
Neuroimaging Insights into the Dreaming Brain

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Abstract

Dreams are sensory, cognitive, and emotional experiences that occur spontaneously during sleep. Dream reports tend to be more frequent, vivid, and longer during rapid eye movement (REM) sleep than during non-REM sleep. This is why our current neurobiological knowledge about dreaming primarily derives from functional neuroimaging data acquired during REM sleep (e.g. electroencephalography, positron emission tomography, and functional magnetic resonance imaging). Recent neuroimaging results showed that REM sleep is characterized by a specific pattern of regional brain activity: (i) activation of the thalamus, pons, temporo-occipital and limbic/paralimbic areas (encompassing amygdala, hippocampal formation and anterior cingulate cortex), and (ii) deactivation of the dorsolateral prefrontal and inferior parietal cortices. This heterogenous distribution of brain activity might relate to some characteristic dream features (e.g. amygdala activation is consistent with frequent threat-related emotions in dream reports). Reciprocally, specific dream features suggest the

activation of specific brain regions during sleep. Based on these observations, we

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previously proposed that a neuropsychological or cognitive neuroscience approach to dreaming can usefully contribute to the interpretation of neuroimaging maps of sleep. The goal of this chapter is to show that connecting recent neurophysiological and neuroimaging data on human sleep and the content of dreams offers new insights into the brain correlates of dreaming and possibly into dream functions.

Keywords: dreaming, sleep, Rapid Eye Movement (REM), functional neuroimaging, neuropsychology, cognitive neuroscience, brain, amygdala.

Introduction

Dreaming represents an important facet of human experience. Dreams consist in sensory-motor, verbal, cognitive and emotional experiences, most often arranged in a narrative manner. Multisensory 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 encompasses several aspects of executive functions (planning, reasoning, etc.), memory (elements in dreams involve retrieval from recent or more remote memory), as well as spatial navigation abilities, among others. Many emotional experiences in dreams are intense and possibly biased toward negative emotions. Yet, probably all the categories of dream experience described above are also subjected to many alterations and distortions that are unlikely to occur in real waking life (Hobson, Stickgold et al. 1998; Schwartz and Maquet 2002). Despite the implausibility of many dream elements with respect to the real world, the dreamer usually remains unaware of being in a dream and he/she experiences the dream as a world analog (Johnson, Kahan et al. 1984). Because of these distinctive properties among others, the study of dreaming offers a fascinating opportunity to better understand the varieties of conscious experiences across dramatic changes in brain states.

Below, we first provide some historical background for a neuroscience conception of dreaming. We then review the available functional neuroimaging data that describe regional cerebral activity during normal human REM sleep, as well as the likely activating neurophysiological mechanisms underlying this pattern of activity. Finally, we discuss how these results might be interpreted in 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.

Modern History of Dream Research

In the modern occidental era, pioneering scientific experimentations on dreaming started during the second half of the 19th century (Macario 1857/1978; Maury 1862; Saint-Denis 1867/1977; Delboeuf 1885/1993). In those days (as today), introspective dream reports were

considered as a valuable material for scientific enquiry, because they provide unique information about what was perceived, felt, or thought in the dream. Many experiments were designed to determine what factors might influence the dream content and what rules may determine the dream scenario. These promising developments were stopped 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 in 1900 ("The Interpretation of Dreams"), studies relying exclusively on the manifest content of dreams were discredited on behalf of a quest of the "true" dream, i.e., the latent content hidden beneath the apparent dream (Freud 1955). On the other hand, the advent of behaviorism was detrimental to the study of dreaming because it denied 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 dreaming occurred in late 1950s, when two concomitant events renewed the interest for a scientific approach to dreaming: (i) the discovery of an objective indicator of the dreaming state and (ii) a new cognitive approach to the phenomenology of dreams (for 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 was related to recurrent periods of high cortical activity during sleep (i.e., high-frequency/low-amplitude electroencephalographic (EEG) activity, analogous to resting wake state) accompanied by rapid eye movements (REM), and increased heart rate and respiratory activity (Aserinsky and Kleitman 1953; Dement and Kleitman 1957). These REM periods were also associated with a paradoxical muscular atonia (Jouvet 1994). Later studies showed that, compared to non-REM periods, dreams collected after REM awakenings are reported more frequently, are better recalled, longer, more emotionally loaded and perceptually vivid, and they contain more bizarre features (Aserinsky and Kleitman 1953; Hobson, Pace-Schott et al. 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 an 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 and Kleitman 1953). While the generation of dreams was first supposed to be restricted to REM sleep, it is increasingly believed that dreaming does not rely on REM-generating brain structures and may also occur during non-REM sleep, especially late in the sleep night (Foulkes 1962; Antrobus 1983; Cicogna, Cavallero et al. 1991; Solms 2000; Fosse, Stickgold et al. 2001; Fosse, Stickgold et al. 2004; Manni 2005). Yet, 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.

The exact same year that Aserinsky and Kleitman wrote their inaugural article on REM sleep, Calvin S. Hall (1953/1966) published *The Meaning of Dreams* in which he described

and classified phenomenological characteristics from 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 (Schneider and Domhoff 2009). From then on, the phenomenological content of the dreams was again considered as useful descriptions of cognitive processes at play during sleep.

Functions of Dreaming

The conception of dreaming has considerably changed through history, which led to many different hypothesized functions of the dreams (Lavie and Hobson 1986; Barbera 2008). Currently, the function of dreaming remains still controversial. For instance, several theories encompassing the mind-brain reductionism claim that dreaming is simply a random by-product of REM physiology related to “unlearning” in an otherwise overloaded brain (Hobson and McCarley 1977; Crick and Mitchison 1995). Contrarily, others proposed it has fundamental functional significance. For instance, dreams might echo dynamic functions like reprocessing and further consolidation of novel and individually relevant features encountered during previous waking experience (Cipolli, Fagioli et al. 2004). Besides the potential benefits for long-term storage of freshly encoded information proposed by the latter theory, Jouvet (1998) proposed that dreaming involves the genetic reprogramming of cortical networks maintaining psychological individuality despite potentially unfavorable pressures arising during waking experiences. Another model, the “threat simulation” model pinpointed the evolutionary context for explaining the realistic representation of fear in nightmares and its potential adaptive function (Revonsuo 2000). In this model, illusory feeling of reality simulating threatening events could afford the rehearsal of threat perception and avoidance in an entirely harmless situation and without any detrimental consequences (Revonsuo 2000; Valli, Revonsuo et al. 2005).

Extending this evolutionary hypothesis, Franklin and Zyphur (2005) suggested that REM sleep may act as a “virtual rehearsal mechanism”, 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. Lastly, following on psychoanalytical models, authors suggested that dreaming is a process of internal activation, arising from a person’s affective and emotional history (Mancia 2005).

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

Neuroimaging View in REM Sleep Physiology

Since the 1990's, human brain imaging became a key player in the sleep field. Based on the hypothesis that dreaming mechanisms are most powerfully engaged during REM sleep, 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. total head immobilization, high noise level, effect of the magnetic field on the EEG). As we discuss below, both these imaging techniques had major impacts on our understanding of the cerebral bases of dreaming.

Distribution of Brain Activity during REM Sleep

Early neuroimaging data first confirmed the sustained neuronal activity observed with EEG (Steriade and McCarley 1990; Jones 1991) by showing a high-level of cerebral energy requirements (Maquet, Dive et al. 1990) and a widespread increase of cerebral blood flow (Madsen, Holm et al. 1991; Madsen, Schmidt et al. 1991; Madsen and 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. Regional cerebral blood flow (rCBF) increases (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 (Maquet, Peters et al. 1996; Braun, Balkin et al. 1997; Nofzinger, Mintun et al. 1997; Maquet 2000; Maquet 2005). Deactivations in regions that subserve important executive and attentional functions during wakefulness demonstrate that the functional neuroanatomy of REM sleep significantly differs from that observed during wakefulness.

Activations in limbic and paralimbic structures, including amygdaloid complexes, hippocampal formation, and anterior cingulate cortex (ACC) during REM sleep in humans (Maquet, Peters et al. 1996; Braun, Balkin et al. 1997; Nofzinger, Mintun et al. 1997) are consistent with available animal data (e.g. Calvo, Badillo et al. 1987; Lydic, Baghdoyan et al. 1991; Calvo, Simon-Arceo et al. 1996) and suggest that memory consolidation processes, in particular emotional memories, may occur during REM sleep (Wagner, Gais et al. 2001; Hu, Stylos-Allan et al. 2006; Wagner, Hallschmid et al. 2006; Sterpenich, Albouy et al. 2007; Nishida, Pearsall et al. 2009; Sterpenich, Albouy et al. 2009; Walker 2009). While a large

body of data support the involvement of sleep in memory (for review, see Dang-Vu, Desseilles et al. 2006), the relationship between processes related to memory consolidation and those underlying dream experience is still poorly understood (e.g. Schwartz 2003; Cipolli, Fagioli et al. 2004; Frank and Benington 2006; Wamsley and Antrobus 2009).

In an important study, Braun and colleagues (1998) found that, during REM sleep, activation within the temporo-occipital regions showed some characteristic functional dissociations. Indeed, extrastriate cortex (visual association areas) activation significantly correlated with striate cortex (primary visual cortex) deactivation during REM sleep, whereas their activities are usually found to positively correlate during wakefulness (Braun, Balkin 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, Balkin 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 1997). Yet, some recent fMRI studies suggest that rapid eye movements during REM sleep might be associated with increased BOLD response in V1 (Hong, Harris et al. 2009; Miyauchi, Misaki et al. 2009). On the other hand, because several studies found that auditory stimuli may be processed to some extent during sleep (Perrin, Garcia-Larrea et al. 1999; Portas, Krakow et al. 2000; Atienza, Cantero et al. 2001; Czisch, Wetter et al. 2002; Wehrle, Kaufmann et al. 2007), we would predict that external auditory stimulation during sleep may effectively synchronize the activation of the primary and associative auditory cortices.

Some regions are hypoactive during REM sleep when compared to wakefulness, in particular portions of the parietal and DLPF cortices (the temporo-parietal junction, the inferior parietal lobule, and the inferior and middle frontal gyri of the DLPF) (Maquet, Peters et al. 1996; Braun, Balkin et al. 1997). Conversely, activity in the superior parietal lobe and in the superior and medial prefrontal cortices is not different from that during waking. Interestingly, transcranial magnetic stimulation data evidenced a reduction of cerebral functional connectivity during non-REM sleep as well as a drastic reduction of interhemispheric connectivity after awakenings from REM sleep (Bertini, De Gennaro et al. 2004; Massimini, Ferrarelli et al. 2005). These findings 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 a disruption of effective connectivity. As we discuss in more detail below, such functional peculiarities during REM sleep may also underlie some distinctive features in dream experiences.

Transient Activations during REM Sleep

In animals (Marini, Gritti et al. 1992; Datta 1995) as well as in humans (Maquet, Peters et al. 1996; Braun, Balkin et al. 1997), REM sleep is believed to be generated by cholinergic processes arising from brainstem structures (pedunculo-pontine 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 and McCarley 2005). In animals, rapid eye movements during REM sleep co-occur with “pontogeniculo-occipital” (PGO) waves. 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 et al. 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 intracerebral recordings in epileptic patients (Salzarule, Liary et al. 1975), surface EEG (Salzarule, Liary et al. 1975), magnetoencephalography (MEG) (Inoue, Saha et al. 1999). In addition, neuroimaging studies using PET and fMRI 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 (Peigneux, Laureys et al. 2001; Wehrle, Czisch et al. 2005). This was confirmed in a recent event-related fMRI study (Miyachi, Misaki et al. 2009).

In sum, these brain imaging data in humans are congruent with early studies in animals showing that REM sleep is generated by cholinergic processes arising from the pons and projecting to the cortex via the thalamus and the basal forebrain. On the other hand, human studies suggest that the amygdala and more largely, the limbic/paralimbic system might orchestrate cortical activity underpinning the processing of internally-generated cortical information within functionally segregated areas. The ensuing network may be shaped by transient activation from PGO-like waves and could thus underlie important functions such as brain plasticity and memory. Because they produce widespread subcortical and cortical activities, such phasic neural events may trigger mental activities during sleep (e.g. dreams).

Integration of Brain Mapping with Dreaming Data

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 during REM sleep (Cavallero, Cicogna et al. 1992; Stickgold, Malia et al. 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 et al. 2001; Stickgold, Malia et al. 2001; Fosse, Stickgold et al. 2004; Nielsen 2004). These findings suggest that REM sleep is not a necessary but a facilitating condition for dreaming to occur.

We have previously proposed that the specific distribution of sustained brain activity during REM sleep may relate to specific dream features and that, reciprocally, specific dream features provide important information about specific brain activities during sleep (Schwartz

and Maquet 2002). Below, we show how sensory, cognitive and emotional experiences in the dreams are consistent with the global patterns of brain activity during REM sleep.

Dream reports contain a variety of sensations across different modalities. The most prevalent sensory modality is vision (nearly 100 percent of the dream contain at least one visual element) and audition (40 to 60 percent), while movements and tactile sensations (15 to 30 percent) or smell and taste (less than 1 percent) are less frequent (Calkins 1893; Strauch, Meier et al. 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, Balkin et al. 1997; Hong, Harris et al. 2009). Congruently, patients with extrastriate occipito-temporal lesions report cessation of visual dream imagery (Solms 1997).

When compared to 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 and Revonsuo 2009). During wakefulness, the amygdala is known to respond to threatening stimuli, stressful situations, or novelty. Its high activity during REM sleep could reflect the intensity of emotions in dreams (Maquet, Peters et al. 1996; Maquet and Phillips 1998). Very strong negative emotions in dreams may be associated with nightmares.

Several theories suggested that dreaming may be beneficial for the regulation of emotional states (for a comprehensive review see Nielsen and Levin 2007). Hartmann proposed that a central function of dreams, in particular nightmares, might be the regulation of emotions through contextualizing, or finding a picture context for, an individual's emotional concern (Hartmann 1996). Contextualizing creates new associations to the emotion, the result of which would be emotionally adaptive. Another "mood regulatory theory" of dreaming was proposed by Kramer. Based on the observation that limbic activity and affective arousal (e.g. heart and respiratory rates) increase during REM sleep, the model suggests that dreaming would allow to progressively suppress these emotional surges across successive REM periods. This would be achieved by decreasing the intensity and variability of the associated emotion thanks to a problem-solving dream structure that unfolds across the night and enables a form of emotional problem solving that would ultimately ameliorate mood (Kramer 1991; Kramer 1993). In general, the notion that intervening dream activity regulates mood is supported by evidence that dreams are influenced by immediate pre-sleep emotional experiences (Piccione, Thomas et al. 1976; Kramer 1993; Nielsen, Kuiken et al. 2004) and that some contents or emotions in the dreams may affect subsequent waking state mood (Kramer 1982). Combining an evolutionary perspective of the function of dreaming with the empirical evidence concerning the frequency of negatively loaded dreams (e.g. nightmares and post-traumatic dreams), Revonsuo and colleagues recently suggested that dreaming might serve to simulate responses to threatening events in a totally secure environment. Such active rehearsal would enhance threat-avoidance skills that would ultimately help the dreamer to respond in an adapted and efficient way to dangerous real-life events (Revonsuo 2000; Valli and Revonsuo 2009). More recently, Nielsen and colleagues have described an "affective network dysfunction" (AND) model that integrates most of the elements from the prior models above to explain the putative function of nightmares (Levin and Nielsen 2007; Nielsen and Levin 2007). In short, the AND states that nightmares result from a "dysfunction in a network of affective processes that, during normal dreaming, serves the adaptive function of fear memory extinction" (Nielsen and Levin 2007, p. 300). The

model stipulates that dreaming may promote the consolidation of fear extinction memories by (1) activating features of fearful memories (largely independently from their episodic, real-world contexts); (2) reorganizing these features by creating novel simulated contexts in which the conditioned stimuli are presented without their pairing with the unpleasant unconditioned stimulus, but rather in non-fearful, contexts; and (3) allowing the experience of these modified emotional reactions to such recombined dream features that would foster the extinction of conditioned responses. By identifying an affective network (i.e. hippocampus, amygdala, anterior cingulate, medial prefrontal cortex) whose dysfunction might account for different types of dysphoric dreaming—from occasional bad dreams to non-traumatic nightmares to replicative post-traumatic nightmares, the AND is a sophisticated model that integrates both cognitive and neural explanatory levels.

Cognitive features of dreams are characterized by bizarreness, discontinuity and incongruity of dream content, uncritical acceptance of bizarreness, alteration in spatio-temporal perception, the delusional belief of being awake during dreams, the lack of control of the dreaming scenario, and the lack of distinction between first- and third-person perspectives (Hobson, Stickgold et al. 1998; Maquet, Ruby et al. 2005). Regional deactivation of the prefrontal and parietal cortex might account for a large portion of these cognitive characteristics (Maquet, Ruby et al. 2005). Indeed, the PFC is functionally divided into distinct subregions, each of them underpinning the monitoring of precise cognitive processes during wakefulness (Miller, Freedman et al. 2002).

For instance, the DLPFC is involved in the selection of stimulus-response associations according to contextual signals, past events, and internal goals. The deactivation of this area during REM sleep is congruent with the apparent lack of control of dreaming scenarios and the uncritical acceptance of bizarreness and incongruity. In addition, the DLPFC and the inferior parietal lobule, both deactivated during REM sleep, take part in the ventral attentional network (Corbetta and Shulman 2002). During wakefulness, this network is involved in a bottom-up attentional control aiming at reorienting the focus of attention toward an unexpected incoming salient stimulus, most often behaviorally relevant. REM sleep is characterized by a decrease of the noradrenergic tone in the locus coeruleus (LC). Since this structure sends important projections to the inferior parietal cortex (Morrison and Foote 1986) and is involved in selective attention to salient unexpected stimuli (Aston-Jones, Rajkowski et al. 2000), a relative quiescence of the ventral attentional network is congruent with the fact 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 (Foulkes 1966; Burton, Harsh et al. 1988). Paraphrasing Freud's suggestion (Freud 1955), we could suggest that dream is the guardian of REM sleep.

The lateral and inferior PFC is involved 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 and Nyberg 2000). The hypoactivity of these areas during REM sleep is congruent with the fact that only a very small percentage of dream reports that contain residues of previous waking activity could be considered as representing the exact replay of full memory episodes (Fosse, Fosse et al. 2003; Schwartz 2003). Taken together it seems that 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).

The dreamers often attribute thoughts, emotions, and intentions to the characters who appear in their dreams (Kahn and Hobson 2005). Neuroimaging studies of “theory of mind” tasks (i.e. the ability to attribute intentions, thoughts, and feelings to oneself and to others) during wakefulness suggest the role of the medial prefrontal cortex (mPFC) in such high-level mental activity (Frith and Frith 2003; Gallagher and Frith 2003; Harris, Todorov et al. 2005). The mPFC has been shown to stay as active during REM sleep as during wakefulness (Maquet, Peters et al. 1996) and could therefore contribute to the persistence of the ability to represent others’ mind during REM sleep dreaming.

Contrasting with preserved activity in mPFC, activity in inferior parietal regions (including the temporo-parietal junction, see above) decreases during REM sleep. Because these regions are believed to contribute to a unified representation of the self and of self-versus others- perspective (Farrer, Franck et al. 2003; Ruby and Decety 2004), deactivation in these regions would be consistent with dream reports showing 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) without any distinction (Maquet, Ruby et al. 2005).

Dream, REM Sleep and Psychiatric Illnesses

Because several psychiatric illnesses may involve sensory, emotional and cognitive abnormalities, it has been suggested that psychiatric disorders may share some common underlying mechanisms with dreaming (in healthy subjects) and REM sleep features. For instance, some authors proposed that the dreaming would provide a valid model for psychosis because both “conditions” share many bizarre features (Scarone, Manzone et al. 2008). Others have even proposed that REM sleep could be a potential endophenotype (Gottesmann and Gottesman 2007). Endophenotypes represent measurable component invisible to the naked eye along the pathway between a disease and the genotype. This is thus a kind of intermediate phenotype between the phenotype and the genotype that can be either neurophysiological, biochemical, endocrinological, neuroanatomical, cognitive or neuropsychological (Gottesman and Gould 2003) and that can help identify the genes responsible for a particular mental illness. For instance, the specific absence of REM sleep rebound after REM sleep deprivation in schizophrenic patients might be an endophenotype (Zarcone, Azumi et al. 1975). Interestingly, a recent study suggests that dream content characteristics in schizophrenia may reflect neurocognitive processes specific to this condition (Lusignan, Zadra et al. 2009). Thus quantitative study of dream reports in schizophrenic patients may represent an alternative to discover an endophenotype subtending impairments of emotional processing in this condition.

Similarly, REM sleep has been considered as an endophenotype in major depression (Modell and Lauer 2007). For instance, in this later illness, the increased activity in the amygdala during REM sleep (Nofzinger, Nichols et al. 1999) might be congruent with the increased pressure of REM sleep (Adrien 2002) observed since the activity within this

structure has been linked to an augmentation of REM sleep in animals (Calvo, Badillo et al. 1987).

Compared to NREM sleep, REM sleep was shown to increase cognitive distortions and in particular negative self-appraisals in patients suffering from anxious depression (McNamara, Auerbach et al. 2009), supporting the REM sleep deprivation therapy in these patients. Alternatively, through successive REM periods, depressed subjects showed a decrease of negative and an increase of positive affect in dreams suggesting that dreaming may actively moderate mood overnight in these subjects (Cartwright, Luten et al. 1998). Refining these observations, the same group showed that depressed subjects who increased REM sleep pressure through repetitive REM sleep deprivation had an antidepressant effect if they were able to construct well-organized dreams (Cartwright, Baehr et al. 2003). Overall, these studies suggest that during REM sleep an interaction between cognition and emotion regulates neuronal networks involved in emotional processing and mood disorders.

Conclusions

In this review, we have shown that the conception of dreaming as intimately linked to brain activity was relatively popular among scientists in the late 19th century. It is only recently and after the discovery of REM sleep, that modern brain imaging techniques emerged as major tools to better understand the neural mechanisms of dreaming. We demonstrated that some general perceptual, cognitive, and emotional characteristics in dream reports are compatible with the pattern of regional activity during REM sleep revealed by neuroimaging studies. While early brain imaging studies (most of them using PET) could only picture 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. Future studies using these advanced imaging methods will further improve our knowledge of brain functions during sleep, and will undoubtedly redefine and tighten the links between brain processes and the varieties of dream experiences.

Acknowledgments

M.D., P.M., L.M., L.M., A.F. and T.T.D.-V are supported by the Fonds National de la Recherche Scientifique (FNRS - Belgium). S.S. is supported by the Swiss National Science Foundation. M.S. was supported by the Austrian Science Fonds (FWF). Additional support was provided by the University of Liège, the Queen Elisabeth Medical Foundation and the Fonds Léon Frédéricq, the Horlait-Dapsens Foundation and a BCNBP-Lundbeck grant (Belgian College of Neuropsychopharmacology and Biological Psychiatry).

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