Chapter 15

Complementarity of dream research and neuroimaging of sleep

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Introduction

Sleep and dream research has recently been invigorated by the use of new methodologies, as well as by convergent data from complementary sources including neuroimaging studies of human sleep, clinical investigations of dreaming in brain-damaged patients, and the analysis of phenomenological characteristics of dream reports.

The aim of the present chapter is to show that dream reports contain valuable information about neural and cognitive processing during sleep. In particular, we propose that the characterization of sensory, cognitive, and emotional dream features, as well as the identification of typical bizarre elements in dreams may help specify how and what type of information is processed during sleep [1–3]. A systematic assessment of dream content can thus significantly contribute to the interpretation of functional imaging data recorded during sleep.

Below, we first consider the main difficulties that neuroscientists or clinicians may face when interpreting brain imaging data of human sleep. Next, we describe some reproducible cognitive and emotional features of dreams and show how they may orient the interpretation of patterns of brain activity recorded during sleep. Although dreaming may incorporate aspects of waking experiences, dreams are not replicas of real-life experiences. Instead, and as we then show, dreams contain many bizarre but typical features, which present similarities with specific neuropsychological deficits in neurological patients. Knowledge about brain damage underlying such deficits (during wakefulness) thus provides useful information about functional changes that may characterize normal human sleep, both at the brain and cognitive levels. Finally, we report some recent studies looking at the neural determinants of dream recall. In this chapter, we also suggest promising new ways of combining cognitive and neuroimaging experimental designs to better characterize cognitive or affective aspects of human sleep.

Interpreting neuroimaging data of human sleep: the problem

Non-invasive brain imaging methods have provided unprecedented insights into human brain functions. Likewise, descriptions of spontaneous brain activity across human sleep states have become increasingly complex and detailed. Yet, scientists may face several problems when attempting to interpret neuroimaging data of sleep, as illustrated by the following example. Let’s imagine that we obtained a set of brain activity maps in people while they were sleeping in a scanner. We may want to compare the level of regional brain activity corresponding to different sleep/wake states, we could also identify changes in functional connectivity across distributed networks, we may also compare activity for different populations such as normal healthy controls and patients, etc. Any of these scenarios will result in statistics indicating differences for certain brain regions or networks, which will call for an interpretation. Several strategies can then be used to interpret such data.

A first approach is to link brain activation observed during human sleep to animal physiological and cellular data (Figure 15.1). For example, we may infer that increased activation of the amygdala during rapid eye movement (REM) sleep is a manifestation of the dense connections of the amygdala with typical sleep-regulating structures described in the animal literature, such as the pons and brainstem nuclei (see [4]; Figure 15.2A). Confirming (or disconfirming) that specific aspects of sleep at the cellular level in animals can translate into macroscopic neuroimaging data in humans is an important research objective. While this strategy has proven very successful as well as inspiring for neuroimaging studies, it could also be seen as having a confirmatory scope, with a relatively limited potential for discoveries. A second approach is to refer to what we know about the functions of different brain systems during wakefulness (Figure 15.1). In our example, we could relate the activation of the amygdala observed during REM sleep to the role of the amygdala in emotional processing and learning [5, 6]. Nevertheless, this interpretation remains speculative in the absence of a direct access to emotional responses during sleep (unlike neuroimaging studies of awake subjects). This is why additional physiological measures of emotional reactivity should be used, whenever available (e.g., skin conductance, heart rate variability; e.g., [7]). Yet, both these approaches appear particularly challenging for more subtle dimensions of emotional experience as well as for understanding higher-level cognitive functions in sleep. In this
### Behavioral /cognitive level

**Pre- vs. post-sleep**
- task performance, self-rating
  - (e.g., emotion, cognition, learning, anxiety, impulsivity)

**During sleep**
- analysis of dream reports (see main text for more details)
- changes in dreaming after brain damage (e.g., Solms, 1997 [64])
- replay of motor behavior in parasomnia (e.g., Oudiette et al. 2011 [40])

### Cellular/microcircuits level

**During sleep**
- neuronal activity (e.g., replay of sequences of neuronal activity)
- synaptic plasticity, neurogenesis, gene expression, etc.

### Neuroimaging/macroscopic systems level

**Pre- vs. post-sleep**
- EEG, PET, MRI, SPECT, etc.
- activity, connectivity, anatomy, etc.
- task-related, resting state, etc.

**During sleep**
- EEG, PET, MRI, SPECT, etc.
- sleep macro/micro structure, etc.
- task-related reactivation/responses to external stimulation, etc.

### Figure 15.1 Examples of methods and data available in sleep research for interpreting brain imaging results from human sleep. Information about neural and cognitive processes during sleep may come from distinct sources and levels of description. Direct (during sleep) as well as indirect (e.g., pre- vs. post-sleep) measurements are represented. Arrows symbolize the contribution of various sources of information (e.g., dream data) to the interpretation of neuroimaging data collected during sleep.

### Figure 15.2 (A) Functional neuroanatomy of human REM sleep. Regions showing increased or decreased brain activity in the positron emission tomography (PET) studies reported in the main text. (Adapted with permission from Desseilles et al. [26] Conscious Cogn, 2011.) (B) Specialized brain regions for the processing of visual motion (MT/V5), colors (V4), layouts and landscapes (parahippocampal place area; PPA), face processing (fusiform face area; FFA). These regions are located within the occipital and temporal lobes.
context, dream reports represent an additional major source of information about cognitive and emotional processing during sleep (Figure 15.1). In our example, the interpretation of amygdala activation in terms of concomitant emotional processing during sleep would be supported by the high prevalence of intense negative emotions in dreams (see Distinct affective and cognitive dimensions in dream reports below), and by changes in dreamed emotions in conditions that modulate amygdala activity (e.g., pharmacological treatments, mood disorders, psychotherapy). Another attractive option is to use dedicated experimental protocols to indirectly probe cognition or emotion during sleep, for instance by using measures of waking performance in behavioral tasks (pre- and post-sleep behavioral measures; e.g., [8, 9]) or by presenting external stimuli during sleep (such as sounds, words, odors; e.g., [10–12]), with the assumption that observed changes in brain activity during sleep correspond to the active processing of information related to pre-sleep experience or external stimulation. A combination of such an experimental approach and the analysis of dream reports may be particularly promising for future studies [13].

We therefore propose that a thorough understanding of human sleep will require an interpretation of functional imaging data in terms of their concomitant cognitive processes, such as those revealed by the analysis of dream content.

**Phenomenology of dreaming**

In this section, we demonstrate that dream reports contain valuable information about the cognitive processes that contribute to their generation and that cognition during sleep can be inferred from common features found in dream reports from different individuals [1, 2, 14]. Here, we consider dream content as accurate descriptions of sensory, emotional, and cognitive experiences spontaneously generated during sleep. Accordingly, vivid visual imagery, emotional intensification, and illusion of reality would represent examples of the defining features of typical dream experiences. We suggest that frequent cognitive features of dreams inform about underlying brain functions, thus allowing the integration of dream data into a unified model of human sleep.

**Methods to collect reliable dream data**

Dreaming raises the following methodological problem, which is also shared by other manifestations of conscious processes: how can we study a phenomenon that is not directly and objectively observable, but only accessible through introspection? Introspection implies that we first look into our own mind and then report any thought, feeling, and sensation that we could discern. It is important to note that the difference between introspective data and objective data derived from overt behavioral responses is often overstated. Indeed, like introspective data, behavioral measurements in cognitive studies frequently rely on inspecting mental representations or sensations and making decisions about them [15, 16]. By the very fact that they constitute a form of memory recall, dream reports may also be influenced by several factors such as forgetting, reconstruction mechanisms, verbal description difficulties, censorship, experimental demands, and lack of independent verification. The impact of each of these factors can be minimized by using appropriate strategies, in particular by a careful training of the participants at reporting their dreams (more information about these strategies in [2]). Different methods can be used to collect representative and reliable dream material such as home-based dream diaries, dream questionnaires measuring precise features of dream experience, and dreams collected after awakening from polysomnographically defined sleep stages. Finally, asking people to report their most recent dream, whether it was “last night, last week, or last month,” can also provide valuable information about dream content, in particular to characterize dreams in specific populations (“most recent dream” method; [17]).

**Statistical approach to dreaming**

Humans have always been intrigued by the varieties of dream experiences. Indeed, the seemingly disorganized and bizarre aspects in dreams contrast with the consistency and reproducibility of certain dream features, including some of the most bizarre dreams. It is thus not surprising that scientific approaches to dreaming have been interested in measuring the frequency of specific dream contents. Here we suggest that frequent dream features must relate to recurrent patterns of brain activity during sleep.

In 1893, a first statistical investigation was conducted on 375 dream reports by Mary Calkins [18], who found a clear predominance of visual experiences in dreams (57%), followed by auditory experiences (37%), and then by gustatory and olfactory experiences (1%) (see [19] for similar results). By programming awakenings at different times in the night, she also observed that more dreams occurred during the late part of the night (between 4 and 8 am), and that these late dreams were more vivid (this observation was replicated in several recent studies; e.g., [20–22]). Much more recently, and almost at the same time as REM sleep was discovered, Hall and Van De Castle published an extensive manual for coding of the content of dream reports [23]. This classification system was initially designed to measure common features in a large sample of dream reports from healthy young students (e.g., people, objects, places, social interactions, activities, emotions, etc.) and provided normative values for different content categories, which have since then been used to study many different samples of dreams (e.g., [24]). Nowadays, scales and coding systems have become standard tools to quantify dream characteristics. This classification approach is very efficient for assessing specific content categories, such as different types of emotions or bizarre features in the dreams of healthy or patient populations, or when testing theoretically driven hypotheses (e.g., [25]). However, coding systems rely on the delimitation of a-priori categories to be quantified and therefore purposefully dismiss a large portion of information in the data. They also require that dream reports are analyzed manually, which may become particularly time-consuming when processing large dream data sets. To overcome some of these limitations, we proposed to use lexical statistical methods.
Distinct affective and cognitive dimensions in dream reports

We applied multidimensional statistical methods to a large longitudinal dream diary containing 1770 dream reports as well as to the original dreams used by Hall and Van de Castle consisting in total of 1000 dreams from 50 male and 50 female students (data set available: www.dreambank.net; [23]). Our results revealed well-segregated and consistent cognitive dimensions in the dreams from different individuals (more details about these results can be found in [1, 26]).

For example, frightening experiences formed a highly consistent category of dream content, which was clearly separated from dream elements referring to affective and working concerns related to the sleeper’s waking life because limbic circuits, in particular the amygdala, contribute to emotional and memory processing [5, 6, 27], amygdala activation during sleep [4, 28, 29] might provide a permissive condition for emotionally relevant elements of memory to be selectively reprocessed in sleep (Figure 15.2A) [30–33]. This is consistent with an overrepresentation of recent elements of real-life and social emotions in the dreams [34–36]. On the other hand, intense fear-related emotions in dreams associated with rather unfamiliar settings as compared to waking life suggest that enhanced activation of the amygdala could also contribute to the rehearsal of genetically programmed or “primitive” behavioral responses to threatening stimuli [25, 37, 38]. A careful analysis of dream data therefore suggests that amygdala activation during REM sleep may be interpreted as contributing to distinct memory functions. Because the replay of recent neuronal activity possibly predominates during slow-wave sleep [39, 40], the finding that current concerns are frequent in dreams would also motivate future studies looking at transient patterns of regional cerebral activity [41, 42] and at the specific distribution of affective contents in dreams across all sleep stages [22].

As another example, the same statistical analyses also revealed that different categories of dream reports are characterized by distinct types of visual processes, such as color vision versus motion perception, or landscapes and outdoor scenes versus familiar people (among other visual characteristics; Figure 15.2B). Dissociation between these different visual properties is consistent with well-known functional specializations in the human brain (e.g., color vision in V4; motion processing in MT/V5; layouts and landscapes in the parahippocampal place area [PPA]; face processing in the fusiform face area [FFA]). While activation of associative visual areas is common in REM sleep [29, 43, 44], the functional dissociations in dreamed visual content, as found here, suggest that activity within associative visual areas during sleep might be more heterogeneous than previously thought, while involving reproducible patterns of brain activity.

Importantly, consistent emotional and cognitive dissociations were found in independent sets of dream data. Thus, the categories of dream content reported here substantiate our initial hypothesis that typical or common features in dream reports provide new information about emotional and cognitive processes at play during sleep.

Neuropsychology of dream bizarreness

When compared to usual experiences of waking life, dreams present innumerable anomalies. In this section, we show that bizarre features in the dreams may reflect specific functional states of the sleeping brain. We propose that (a) some bizarre features reported in dreams present remarkable similarities with specific neuropsychological deficits observed in brain-damaged patients, and that (b) the lesional topography causing these deficits in patients provides useful information about brain regions activated or deactivated during normal sleep [2]. Below, we illustrate with a few examples how bizarre aspects of visual processing in dreams may resemble some neurological syndromes. Note that the existence of striking similarities between certain neuropsychological syndromes and typical dream productions suggests commonalities in their underlying brain organization, but this does not imply at all that sleep or dreaming is a pathological state.

Misidentification for faces

One common bizarre feature in dreams is the disruption in visual recognition, whereby a dreamed character or object is clearly recognized although its physical appearance is drastically modified in the dream [2, 45]. In dreams, such dissociations between appearance and meaning commonly occur for faces or characters. The following dream reported by a 25-year-old man after an experimental awakening from REM sleep illustrates a typical mismatch between the identity of a character and its appearance: “Ah yes, exactly, I had a talk with your colleague, but she looked differently, much younger, like someone I went to school with, perhaps a 13-year-old girl …” ([19], p. 71). Normal identification of faces relies on a specific network of specialized brain areas including the FFA (Figure 15.2B) for the visual extraction of facial traits, the amygdala for detection of emotional significance [46], and infero-temporal and prefrontal regions that provide semantic information about particular people. Delusional misidentification or hyperidentification for people corresponds to a well-known neurological condition (sometimes called the Frégoli syndrome), whereby an unknown person face’s is erroneously recognized as a familiar person, despite the lack of any obvious physical resemblance [47–49]. Brain lesions in this disorder may encompass temporo-occipital regions and the prefrontal cortex [47, 50, 51]. As exemplified by the dream excerpt above, misidentification for faces is a common feature of dream experience [45], which might relate to an activation of the FFA and temporal areas in the absence of selective reciprocal constraints between these regions, and in the absence of monitoring from prefrontal areas (whose activity is reduced during human sleep; [4, 29, 52]). Moreover, activation of limbic circuits during REM
sleep may promote an abnormal bias in attributing a personal meaning or relevance to unknown faces [4, 29].

Misidentification for places

Misidentifications for places are also extremely frequent in dream reports, in which one place can be recognized as familiar in the absence of any apparent similitude to the corresponding original place. Neuroimaging studies in awake subjects have identified a specific brain area that is specialized for the processing of places and layouts, i.e., the PPA (just anterior to the FFA; Figure 15.2B). Delusional misidentification syndromes or “redundicual paramnesia” for places can occur after temporal and prefrontal lesions, with a right hemisphere predominance [53–55]. Like the misidentifications for faces, misidentifications for places in dreams likely result from a disconnection between the PPA (mediating perceptual features), temporal regions (semantic information), and frontal regions (monitoring).

Other visual distortions

A non-exhaustive list of other typical visual distortions in dreams includes the multiplication of a visual percept in time (“palinopsia”) or in space (“polyopia”), which is observed in patients with lesions in visual associative areas [56, 57], and abnormal visual size perception with apparent reduction (“micropsia”) or increase (“macropsia”) of the size of objects, previously reported after right occipital damage [58]. A typical example of macropsia is offered in the following excerpt from a dream of a 23-year-old woman (laboratory recording, awaking from REM sleep): “I was together with two boys, about 17 years old. They were fixing an enormous steak, a T-bone steak. I noticed how they had prepared it. It was a gigantic piece, one might have thought from an elephant, incredibly huge.” ([19], p. 147). These distortions are present in a significant fraction of dream reports, suggesting that selective visual areas are hypo-activated or disconnected from other higher-level areas during this type of dream experiences. The loss of color saturation in visual perception (“achromatopsia”) found in patients with occipital lesions in lingual and fusiform gyri [59] is also frequently found in dream imagery [60] and suggests a hypoactivation of occipital color areas (Figure 15.2B) or a disconnection between color regions and other visual or parietal regions sub- tending multimodal integration.

Interestingly, recent combined electroencephalogram (EEG) and TMS (Transcranial magnetic stimulation) studies have shown that functional connectivity across cortical regions is reduced during non-rapid eye movement (NREM) sleep but possibly restored during REM sleep [61, 62]. Although the functional dialog across brain regions during some sleep stages may be quantitatively comparable to that observed during wakefulness, cognitive dissociations in dream reports suggest some alterations of the functional integration of neural activity across regions, which may be due to decreased perceptual and physiological constraints (e.g., reduced sensory inputs, limited monitoring mechanisms, variations in neurotransmitters balance) during sleep as compared to wakefulness. The analysis of specific bizarre features in dreams might thus offer specific and useful constraints to the interpretation of functional imaging data collected during sleep.

Neural determinants of dream recall

Several studies are directly aimed at revealing the neural correlates of dreaming. In particular, selective disorders of dreaming may result from regionally specific brain damages [63, 64], showing a high degree of overlap with regions found to be activated during REM sleep, thus confirming the hypothesis that activation during REM sleep may, at least in part, support dreaming [3]. Lately, some studies looked at the EEG power spectra during periods of sleep preceding awakenings with and without dream recall [65, 66]. Although not always consistent, the results showed that changes in cortical oscillatory activity may predict successful dream recall, with more frequent recall when frontal theta is high during REM sleep and when NREM sleep oscillations are attenuated (e.g., lower frontal delta and higher temporal alpha). A preliminary study also used transcranial direct current stimulation during stage 2 sleep to directly modulate brain activity and dreaming, and found increased frequency of dreams with visual imagery during stimulation of posterior regions (and deactivation of frontal regions) [67]. These studies confirm that dreaming is not confined to periods of REM sleep and that dreaming may occur on variable backgrounds of neural activity over a night of sleep. While these studies point to a distribution of neural activation that may optimize consciousness and memory for dream experiences, links with specific dream contents still need further research. Related to this issue, a recent study investigated whether anatomical measures of the amygdala and hippocampus correlated with quantitative and qualitative aspects of dream reports in healthy subjects, and showed that the volume and mean diffusivity of the amygdala correlated with emotional and bizarre features in the dreams [68]. These findings demonstrate that individual differences in dream experiences are underlined by differences in brain structure. An important extension of this work will be to test how individual difference in dream content (and brain anatomy) covary with behavioral and brain measures during wakefulness (i.e., emotional responses and amygdala activity). This non-exhaustive selection of studies indicates very clearly that brain imaging methods can be used to investigate mental processes during sleep and their underlying neural substrate. Conversely, future studies are expected to show that dream characteristics may represent biomarkers of important brain functions, such as emotional regulation processes [26]. Thus, future studies of sleep in health and disease would benefit from collecting dreams in a systematic manner.

Conclusions

In the present chapter, we showed that the study of dreams provides meaningful and valuable information about cognitive and affective processes occurring during sleep. We first demonstrated that typical features in large dream samples can be identified using statistical methods and that these features are in good correspondence with known patterns of brain activity
during sleep, in particular REM sleep. These analyses are based on the frequency of occurrence and degree of uniformity of dream contents, irrespective of whether the dreams mimicked real-life experiences or were extremely bizarre. We then showed that bizarre but common aspects in dreams have much in common with known neuropsychological syndromes. This approach has taken into account the typical pattern of activation during REM sleep (high limbic and low prefrontal/parietal activity), but it further suggests that sensory areas are heterogeneously activated (i.e., in different dreams) and that the functional connectivity between brain regions, including associative regions beyond early sensory cortices, may be modulated as well. Future research should objectively characterize these region- and episode-specific patterns of activation across all sleep stages and help specify the hypothesized mechanisms that might explain them, such as ponto-geniculocortical activity [69] or experience-dependent cortico-limbic interplay [39, 70]. Unlike early brain imaging studies (most of them using PET) that were restricted to reporting mean levels of regional cerebral activity during distinct 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 [41, 42, 71]. Altogether, this new, integrated approach to sleep and dreaming will undoubtedly contribute to redefining the links between brain processes and the varieties of dream experiences, and lead to a more comprehensive model of human brain function during sleep.

References


