Five

Neuroimaging of REM Sleep and Dreaming

Thien Thanh Dang-Vu, Manuel Schabus, Martin Desseilles, Sophie Schwartz, and Pierre Maquet

Dreams are sensory experiences occurring spontaneously during sleep. Their distribution during sleep is not homogeneous, as they are more frequent, vivid, and longer during rapid eye movement (REM) sleep. REM sleep might, therefore, constitute a permissive condition for the generation of dream experiences.

Over the last decade, functional brain imaging allowed us to characterize the distribution of regional cerebral activity during human REM sleep. The emerging picture reveals activation of the pons, the thalamus, temporo-occipital, and limbic/paralimbic areas (including amygdala), along with a relative quiescence of dorsolateral prefrontal and inferior parietal cortices. This pattern of activation offers new insights into the neural correlates of dreaming experience. For instance, amygdala activation is consistent with the predominance of negative emotions, anxiety, and fear in dream reports. Temporo-occipital activation is in keeping with a pervasiveness of visual dream content. Prefrontal deactivation might explain several cognitive impairments of the dreamer's mind relative to normal waking abilities, such as poor voluntary access to episodic memories, altered spatio-temporal orientation, deficient working memory, attention and self-awareness, altered reasoning and decision-making, including the usual lack of criticism toward bizarre elements in dreams. Prefrontal deactivation might also account for several characteristics of the dream scenario, such as spatio-temporal discontinuity associated with contextual misbinding.

INTRODUCTION

Dreaming is experienced every night by most humans as multisensory mental representations occurring spontaneously during sleep, often organized in a narrative manner. Dreams are characterized by their perceptual (mostly visual and auditory) and emotionally loaded content (including frequent threat-related content). They typically appear bizarre because of the incongruity, discontinuity, and instability of time, places, and persons (Hobson, Stickgold, & Pace-Schott, 1998; Schwartz & Maquet, 2002). Yet, they are usually taken as real by the dreamer. In a dream, it is, for example, not suspicious to us if we are suddenly able to fly or if a cat starts talking proper English. Indeed, the dream world is (mistakenly) experienced as real, very much like our waking perceptions and actions (Johnson, Kahan, & Raye, 1984). Some scientists even think of this illusory feeling of reality as a necessity for certain functions of the dream (Revonsuo, 2000; Valli et al., 2005). For example, Revonsuo (2000) and Valli (2005) have proposed that, by simulating threatening events, the biological function of dreaming is to afford the rehearsal of threat perception and avoidance, in a completely safe "virtual" environment and without any immediate damaging repercussion. Finally, the memory of the dream is generally quite poor and labile as compared to memory for waking events. As Pace-Schott, Stickgold, and Hobson (1997) suggested, the description of half an hour of waking life would be ten times longer than all the dream reports from one night.

The scientific study of dreaming constitutes a tough but fascinating challenge. Indeed, the dreamer is the unique observer of his dream and, as any subjective experience, dream content is not accessible to direct (third-person) observation. Consequently, information about a dream is obtained introspectively through memory recall. Several confounding factors may, therefore, affect the genuineness of dream reports such as forgetting, reconstruction mechanisms, verbal description difficulties, and censorship (Schwartz & Maquet, 2002). When studying dreams, one should always remain aware of these limitations and use appropriate strategies to prevent them from hindering valuable dream information.

The conception of dreams has slowly evolved through the centuries. In Greek antiquity, dreams were divine messages delivered to humans to warn them about upcoming disasters or misfortune. However, Aristotle challenged this common belief by bringing down any seemingly prophetic dream content to mere coincidence. He emphasized that dreams are endogenously generated and arise from the amplification of real external stimulation occurring during sleep. During the second half of the nineteenth century, several scientists conducted ingenious experimental studies on dreaming,

focusing on the phenomenological descriptive features of dreams rather than their meaning. They proposed theories about the cerebral mechanisms underlying dreams that are strikingly close to some recent theories (Schwartz, 2000). This wave of dream studies was slowed down when the psychoanalytic interpretation of dreams emerged. Indeed, more than 100 years ago, Freud believed that dreams were the expression of hallucinatory satisfaction of repressed desires or the "royal road to the unconscious" (Freud, 1900/1955). Then it was only in the 1950s that a neurophysiological marker of dreaming was described, leading to a renewed interest for the scientific study of dreaming. In 1953, Aserinsky and Kleitman (1953) described for the first time recurrent periods of rapid eye movements during sleep. Since these periods were also characterized by high-frequency/low-amplitude electroencephalographic (EEG) activity and muscular atonia, they were identified as a specific sleep stage called "Rapid-Eye-Movement sleep" (REM sleep) or paradoxical sleep (Jouvet, 1962). Critically, awakenings from this sleep stage were associated with a high probability of vivid dream reports (Dement & Kleitman, 1957). This discovery shaped a new field of research for dreaming: sleep was no longer considered as a homogeneous resting state but included periods of enhanced neurophysiological activity underlying the production of dream experiences (Aserinsky & Kleitman, 1953). The generation of dreams was thus supposed to be restricted to REM sleep, but this concept has changed since then as dreaming also seems to occur during non-REM sleep (Antrobus, 1983; Cicogna, Cavallero, & Bosinelli, 1991; Mannim, 2005; Solms, 2000). It is still discussed whether dreaming mentation in REM and non-REM sleep depends on one common set of processes or rather on two separate generators (Foulkes, 1996; Nielsen, 2000).

Yet, the study of dreams and REM sleep physiology remain closely associated, because dreams during this sleep stage are reported much more frequently, are better recalled, longer, more emotionally charged and perceptually vivid, and they contain more bizarre features (Aserinsky & Kleitman, 1953; Hobson, Pace-Schott, & Stickgold, 2000). REM sleep neurophysiology is dominated by complex neuromodulatory changes (Hobson et al., 1998; Hobson et al., 2000). In cats and rodents, REM sleep is generated by cholinergic input arising from brainstem nuclei located in the pedunculopontine tegmentum (PPT) and laterodorsal tegmentum (LDT) (Baghdoyan, Lydic, Callaway, & Hobson, 1989; Capece, Efange, & Lydic, 1997; Datta, 1995; Hobson, Datta, Calvo, & Quattrochi, 1993; Kodama, Takahashi, & Honda, 1990; Velazquez-Moctezuma, Gillin, & Shiromani, 1989; Velazquez-Moctezuma, Shalauta, Gillin, & Shiromani, 1991; Yamamoto, Mamelak, Quattrochi, & Hobson, 1990). These cholinergic

generators are mainly controlled by inhibition from aminergic neurotransmitters (noradrenalin [NA] and serotonin [5-HT]), which are repressed during REM sleep, leading to cholinergic firing increase (Gentili et al., 1996; Horner, Sanford, Annis, Pack, & Morrison, 1997; Imeri, De Simoni, Giglio, Clavenna, & Mancia, 1994; Leonard & Llinas, 1994; Nicholson & Pascoe, 1991; Portas & McCarley, 1994; Singh & Mallick, 1996). Other neuromodulatory systems might also participate in REM sleep modulation, such as gamma-aminobutyric acid (GABA) (Nitz & Siegel, 1997), nitric oxide (NO) (Leonard & Lydic, 1997), glutamate (Onoe & Sakai, 1995), glycine (Chase, Soja, & Morales, 1989), neuropeptides (Bourgin et al., 1997), as well as other non-pontine systems involving structures such as the basal forebrain (Szymusiak, 1995), hypothalamus (Lu et al., 2002), thalamus (Marini, Imeri, & Mancia, 1988; Marini, Gritti, & Mancia, 1992), amygdala (Sanford, Tejani-Butt, Ross, & Morrison, 1995), periaqueductal grey area (Sastre, Buda, Kitahama, & Jouvet, 1996), and medulla (Chase & Morales, 1990).

The function of dreaming is a source of intense debate and a fascinating topic in the field of cognitive neuroscience (for review see, Revonsuo, 2000). Although several theories claim that dreaming is simply a random by-product of REM physiology, others suggest it has quite important, if not vital, functional significance.

For example, Hobson and McCarley suggested that dreams merely result from the forebrain responding to (and trying to interpret) random activation initiated at the brainstem, or as a by-product related to "unlearning" in an otherwise overloaded brain (Crick & Mitchison, 1995; Hobson & McCarley, 1977).

Other researchers have proposed that dreams might reflect active functions like reprocessing and further consolidation of novel and (individually) relevant features encountered during previous waking experience. According to these authors (Cipolli, Fagioli, Mazzetti, & Tuozzi, 2004), the restructuring occurring during sleep and dreaming should be beneficial for long-term storage of freshly encoded information. By contrast, Jouvet proposed that dreaming involves the genetic reprogramming of cortical networks that might promote the maintenance of psychological individuality despite potentially adverse influences from the waking experiences (Jouvet, 1998).

More extreme views have suggested vital and adaptive functions to dreams in the course of brain development and evolution. Extending the evolutionary hypothesis of the function of dreaming (that is, "threat simulating theory") from Revonsuo and colleagues (2000), Franklin and Zyphur (2005) proposed that REM sleep may be so prominent early in life because it might function as a "virtual rehearsal mechanism." For optimizing brain

development and connectivity, a young organism would benefit from adaptively experiencing rich and vivid environments during dreams.

Finally, following on psychoanalytical theories, others have argued that dreaming is a process of internal activation, arising from a person's affective and emotional history (Mancia, 2005).

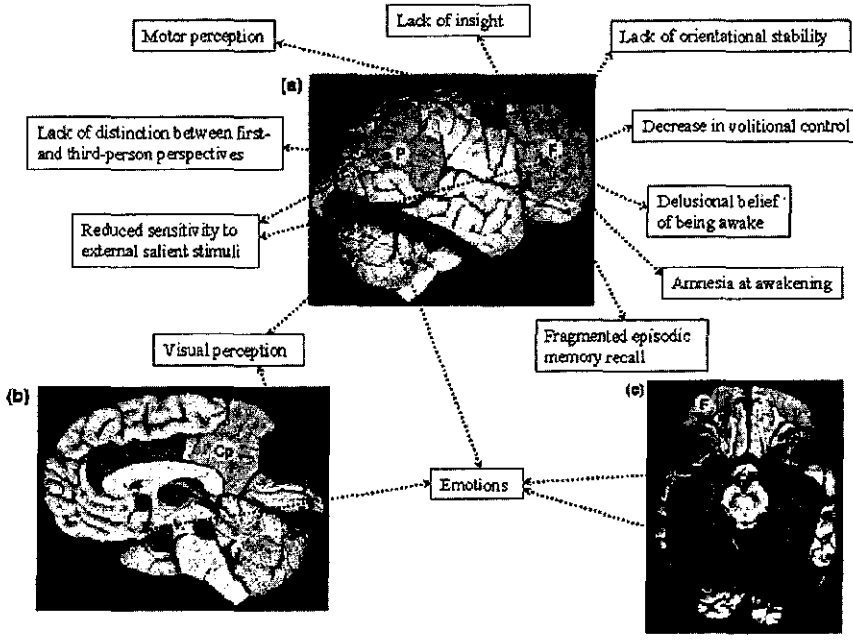
Over the last decades, the development of neuroimaging techniques allowed researchers to investigate in a noninvasive way functional changes in brain activity across various experimental conditions. In the field of sleep research, positron emission tomography (PET) was the main technique used to assess the global and regional cerebral activity during the different sleep stages. When applied to brain imaging, PET technique allows an assessment of cerebral activity using compounds labeled with positron-emitting isotopes. In sleep studies, different probes can be used, such as [^{18}F]fluorodeoxyglucose (^{18}FDG), which is a marker of glucose metabolism, and oxygen-15-labeled water ($H_2{}^{15}O$), which is a marker of blood flow. The neuroimaging data confirmed and extended some sleep physiological theories raised from animal data. Below, we first review the available functional neuroimaging studies that describe the pattern of regional cerebral activity during normal human REM sleep, as well as the likely activating neurophysiological mechanisms underlying this pattern of activity. Then, we discuss how these results could also be interpreted in more cognitive terms based on common dream features. This integrated view contributes to the characterization of the neural correlates of dreaming and may provide important elements for the understanding of the organization and functions of dreaming.

REM SLEEP PHYSIOLOGY VIEWED FROM A NEUROIMAGING PERSPECTIVE

Electrophysiological data showed that REM sleep is characterized by sustained neuronal activity (Jones, 1991; Steriade & McCarley, 1990). Early neuroimaging results demonstrated that REM sleep also displays a *global* high-level of cerebral energy requirements (Maquet et al., 1990) and cerebral blood flow (Madsen et al., 1991; Madsen & Vorstrup, 1991), which are comparable to wakefulness values. Subsequent neuroimaging studies, mostly conducted with PET, described REM sleep *regional* patterns of activity compared to wakefulness and/or non-REM sleep (Braun et al., 1997; Maquet et al., 1996; Maquet et al., 2000; Maquet et al., 2005; Nofzinger, Mintun, Wiseman, Kupfer, & Moore, 1997) (see Figure 5.1). The resulting maps showed a distribution of brain areas that displayed a higher (activation) or

FIGURE 5.1

Schematic representation of the functional neuroanatomy of normal human REM sleep. Regions with dark shading are those in which there is a relative increase in neural activity associated with REM sleep; those with light shading show relative decreases in neural activity during REM sleep. Arrows show the proposed relationships between brain areas and several dreaming features, which may be accounted for by regional patterns of activity during REM sleep. (a) lateral view; (b) medial view; (c) ventral view. A: amygdala; B: basal forebrain; Ca: anterior cingulate gyrus; Cp: posterior cingulate gyrus and precuneus; F: dorsolateral prefrontal cortex (middle and inferior frontal gyri); H: hypothalamus; M: motor cortex; P: parietal cortex (inferior parietal lobule); PH: parahippocampical gyrus; O: occipital-lateral cortex; Th: thalamus; T-O: temporo-occipital extrastriate cortex; TP: pontine tegmentum.



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lower (deactivation) regional cerebral blood flow (rCBF) during REM sleep in comparison to wakefulness and/or non-REM sleep. Regional activations were found in the pontine tegmentum, thalamus, basal forebrain, amygdala, hippocampus, anterior cingulate cortex, and temporo-occipital areas. Regional deactivations were found in the dorsolateral prefrontal cortex (DLPF), posterior cingulate gyrus, precuneus, and the inferior parietal cortex.

Reported activation of *pontine tegmentum*, *thalamic nuclei*, and *basal forebrain* (Braun et al., 1997; Maquet et al., 1996) is in agreement with REM sleep-generation mechanisms in animals (Datta, 1995, 1997; Marini et al., 1992). Namely, REM sleep is believed to be generated by cholinergic processes arising from brainstem structures (PPT and LDT) that mediate widespread cortical activation via a dorsal pathway innervating the thalamus and a ventral pathway innervating the basal forebrain (Steriade & McCarley, 2005).

A major finding from PET studies is the demonstration that *limbic and paralimbic* structures, including amygdaloid complexes, hippocampal formation, and anterior cingulate cortex, were consistently activated during REM sleep in humans (Braun et al., 1997; Maquet et al., 1996; Nofzinger et al., 1997). This result is also in line with earlier studies in animals showing a high regional glucose metabolism in the limbic system of rats (Ramm & Frost, 1983) and cats (Lydic et al., 1991; Ramm & Frost, 1986). Amygdala is known to play a key role in REM sleep modulation. For instance, in cats the stimulation of the central nucleus of amygdaloid complexes, either by electrical stimulation (Calvo, Badillo, Morales-Ramirez, & Palacios-Salas, 1987) or by injections of a cholinergic agonist (Calvo, Simon-Arceo, & Fernandez-Mas, 1996) enhances REM sleep activity. Besides the amygdala, the hippocampal formation is also activated during REM sleep in some studies (Nofzinger et al., 1997), suggesting an activation of the whole limbic system rather than the amygdala alone. The activation of the amygdala and the hippocampus, which are both involved in memory processing (Bechara et al., 1995), also suggests memory consolidation processes during REM sleep. Numerous data support the involvement of sleep in memory (for review, see Dang-Vu, Desseilles, Peigneux, & Maquet, 2006; Maquet, 2001; Maquet, Smith, & Stickgold, 2003; Peigneux, Laureys, Delbeuck, & Maquet, 2001a; Rauchs, Desgranges, Foret, & Eustache, 2005), but the relationships with dream content remain to be demonstrated.

Activated cortical *temporo-occipital* areas encompass the inferior temporal cortex and the fusiform gyrus (Braun et al., 1997), which belong to visual association areas (extrastriate cortex), but they do not include the primary visual cortex (striate cortex). Furthermore, striate and extrastriate cortices were shown to be functionally dissociated during REM sleep (Braun et al., 1998): extrastriate cortex activation is significantly correlated with striate cortex deactivation during REM sleep, whereas their activities are usually positively correlated during wakefulness. This dissociation between visual association areas and primary visual areas seems to be a hallmark of REM sleep and has led Braun and colleagues to hypothesize that REM sleep allows internal information processing (between extrastriate areas and their

paralimbic projections, both activated during REM sleep) in a closed system dissociated from interactions with the environment (via striate cortex and prefrontal cortex, both deactivated during REM sleep) (Braun et al., 1998).

Deactivated areas during REM sleep were first found in the *DLPF*, the *precuneus*, the *posterior cingulate* cortex, and the *parietal* cortex (Braun et al., 1997; Maquet et al., 1996). A recent PET study, however, showed that only parts of the parietal and DLPF cortices are hypoactive during REM sleep when compared to wakefulness (Maquet et al., 2005): the temporo-parietal region, the inferior parietal lobule, and the inferior and middle frontal gyrus of the DLPF. Conversely, activity in the superior parietal lobe and in the superior and medial prefrontal cortex is not different from waking level. The neurophysiological mechanisms underlying this functional segregation are still hypothetical. The amygdala might play a role in this cortical mapping: in monkeys, the amygdala sends abundant projections to the extrastriate and anterior cingulate cortices, which are activated during human REM sleep, but sends only sparse or indirect projections to the parietal cortex and DLPF, which are deactivated during REM sleep (Amaral & Price, 1984). These data suggest that the amygdala might "orchestrate" cortical activity during REM sleep. In line with this hypothesis, PET data also showed functional interactions between the amygdala and the temporal cortex, whereby amygdala activity was significantly and positively correlated with activity in the ipsilateral temporal cortex during REM sleep, but not during other states of vigilance (Maquet & Phillips, 1998). One proposed function for this amygdalo-cortical network may be the selective processing of emotionally-relevant memories during REM sleep (Maquet et al., 1996).

In animals, rapid eye movements during REM sleep are closely related to the occurrence of the so-called ponto-geniculo-occipital (PGO) waves. These *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). They are observed at many locations in the animal brain (Hobson, 1964), but most easily recorded in the pons (Jouvet, 1967), the lateral geniculate bodies of the thalamus (Mikiten, Niebyl, & Hendley, 1961) and the occipital cortex (Mouret, Jeannerod, & Jouvet, 1963). PGO waves might have important functional roles, such as the promotion of brain development and the facilitation of brain plasticity (Datta, 1999). There is also some evidence that PGO waves may exist in humans, as suggested by direct intracerebral recordings in epileptic patients (Salzarule et al., 1975), surface EEG (Salzarule et al., 1975), and magnetoencephalography (MEG) (Inoue, Saha, & Musha, 1999). A human PET study also found correlations during REM sleep, but not during wakefulness, between spontaneous eye movements and rCBF in the occipital cortex and

the lateral geniculate bodies of the thalamus, giving further support for the existence of PGO-like activities during REM sleep in humans (Peigneux, et al., 2001b). This finding was recently corroborated by a functional magnetic resonance imaging (fMRI) study (Wehrle et al., 2005).

Overall, neuroimaging studies have shown that the functional neuroanatomy (Braun et al., 1997; Maquet et al., 1996; Maquet et al., 2005; Nofzinger et al., 1997) but also the functional interactions between brain areas (Braun et al., 1998; Maquet & Phillips, 1998) were significantly different during REM sleep compared to wakefulness and to other sleep stages. These patterns of activity contribute to build a model of REM sleep physiology integrating human and animal data: (1) REM sleep is generated by processes arising from the pons and projecting to the cortex via the thalamus and the basal forebrain. (2) The limbic/paralimbic structures, mostly the amygdala, may serve as important modulators of internally-generated cortical input. (3) The hallmark of this segregated cortical activity is the activation of temporo-occipital visual association areas, contrasting with DLPF and inferior parietal deactivations. (4) The resulting network may be shaped by PGO-like activities and could underlie important functions such as brain plasticity and memory.

DREAMING VIEWED FROM A NEUROIMAGING PERSPECTIVE: INTEGRATION OF REM SLEEP CEREBRAL MAPPING AND MAJOR DREAM FEATURES

The previous maps reflect some aspects of REM sleep physiology, but may also convey information about the neural basis of dreaming. Indeed, the functional patterns of cerebral activity during REM sleep can be interpreted in the light of common features of dream content, and therefore potentially account for the generation of oneiric activity (see Figure 5.1).

Dream reports usually include different sensory modalities, largely dominated by *visual* (close to 100 percent) and *auditory* (40 to 60 percent) percepts, whereas movement and tactile sensations (15 to 30 percent) or smell and taste (less than 1 percent) are much less frequent (Strauch, Meier, & Foulkes, 1996). The occipito-temporal activation during REM sleep may underpin these perceptual aspects of dreams, consistently dominated by visual and auditory elements (Braun et al., 1997). Accordingly, cessation of visual dream imagery was reported for patients with occipito-temporal lesions (Solms, 1997).

Dream content is also characterized by the prominence of *emotions*, and especially negative emotions such as fear and anxiety (Strauch et al., 1996). Responses to threatening stimuli or stressful situations are modulated by the

amygdala during wakefulness (Sah, Faber, Lopez, & Power, 2003). The high limbic—and amygdalar—activity during REM sleep may thus underlie the emotional intensity occurring during dreams (Maquet et al., 1996). Moreover, PET data have shown positive functional interactions between amygdala and occipito-temporal cortices during REM sleep (Maquet & Phillips, 1998), while a recent fMRI study has found a positive relationship between the emotional load of visual stimuli and the functional activity in both amygdala and infero-temporal cortex (Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005). Together, these data suggest that the emotional experience during dreams might involve specific brain networks encompassing the amygdala and the occipito-temporal cortex.

The regional hypoactivity patterns during REM sleep, and especially the deactivation of parts of the prefrontal and parietal cortex (Maquet et al., 2005), have been proposed to explain several other dreaming features such as the uncritical acceptance of bizarre dream content, the alteration in time perception, the delusional belief of being awake during dreams, and the amnesia at awakening (Hobson et al., 1998). As discussed below, these deactivations could also account for the discontinuity and incongruity of dream content, the lack of control on the dreaming scenario, the fragmented recall of dreaming episodic elements, the reduced sensitivity of the dreaming narrative to external information, and the lack of distinction between first- and third-person perspectives in mind representation during dreaming (Maquet et al., 2005).

The prefrontal cortex can be functionally divided in distinct subregions, each of them underlying the monitoring of specific *cognitive processes* during wakefulness (Koechlin, Ody, & Kouneiher, 2003). In this model, the DLPF areas deactivated during REM sleep (Maquet et al., 2005) correspond to the prefrontal subregions involved in the selection of stimulus-response associations according to contextual signals, past events, and internal goals. The decreased activity of these areas would, therefore, prevent the brain from supervising the meaningful integration and continuity of dream information with respect to waking routines, physical rules, and social conventions. It may also explain the dreamer's failure to organize his/her mental representation toward specific goals or to control the flow of dream events.

During wakefulness, the retrieval of *episodic memory*, which refers to the ability to recollect personally experienced events anchored within a particular spatio-temporal context (Tulving, 1983), has been shown to involve the activation of lateral and inferior prefrontal cortices (Buckner, Wheeler, & Sheridan, 2001; Cabeza & Nyberg, 2000; Fletcher & Henson, 2001; Rugg & Wilding, 2000; Rugg, Otten, & Henson, 2002), which are typically deactivated during REM sleep (Maquet et al., 2005). It is indeed believed that

prefrontal areas participate in the processing of information retrieved from episodic memory; for instance, by checking its accuracy and completeness (Maquet et al., 2005). The hypoactivity of these regions during REM sleep is in line with the demonstration that, although 65 percent of dream reports contain residues of previous waking activity, only 1.4 percent of them are considered as representing the replay of full memory episodes (Fosse, Fosse, Hobson, & Stickgold, 2003). In other words, the dreamer reactivates episodic elements in a fragmented fashion (probably via the activation of the hippocampus and posterior cortical areas), but is unable to integrate the details of past events into an identifiable life episode because of the deactivation of the DLPF (Maquet et al., 2005; Schwartz, 2003).

The DLPF (inferior and middle frontal gyri) and the inferior parietal lobule, both deactivated during REM sleep, are included in the *ventral attentional network* (Corbetta & Shulman, 2002). This network acts as an alerting mechanism that is specialized in the detection of salient, unexpected, behaviorally relevant stimuli and helps to reorient the focus of attention toward the incoming stimulus (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000). A relative quiescence of the ventral attentional network during REM sleep might be induced by the decrease of noradrenergic tone, given that the locus coeruleus sends heavy projections to the inferior parietal cortex (Morrison & Foote, 1986) and also participates in selective attention, especially to salient and unexpected stimuli (Aston-Jones & Rajkowski, 2000). These functional patterns then predict that the dream narrative, reported after awakening from REM sleep, would hardly be modified by external stimulation, even if behaviorally relevant (Maquet et al., 2005). This view is supported by observations describing that external stimuli delivered during REM sleep are either ignored or automatically incorporated into the dream narrative, instead of interrupting the flow of the dream storyline (Burton, Harsh, & Badia, 1988; Foulkes, 1966).

The ability to attribute intentions, thoughts, and feelings to oneself and to others is commonly referred to as the "Theory of Mind." Instances of *mind representation* appear in dreams: the dreaming mind creates characters and attributes thoughts, emotions, and intentions to those characters (Kahn & Hobson, 2005). Neuroimaging studies of theory of mind tasks during wakefulness have demonstrated a consistent involvement of the medial prefrontal cortex (MPF) (Frith & Frith, 2003; Gallagher & Frith, 2003; Harris, Todorov, & Fiske, 2005). While the DLPF is deactivated during REM sleep, the MPF has been shown to remain as active during REM sleep as during wakefulness (Maquet et al., 2005). This stands in contrast with its significant deactivation during non-REM sleep (Dang-Vu et al., 2005; Maquet et al., 1997; Maquet et al., 2005). The similar level of activity in the MPF

during REM sleep and wakefulness could therefore contribute to the persistence of the ability to represent others' mind during REM sleep dreaming. On the other hand, the inferior parietal lobule and temporo-parietal junction would be involved in the *distinction of first- versus third-person perspectives* in the representation of actions, thoughts, and emotions during wakefulness (Chaminade & Decety, 2002; Farrer et al., 2003; Ruby & Decety, 2001; Ruby & Decety, 2003, 2004). Contrasting with the MPF preserved activity, the hypoactivity of these parietal areas would predict a decrease of the ability to distinguish the perspective of others as compared to our own during REM sleep and dreaming. Accordingly, dream reports show that the self can participate to the dream scenario both in a first-person (the self sees and acts) and in a third-person perspective (the dreamer sees the self acting in the dream) (Maquet et al., 2005).

CONCLUSION

Over the last decade, neuroimaging studies have successfully described the distribution of brain activity across the sleep-wake cycle. When compared to non-REM sleep, REM sleep is characterized by an overall elevated level of activity, together with a specific pattern of regional brain activations and deactivations. This functional mapping of human REM sleep also allowed confirming theories of REM sleep neurophysiology derived from animal experiments. It has also been proposed that the cerebral correlates of REM sleep could underpin some important dreaming characteristics, including the predominance of threat-related emotions and visual percept, the loss of orientational stability and volitional control, the fragmented episodic memory recall, the reduced sensitivity to external relevant information, as well as the possibility of attributing feelings and goals to other characters in the dream.

To further improve the accuracy of the neural correlates of dreaming, future functional brain imaging studies should be combined with refined neuropsychological analysis of dream reports (Schwartz & Maquet, 2002). Dreams are indeed multifarious, often bizarre, and cannot be reduced to a list of broad and typical sensory or cognitive features. Some specific and bizarre but common dream features of normal human sleep resemble clinical signs of neuropsychological syndromes resulting from focal brain damages, thus potentially predicting the topography of the corresponding brain functional changes (Schwartz & Maquet, 2002). On the basis of these observations, it has been proposed to quantify and categorize the dream narrative in terms of different perceptual, emotional, or bizarre elements to provide useful constraints to the analysis and interpretation of future REM sleep data (Schwartz & Maquet, 2002). Perhaps a special type of dreaming during

which the dreamer is conscious of being in a dream ("lucid dreaming") might provide an interesting test case for future neuroimaging studies (LaBerge & DeGracia, 2000). The fact that lucid dreamers can remember to perform predetermined actions during a dream might allow assessing the neural correlates of a large variety of dreaming features. Non-REM sleep dreaming should also be investigated in upcoming dedicated studies, and the differences (or similarities) between REM on non-REM dreaming mentation should be further clarified.

The reviewed neurophysiological and neuroimaging research on REM sleep offers an increasingly detailed picture of the cerebral correlates of dreaming, which may finally bring significant insight into dreaming mechanisms and possible functions.

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