sleep onset (Pillar, Malhotra, & Lavie, 2000), which may reflect an abnormal activation of attentional networks in these patients during sleep.

Hypoactivity in the lateral and inferior PFC during REM sleep might imply deficits in the retrieval of episodic memory during wakefulness (i.e. the ability to recollect personally experienced events anchored within a particular spatio-temporal context) (Cabeza & Nyberg, 2000). In accordance with this hypothesis, only a very small percentage of dream reports that contain residues of previous waking activity have been found to represent an exact replay of full memory episodes (Fosse, Fosse, Hobson, & Stickgold, 2003; Schwartz, 2003). Isolated episodic elements are reactivated during sleep (most likely via the activation of the hippocampus, limbic structures, and posterior cortical areas), but these elements do not form replicates of real life episodes (because of the deactivation of the DLPFC among other possible causes; see Fig. 2 for examples of waking life elements reorganized in the dream).

Unlike lateral and inferior PFC, the medial PFC (mPFC) has been shown to remain as active during REM sleep as during wakefulness (Maquet et al., 1996). The mPFC has been found to play a role in the ability to attribute intentions, thoughts, and feelings to oneself and to others (“Theory of Mind” Frith & Frith, 2003). Thus, persistent mPFC activity could underlie the ability to represent others’ mind during REM sleep dreaming. Indeed, the dreamers very often attribute thoughts, emotions, and intentions to the characters who appear in their dreams (Kahn & Hobson, 2005). However, contrasting with this preserved activity in mPFC, activity in inferior parietal regions (including the temporo-parietal junction, see above) decreases during REM sleep. Because the latter regions are believed to contribute to a unified representation of the self and of self-versus others-perspective (Farrer et al., 2003; Ruby & Decety, 2004), deactivation in these regions would allow the dream self to participate to the dream both in a first-person (where the dreamer is the self who sees and acts) and in a third-person perspective (where the dreamer sees the self acting in the dream) without any distinction (Maquet et al., 2005). This offline role-play may facilitate the resolution of social or emotional conflicts. In particular, such potentiality for the dreamer to participate to the action (first-person) and be part of the audience (third-person), much like in a theatre, would foster a so-called “Aristotelian catharsis” (Kruse, 1979). Catharsis has been frequently identified as the proper purgation of audience members’ emotions, in particular pity and fear, through the representation of pitiable and frightening incidents in a dramatic form leading to a psychological release for the spectators. Thus, dreams may have an adaptive function in emotion regulation by preparing the individual (and its brain) to react to threats and resolve emotional conflicts (see Section 1.2, above). Notably, compared to the real-life spectrum of emotions, emotional content in dream reports tend to be predominantly negatively-loaded, with a high proportion of fear- or anxiety-related emotions (Valli & Revonsuo, 2009). During wakefulness, the amygdala is known to respond to threatening stimuli, stressful situations, or novelty (Vuilleumier, 2005). Its high activity during REM sleep could reflect the intensity and reprocessing of emotions in dreams (Maquet & Phillips, 1998; Maquet et al., 1996). Fig. 2D illustrates a typical frightening dream in which the dreamer runs away from a danger.

Further supporting a role of sleep in emotional regulation, the consolidation of emotional memories, including conditioned responses, is strengthened by a period of sleep following the emotional experience, particularly for hippocampus-dependent emotional memories (Sterpenich et al., 2007, 2009; Wagner et al., 2001, 2006; Wamsley & Antrobus, 2009). Animal (Silvestri, 2005) and human studies (Pace-Schott et al., 2009) also suggest that the extinction of a conditioned response is affected by sleep, mainly in a hippocampus-independent manner (i.e. when tested in a new extinction context) (Fu et al., 2007). Note however that no study to date has been able to directly relate, in the same individuals, brain activation during sleep with emotions experienced in dreams. Future research is thus needed to clarify the exact neurophysiological mechanisms by which sleep (and possibly dreams) might modify the emotional impact of some recent events.

Another clinically-relevant issue for future studies is to better understand sleep-related effects on the processing of traumatic events in people suffering from PTSD (Wittmann, Schredl, & Kramer, 2007), as well as the underlying neural mechanisms involved, which might be distinct from those involved in the processing of strong emotions not associated with PTSD symptoms.

Finally, because one of the main obstacle to the experimental study of the neural correlates of dreaming is the highly variable and unpredictable content of the dreams, one potentially promising avenue for the integration of dream data and brain activation maps might be to study lucid dreaming, namely dreams in which the dreamer is conscious of being in a dream (Cicogna & Bosinelli, 2001) and, to some extent, capable of modifying the content of the ongoing dream. However, recent

EEG findings indicate that lucid dreaming might correspond to an hybrid state of consciousness, with some EEG features more similar to those seen in wakefulness than in REM sleep (e.g. overall coherence levels, gamma power in frontal regions) (Voss, Holzmann, Tuin, & Hobson, 2009). While lucid dreaming is certainly an imperfect model of the dreaming brain, it offers some uniquely dissociated features of REM sleep and wakefulness, both at the mind and brain levels, which may usefully contribute to our understanding of the neural bases of consciousness.

5. Conclusions

In this review, we demonstrate that modern brain imaging techniques has emerged as major tools to better understand the neural mechanisms of dreaming. We show that there is a good correspondence between the distribution of sustained brain activity during REM sleep and some general perceptual, cognitive, and emotional characteristics in dream reports. Reciprocally, the data reviewed above also suggest that specific dream features, such as emotions in dreams, may provide valuable and unique information about brain functions during sleep.

Unlike early brain imaging studies (most of them using PET) that were restricted to reporting mean levels of regional cerebral activity during sleep stages, a few recent neuroimaging studies, in particular functional MRI studies, showed that it is now possible to capture more transient, dynamic changes of brain activity with a high anatomical resolution. While these advanced imaging methods are not easy to use to study sleep-related phenomena, they will undoubtedly contribute to redefining the links between brain processes and the varieties of dream experiences. Another important challenge for future studies will be to systematically investigate changes in brain activity and mental content across all sleep–wake states, and achieve a detailed characterization of the neural constraints affecting the daily oscillations of human conscious experiences. Such an integrated framework for the study of human sleep and dreaming is necessary to accommodate the diversity and increasing sophistication of modern neuroimaging research and to improve our understanding of the neuroanatomy and functions of dreaming.

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