

Human cognition during REM sleep and the activity profile within frontal and parietal cortices: a reappraisal of functional neuroimaging data

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Abstract: In this chapter, we aimed at further characterizing the functional neuroanatomy of the human rapid eye movement (REM) sleep at the population level. We carried out a meta-analysis of a large dataset of positron emission tomography (PET) scans acquired during wakefulness, slow wave sleep and REM sleep, and focused especially on the brain areas in which the activity diminishes during REM sleep. Results show that quiescent regions are confined to the inferior and middle frontal cortex and to the inferior parietal lobule. Providing a plausible explanation for some of the features of dream reports, these findings may help in refining the concepts, which try to account for human cognition during REM sleep. In particular, we discuss the significance of these results to explain the alteration in executive processes, episodic memory retrieval and self representation during REM sleep dreaming as well as the incorporation of external stimuli into the dream narrative.

Introduction

During the last decade, functional neuroimaging by positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) characterized a very reproducible functional neuroanatomy of human sleep, which we will briefly summarize below.

During slow wave sleep (SWS), as compared to wakefulness, the cerebral energy metabolism and blood flow globally decrease (Maquet, 2000). The most deactivated areas are located in the dorsal pons and mesencephalon, cerebellum, thalami, basal ganglia, basal forebrain/hypothalamus, pre-

frontal cortex, anterior cingulate cortex and precuneus. As detailed elsewhere (Maquet, 2000), these findings are in keeping with the generation of non-rapid eye movement (REM) sleep in mammals, whereby the decreased firing in brainstem structures causes an hyperpolarization of thalamic neurons and triggers a cascade of processes responsible for the generation of various non-REM sleep rhythms (spindles, theta, slow rhythm).

During REM sleep, as compared to wakefulness, significant activations were found in the pontine tegmentum, thalamic nuclei and limbic and paralimbic areas (e.g., amygdaloid complexes, hippocampal formation and anterior cingulate cortex). Posterior cortices in temporo-occipital areas are also activated and their functional interactions are different in REM sleep than in wakefulness

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(Braun et al., 1998). In contrast, the dorso-lateral prefrontal cortex, parietal cortex as well as the posterior cingulate cortex and precuneus are the least active brain regions (Maquet, 1996; Braun et al., 1997). Although early animal studies had already mentioned the high limbic activity during REM sleep (Lydic et al., 1991), functional neuroimaging in humans highlighted the contrast between the activation of limbic, paralimbic and posterior cortical areas, and the relative quiescence of the associative frontal and parietal cortices. The pattern of activity in subcortical structures is easily explained by the known neurophysiological mechanisms which generate REM sleep in animals. In contrast, the distribution of the activity within the cortex remains harder to explain and its origin remains speculative.

The particular pattern of cerebral activity observed during REM sleep has generated a number of papers and commentaries emphasizing the link between the organization of human brain function during sleep stage and the main characteristics of dreaming activity (Maquet et al., 1996; Hobson et al., 1998, 2003; Maquet, 2000). The main relationships between brain structure and dream features are as follows. First, the perceptual aspects of dreams would be related to the activation of posterior (occipital and temporal) cortices. Accordingly, patients with occipito-temporal lesions may report a cessation of visual dreams imagery (Solms, 1997). Second, emotional features in dreams would be related to the activation of amygdalar complexes, orbito-frontal cortex, and anterior cingulate cortex (Maquet et al., 1996; Maquet and Franck, 1997; Hobson et al., 1998, 2003; Maquet, 2000). Third, the activation of mesio-temporal areas would account for the memory content commonly found in dreams. Fourth, the relative hypoactivation of the prefrontal cortex would explain the alteration in logical reasoning, working memory, episodic memory, and executive functions that manifest themselves in dream reports from REM sleep awakenings (Maquet et al., 1996; Hobson et al., 1998, 2003; Maquet, 2000). Oddly enough, at this stage, the deactivation of the parietal cortex has received little attention.

Although we globally agree with these interpretations of the available PET results, we reasoned

that analyzing a large set of PET data acquired during sleep in normal human subjects would improve the characterization of the cerebral functional organization during sleep, especially REM sleep. In particular, we were interested in better specifying the topography of the relatively decreased activity in frontal and parietal areas, which are believed to decisively shape human cognition during REM sleep. At the outset, we draw the attention of the reader on the speculative nature of the present paper. Although the hypotheses presented here are based on sound experimental work, the functional relationships between the distribution of regional brain activity and dream features are still to be confirmed experimentally.

Meta-analysis of PET data during human sleep

We ran a meta-analysis on 207 PET scans obtained in 22 young, male, healthy subjects (age range: 18–30 years), during awake resting state (eyes closed, 58 scans), SWS (66 scans), and REM sleep (83 scans). These data were obtained in the framework of two already published experimental protocols (Maquet et al., 2000; Peigneux et al., 2004).

Briefly, sleep was monitored by polysomnography during two consecutive nights spent on the scanner table. Polygraphic recordings included electroencephalogram (EEG recorded between electrode pairs C3-A2 and C4-A1), electro-oculogram and chin-electromyogram and were scored using international criteria (Rechtschaffen and Kales, 1968). Only subjects who showed at least two periods of 15 min spent in each stage of sleep were scanned with PET during the third night. PET data were acquired under polygraphic recording, during wakefulness and sleep, on a Siemens CTI 951 R 16/31 scanner in 3D mode. The subject's head was stabilized by a thermoplastic facemask secured to the head holder (Truscan imaging, MA), and a venous catheter was inserted into a left antebachial vein. Regional cerebral blood flow (rCBF) was estimated during 12–14 90-s emission scans using automated, non-arousing, slow intravenous water ($H_2^{15}O$) infusion (6 mCi/222 MBq in 5 cc saline). Data were reconstructed using a Hanning filter (cutoff frequency: 0.5 cycle/pixel) and

corrected for attenuation and background activity. A transmission scan was acquired to perform measured attenuation correction.

The analysis was run using the statistical parametric mapping software (SPM2, Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). In short, a general linear model was designed for each individual subject and tested for the effect of condition (wakefulness, SWS, REM sleep). Global flow adjustment was performed by proportional scaling. Areas of significant changes were determined using linear contrasts. The contrasts of interest simply estimated the main differential effects of conditions, with a special emphasis on the least active brain regions during REM sleep. A comprehensive characterization of these areas required three contrasts, which looked for the brain areas more active in wakefulness than in REM sleep, in REM sleep than in SWS, and finally in wakefulness than in SWS. Taking advantage of the large data set available, the summary statistics images were then entered in second-level design matrices testing for random effects, which were assessed for each contrast of interest using a sample *t*-test. The resulting set of voxel values for each contrast constituted a map of the *t*-statistic {SPM(*T*)}, thresholded at $p < 0.001$. Corrections for multiple comparisons were then performed using the theory of random gaussian fields, at $p < 0.05$ at the voxel level over the entire brain volume. The random effects analysis allows us for the first time to take into account the inter-subjects variability in our analysis. As a consequence, the reported findings can be thought as representative of regional brain activity during sleep in the general population.

In this paper, we focus on the results pertaining to the least active brain areas during REM sleep. Concerning the most active brain areas during REM sleep, our data confirmed the metabolic pattern reported earlier (for review see Maquet, 2000), which has already been extensively discussed (Maquet et al., 1996; Maquet and Franck, 1997; Hobson et al., 1998, 2003; Maquet, 2000). The results are summarized in Tables 1–3 and in Fig. 1. Among the cortical areas that are relatively less active during REM sleep than during quiet wakefulness, it appears clearly that neither the

whole frontal lobe nor the entire parietal cortex is hypoactive. In the parietal lobe, the quiescent area encompasses only the temporo-parietal region and the inferior lobule of the parietal cortex, well below the intra-parietal sulcus (Fig. 1). In the prefrontal cortex, the least active area is located in the inferior frontal gyrus. The significantly hypoactive region spreads to the middle frontal gyrus but does not reach neither the superior frontal gyrus nor the medial aspect of the frontal lobe. The pattern of activity in the latter region is remarkable. In the medial prefrontal cortex, the rCBF is significantly decreased during SWS as compared to wakefulness, but no difference in regional activity is observed between REM sleep and wakefulness (Fig. 1, inset). These findings indicate a quite remarkable redistribution of the regional activity within the frontal and parietal cortices that probably constrain human cognition during REM sleep in a unique way.

Lateral prefrontal cortex and executive functions

Executive processes coordinate external information, thoughts, and emotions and organize actions in relation to internal goals. The selection of motor actions may directly rely on external stimuli, but in other cases it is based on the perceptual context or a whole temporal episode during which the individual is acting. The set of processes that subtend these operations may require the integration of information from various sources but referring to a specific, sometime extended, period of time (Baddeley, 2000). Another model, based on information theory, rather suggests a cascade of nested levels of control (Koechlin et al., 2003). These various executive processes are anatomically segregated. The selection of stimulus–response association involves the dorsal premotor cortex; the caudal prefrontal cortex would carry out the contextual control; and the episodic¹ control would be subserved by the rostral and ventral prefrontal cortex.

¹In this paragraph, we use the term episodic in the sense that this control system selects information according to events that occurred in the past. It does not necessarily refer to the way information is stored in long-term memory (Koechlin et al., 2003).

Table 1. Frontal and parietal areas where regional cerebral blood flow is decreased during REM sleep as compared to wakefulness

Region	<i>x</i>	<i>y</i>	<i>z</i>	<i>Z</i> score	<i>p</i> value
Right inferior frontal gyrus	50	52	2	7.24	< 0.001
Right middle frontal gyrus	42	60	14	6.50	< 0.001
Right orbito-frontal cortex	22	32	−26	6.40	< 0.001
Left inferior frontal gyrus	−50	40	2	6.42	< 0.001
Left middle frontal gyrus	−36	56	0	6.40	< 0.001
Left orbito-frontal cortex	−32	54	−14	6.09	< 0.001
Right inferior parietal lobule	64	−48	40	7.32	< 0.001
Left inferior parietal lobule	−54	−56	50	6.38	< 0.001

Note: Only one peak voxel is reported for each cortical region. *x*, *y*, *z*: coordinates in the stereotactic MNI (Montreal Neurological Institute) space (mm); *Z* score and *p* (corrected for multiple comparisons at the voxel level over the entire brain volume).

Table 2. Frontal and parietal areas where regional cerebral blood flow is higher during REM sleep than during slow wave sleep

Region	<i>x</i>	<i>y</i>	<i>z</i>	<i>Z</i> score	<i>p</i> value
Anterior cingulate cortex	2	34	10	6.94	< 0.001
Ventral medial prefrontal cortex	2	46	−6	6.77	< 0.001
Dorsal medial frontal cortex	4	4	60	6.36	< 0.001
Right inferior frontal gyrus	26	10	−10	6.52	< 0.001
Left superior parietal cortex	−14	−50	66	6.24	< 0.001
Precuneus	−4	−50	66	6.44	< 0.001

Table 3. Frontal and parietal areas where regional cerebral blood flow is higher during wakefulness than during slow wave sleep

Region	<i>x</i>	<i>y</i>	<i>z</i>	<i>Z</i> score	<i>p</i> value
Anterior cingulate cortex	2	40	8	6.94	< 0.001
Ventral medial frontal cortex	−2	30	−14	6.17	< 0.001
Dorsal medial frontal cortex	4	2	60	4.56	0.048
Right inferior frontal gyrus	60	12	0	6.20	< 0.001
Right middle frontal gyrus	40	54	4	6.60	< 0.001
Right orbito-frontal cortex	38	42	−26	6.65	< 0.001
Left middle frontal gyrus	−38	44	24	6.61	< 0.001
Left orbito-frontal cortex	−34	42	−26	7.58	< 0.001
Right inferior parietal lobule	68	−48	34	7.36	< 0.001
Left inferior parietal lobule	−56	−50	42	6.36	< 0.001
Precuneus	−6	−76	60	6.14	< 0.001

The topography of the quiescent prefrontal areas during REM sleep overlap with the regions that support the contextual and episodic control systems. This finding suggests that if the perceptual control is maintained in this stage of sleep, the contextual and the episodic controls are probably less

efficient than during wakefulness. This would explain the lack of “orientational stability” observed in dream reports, whereby the dreamer is unable to coordinate information of a whole episode: the “person, times and place are fused, incongruous and discontinuous” (Hobson et al., 2003). Likewise,

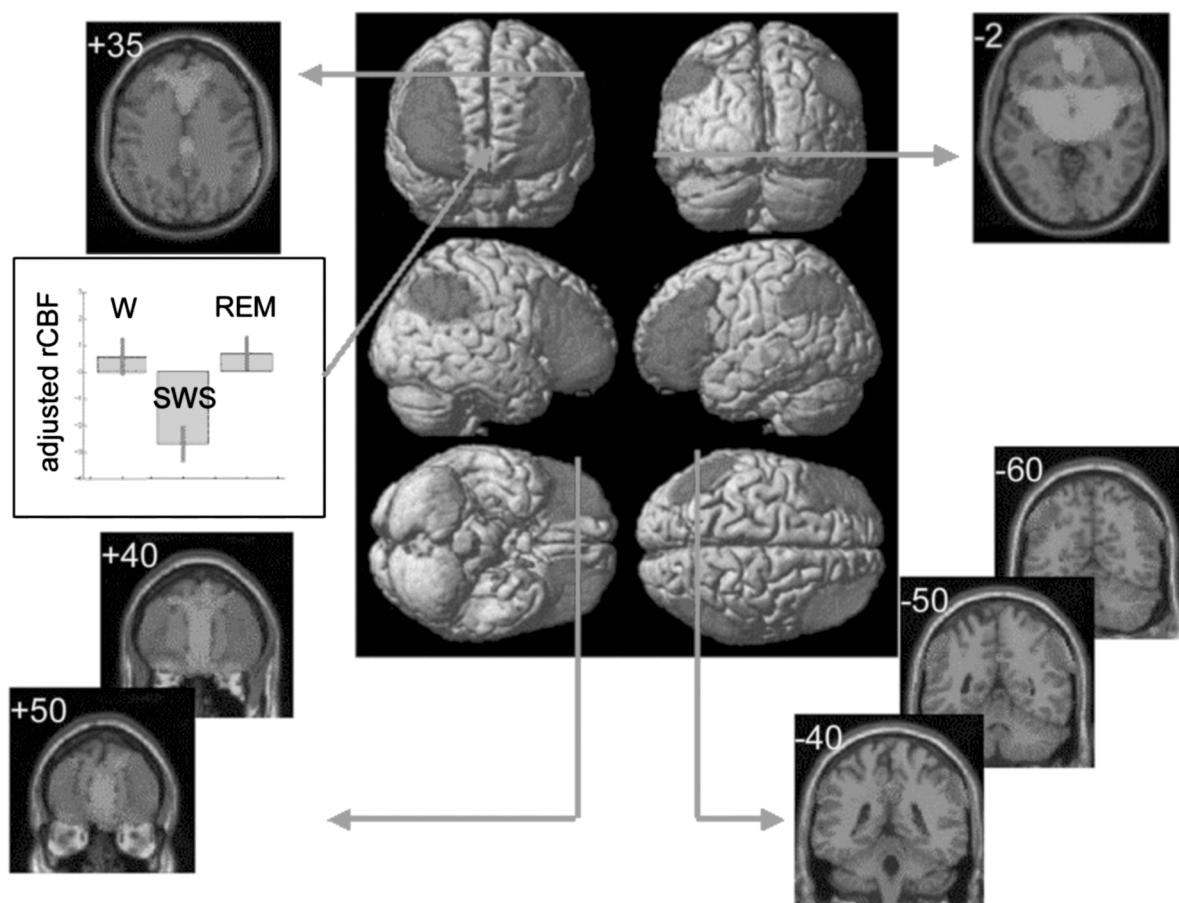


Fig. 1. *Central panel*: Three-dimensional rendering of the brain areas that are less active during REM sleep than during wakefulness (in red). These areas involve the lateral part of the frontal cortex, the inferior lateral lobule, and medial aspects of the parietal cortex. Anterior and posterior views (first row), lateral views (second row) and bottom and top views (third row). *Side panels*: For comparison, the brain areas that are significantly less active during slow wave sleep (SWS) than during wakefulness are indicated in green. Orange areas indicate regions where regional cerebral blood flow is decreased in both SWS and REM sleep as compared to wakefulness. *Left and right upper panels*: Transverse sections 35 (left) and -2 (right) mm from the anterior-posterior commissural plane. The least active areas during REM sleep (as compared to wakefulness, in red) do not reach the medial frontal cortex. In contrast, the medial frontal cortex is one of the least active area during SWS (as compared to wakefulness, in green). *Left lower panel*: Frontal sections through the frontal cortex, at 40 and 50 mm from the anterior commissure. The least active areas during REM sleep (as compared to wakefulness, in red) involve only the inferior and middle frontal gyri but do not reach the superior frontal gyrus or the medial prefrontal cortex. The latter are significantly deactivated during SWS (green). *Right lower panel*: Frontal sections through the parietal cortex, at -40 , -50 , and -60 mm from the anterior commissure. The least active areas during REM sleep (as compared to wakefulness, in red) involve only the inferior parietal lobule but do not reach the intraparietal sulcus or the superior parietal cortex. They overlap (orange) with the least active area during SWS (green). *Inset*: The adjusted cerebral blood flow in the medial prefrontal area is similar during wakefulness and REM sleep and is decreased during SWS. See Plate 16.1 in Colour Plate Section.

the dreamer would fail to organize his mental representation toward a well-identified internal goal and is seldom able to “control the flow of dream events” (Hobson et al., 2003). Volitional control is notoriously decreased in dreams. In contrast, the

dreamer’s behavior would be usually adapted to the objects and locations internally perceived, which are putatively related, as previously mentioned, to the activity in the posterior (temporal and occipital) cortices, highly active during REM sleep.

Lateral prefrontal cortex and episodic memory

Episodic memory refers to the capacity to encode and recollect past episodes with their specific integrated details, place and time (Tulving, 2004). Prefrontal cortex is not necessary to store, or to access to, episodic memories, since damage to frontal lobes does not impair episodic memory to the same extent as lesions to mesio-temporal areas (Henson et al., 1999). However, there are reports of densely amnesic patients after frontal lobe lesions. For instance, a remarkable patient presented with isolated retrograde amnesia due to a post-traumatic lesion in the right ventral prefrontal cortex (Levine et al., 1998). On the other hand, functional neuroimaging studies consistently reported the activation of prefrontal cortex, especially on the right side, during episodic memory retrieval (Rugg et al., 2002). The usually held view considers that prefrontal areas participate in processing information retrieved from episodic memory, essentially by checking its accuracy and completeness. The cognitive processes underpinning these frontal activations remain debated and would represent either a specific retrieval mode, retrieval effort or retrieval success (Rugg et al., 2002). The frontal areas activated during retrieval of episodic information are located in the right and left anterior prefrontal cortices and in the right dorso-lateral prefrontal cortex (Rugg et al., 2002).

It is intriguing to observe that the brain areas activated in functional imaging studies of episodic memory or this brain-lesioned amnesic patient overlap with the cortical regions hypoactive during REM sleep. The relative quiescence of the anterior prefrontal areas, and to some extent of the dorso-lateral prefrontal cortex would explain that recent waking life episodes, characterized by their specific location, characters, objects, and actions are seldom described as such in dream reports (1.7%) (Fosse et al., 2003). In contrast, “snips” of recent waking activity are frequently (65%) observed in dream reports (Fosse et al., 2003). Although the dreamer has access to “day residues,” probably spontaneously generated by the coordinated activity of the mesio-temporal areas and the posterior cortices, he would be prevented by the relative hypoactivity in the anterior prefrontal cortex from

tying up the various details of a specific past episode into an identified autobiographical event.

The ventral parieto-frontal system of attention

Recent neuroimaging data studying the neural correlates of human attention have established that two systems exist and interact in the normal human brain (Corbetta and Shulman, 2002). One system exerts a top-down control on perception. It carries neuronal signals related to the selection of stimuli and allows for the preparation of goal-directed motor responses. This system includes part of the intraparietal sulcus and the superior frontal cortex. The second system is not involved in top-down selection. On the contrary, it is specialized in the detection of salient, unexpected, behaviorally relevant stimuli and reorients the focus of attention. For instance, the activity in this network is enhanced in response to targets occurring at unexpected locations or to low frequency targets, especially when relevant to the task at hand (Corbetta et al., 2000). This system would work as an alerting mechanism when salient stimuli arise outside the present focus of processing. The activation of this system would result in an interruption in the current attentional set and in an attentional shift toward the incoming stimulus. As compared to the top-down system, this system is more ventral, mainly lateralized on the right hemisphere and involves the temporo-parietal cortex and the inferior and middle frontal gyri (Corbetta and Shulman, 2002). Several data suggest the activity in the ventral network would be modulated by the locus coeruleus. For instance, the locus coeruleus is involved in selective attention, especially to salient and unexpected stimuli (Aston-Jones et al., 2000). Furthermore, in the macaque, the inferior parietal cortex is known to receive heavy projection from the locus coeruleus (Morrison and Foote, 1986).

As far as a precise anatomical localization is allowed by PET, the topography of the relatively quiescent areas during REM sleep is similar to this ventral attentional network. The parietal area, hypoactive during REM sleep extends through the posterior part of the inferior parietal lobule toward the posterior end of the sylvian fissure. It

does not seem to extend to temporal areas. The hypoactive frontal region is located in the anterior part of the inferior frontal gyrus, on the anterior aspect of the region identified in the ventral attentional system. Moreover, although bilateral, the hypoactive areas are more extended on the right side, as is the ventral attention system (Corbetta and Shulman, 2002). Finally, the firing rate of noradrenergic locus coeruleus neurons dramatically decreases during REM sleep, depriving the parietal areas from an important positive modulation (Steriade and McCarley, 1990). These considerations suggest that the ventral attentional network is relatively quiescent during REM sleep. If this hypothesis were true, one predicts that the focus of attention during REM sleep should be less sensitive to salient, behaviorally relevant, external stimuli than during wakefulness. The focus of attention is difficult to assess experimentally during REM sleep. However, it may transpire in dream reports. One would expect that the dream narrative (obtained after awakening from REM sleep) would not be easily modified by external stimulation, even if behaviorally relevant. Some observations support this hypothesis. During REM sleep, external stimuli instead of interrupting the flow of the dream storyline, are incorporated into it (Foulkes, 1966). Similarly, responsiveness to external auditory stimulation is reduced during sleep, at least in part, due to incorporation of the external information into ongoing cognitive activity (Burton et al., 1988).

The frontal and parietal areas and mind representation during REM sleep

The medial frontal areas are active during REM sleep as during wakefulness. In this respect, REM sleep is very different from SWS because the same regions are relatively less active in SWS, as compared to either wakefulness or REM sleep. Theory of mind refers to the ability to attribute intentions, thoughts and feelings to oneself and to others (Carruthers and Smith, 1996). It is an inductive reasoning allowing interpretation and understanding of others' actions and speech, and prediction of their behavior. In comparison to reasoning applied to physical events or to lower level tasks, theory of

mind was shown to reliably involve medial prefrontal cortex, temporo-parietal junction especially in the right hemisphere and temporal poles (Fletcher et al., 1995; Brunet et al., 2000, for a review Frith, 2001).

Dreaming usually appears as a multisensorial narrative involving characters interacting with each other. These oneiric characters are credited thoughts, intentions, and emotions by the dreamer himself. Mind representation is thus a key feature of dreaming. We hypothesize that the persistence of a level of activity in the medial frontal areas similar to the activity observed during wakefulness might participate to mind representation during REM sleep.

However, during REM sleep, the preserved activity in the medial prefrontal areas (as compared to wakefulness) contrasts with the low activity in the inferior parietal cortex. In the right hemisphere, this area is a part of the network activated during mind representation at wakefulness and is involved in the distinction of first versus third person perspective in the representation of action, mind and emotion (Ruby and Decety, 2001, 2003, 2004; Chaminade and Decety, 2002; Farrer et al. 2003). During REM sleep, the low activation of the right temporo-parietal junction might be related to a loosening in the distinction between first and third level perspectives. Accordingly, in dream report, the self can participate to the dream action both in a first-person (i.e., the self sees and acts) and in a third-person perspective (i.e., the dreamer sees the self acting in the dream).

Finally, social emotion such as jealousy, pride, embarrassment, infatuation, sexual love, shame, guilt and pride are often reported in dreaming (Adolphs, 2002; Schwartz and Maquet, 2002). Neuropsychological and neuroimaging studies in humans have demonstrated that medial prefrontal cortex and amygdala are consistently involved in basic and social emotions processing and more generally in social cognition (Adolphs, 1999; Phan et al., 2002; Ruby and Decety, 2004). The amygdala are known to be very active during REM sleep (Maquet et al., 1996). The preserved activity in the medial prefrontal cortex might also account for the high proportion of dreams involving social emotions.

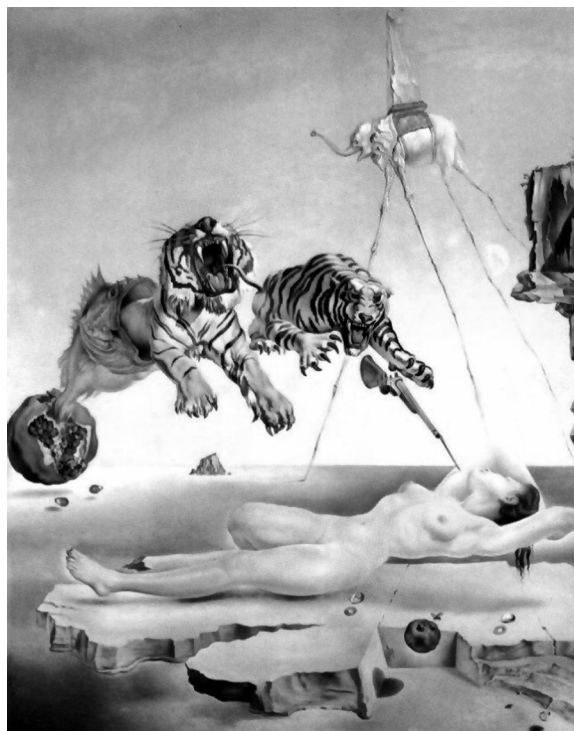


Fig. 2. Dream Caused by the Flight of a Bee Around a Pomegranate One Second Before Awakening, Salvador Dalí, 1944. © Fundació Gala-Salvador Dalí, c/o Beeldrecht Amsterdam 2005.

Conclusions

Our meta-analysis refines the description of the functional neuroanatomy of normal human sleep and provides a tentative framework to explain the relationship between human cognition during REM sleep and regional patterns of decreased activity within frontal and parietal areas. In particular, the hypoactivity in frontal and parietal areas during REM sleep is more precisely characterized. It involves the inferior and middle frontal gyrus as well as the posterior part of the inferior parietal lobule. Interestingly enough, the superior frontal gyrus, the medial frontal areas, the intraparietal sulcus, and the superior parietal cortex are not less active in REM sleep than during wakefulness. We suggest that this peculiar distribution of regional brain activity during REM sleep might correlate with some features of cognition, as reflected in

dream reports (Fig. 2). Especially, this regional metabolic pattern provides new insights on the possible neural bases of some characteristic dream features such as self and characters' mind representations, the poor episodic recall, the lower ability of external stimuli to break the dream narrative and the difficulty to organize one's oneiric behavior toward a well identified and persistent goal.

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