

Dreaming: a neuropsychological view¹

■ S. Schwartz^{a, b, 2}, T. T. Dang-Vu^{c, d, 3}, A. Ponz^{a, 2}, S. Duhoux^{a, 2}, P. Maquet^{c, d, 3}

^a Laboratory for Neurology and Imaging of Cognition, Department of Neurosciences, University Medical Centre, Geneva

^b Department of Clinical Neurology, Geneva University Hospital

^c Cyclotron Research Centre, University of Liège (B)

^d Neurology Department, Centre Hospitalier Universitaire (CHU), Liège (B)

Summary

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Sleep and dream research has recently been invigorated by convergent data from complementary neuropsychological sources such as brain-imaging studies of normal sleep, clinical investigations of dream disorders in brain-damaged patients and analyses of dream reports from healthy individuals. Here we show that by adopting a neuropsychological approach to dream phenomenology we can gain important insights into the processing of information within specialised brain regions during sleep. We first review clinical studies revealing that dreaming can cease or be reduced after lesions within parieto-occipital and deep bifrontal regions, but that dreaming remains largely unaffected by dorsolateral prefrontal lesions. Damages in occipito-temporal visual regions can selectively affect the visual quality of the dreams and often co-occur with similar visual impairments while awake. Based on these clinical observations, it is thus possible to infer which brain structures might underlie normal dreaming. We then describe some cardinal phenomenological features of normal dream experience. Using multidimensional statistical methods, we identified recurrent cognitive dimensions in large samples of dream reports without any a priori coding of their content. Our analyses revealed well-segregated and consistent cognitive dimensions in the dreams from different individuals, including verbal and motor activities,

visual processing such as colour vision and motion processing, and strong emotions such as fearful experiences. These findings suggest that dreaming might implicate distinct but reproducible patterns of activation across the motor, visual and limbic systems. In the last part, we introduce a neuropsychological approach to normal dreaming (i.e. dreams from neurologically healthy individuals). In particular, we show that some bizarre but common features in normal dreams present striking similarities with neuropsychological symptoms observed in brain-damaged patients while being awake, suggesting specific commonalities in brain organisation. For example, dreams present many instances of delusional misidentification for people or places characterised by a mismatch between the identity and the physical appearance of a character or a place. Dreams contain many other visual distortions such as the multiplication of a visual percept in time or space, deficits in size perception, reduced colour vision, etc. These bizarre features of visual processing during sleep suggest reduced neural activity within specialised visual areas and/or functional disconnections within the visual system as well as from other higher-level brain regions. In conclusion, by providing specific predictions about likely patterns of cerebral activity during sleep, dream studies open up a new road for the interpretation of future brain maps of human sleep while shedding light on the varieties of conscious brain states.

Keywords: *dreaming; sleep; neuropsychology; cognition; emotion; REM*

Correspondence:
Sophie Schwartz, PhD
Laboratory for Neurology and Imaging of Cognition
Department of Neurosciences
University Medical Centre (CMU)
1, rue Michel-Servet
CH-1211 Geneva
e-mail: sophie.schwartz@medecine.unige.ch

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Introduction

"A dream is this. I perceive objects and there is nothing there. I see men; I seem to speak to them and I hear what they answer; there is no one there and I have not spoken. It is all as if real things and real persons were there, then on waking all has disappeared, both persons and things. How does this happen?" (H. Bergson 1914, p. 15 [1])

For modern neuroscience research dreaming stands out as a most intriguing topic of investigation. Dreaming constitutes a prevailing facet of human experience associated with specific brain states that occurs spontaneously for several hours each night while we are sleeping. Dreaming can thus be of significant interest to a large number of researchers including neurophysiologists, sleep medicine specialists, psychiatrists, behavioural neurologists and cognitive psychologists. Yet, still little is known about dreaming from a scientific perspective. Over the past fifty years, ingenious and productive work has been dedicated to the study of waking behaviour and waking consciousness, but attempts to understand dream processes have remained comparatively sparse. Two main factors have contributed to this relative neglect of dreaming as a topic of scientific inquiry. First, dreaming has for a long time been associated with psychoanalysis, thus generating suspicion about the nature and reliability of dream data. Second, a traditional experimental approach is not straightforwardly applicable to dreams since dreaming occurs during sleep and is therefore not directly observable or measurable. However, sleep and dream research has recently been invigorated by the use of new methodologies, as well as by convergent data from complementary sources including brain imaging studies (reviewed by Dang-Vu et al. in this issue), clinical investigations in brain-damaged patients, statistical analyses of dream reports and neuropsychological interpretation of bizarre but common features of dream experiences.

The present review substantiates the assumption that dream reports contain valuable information about the cognitive processes and brain functions that participate in their generation. The idea of a "cognitive" approach to dreams dates back to the late 1950s when cognitive psychology arose as a distinct subfield of scientific psychology. Since then, mental phenomena were (again) studied, including one of the most pervasive and impressive forms of human experience – dreaming. However, it was only in the mid-1990s that a renewed interest for the cerebral bases of dreaming emerged [2, 3], promoting dreaming as a valuable topic for neuroscience research. In this context it was proposed that the identification of common sensory, cognitive and emotional dream features, as well as

typical bizarre elements in dreams, could provide unique insights into the processing of information within specialised brain regions during sleep [4–6]. At the same time, advanced neuroimaging techniques such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) started to be used to measure regional brain activity during distinct states of sleep and wakefulness in healthy volunteers (reviewed by Dang-Vu et al. in this issue). In addition, thorough anatomical descriptions provided by modern brain scanning could be used to identify brain lesions that disrupt or alter dream experience in neurological patients [7, 8]. Hence, over the last decade or so, sleep and dream research began to raise fundamental questions pertaining to the diversity of functional brain states, as well as the richness of coincident corporeal and mental experiences.

Here, we first review evidence for quantitative and/or qualitative changes in dream experiences resulting from selective brain lesions. Based on such clinical observations, we can infer which brain structures are normally involved in dreaming and likely to be activated during specific periods of sleep (although any direct mapping from a brain lesion to a cognitive function will always remain tentative). Then, we show that some well-delineated dimensions of dream experiences (e.g. perception, emotion or cognition) are frequent in large dream samples, suggesting that specific but common underlying patterns of cerebral activity might occur iteratively during sleep. Importantly, there is a good match between the neural activity predicted from these cognitive features and functional imaging maps of human sleep (Dang-Vu et al., this issue). In the last part, we introduce a neuropsychological approach to normal dreaming (i.e. dreams from neurologically healthy individuals [5]). This approach arises from conspicuous analogies between bizarre features in dreams and specific neuropsychological syndromes observed in brain-damaged patients while being awake. We demonstrate that knowing about the lesional topography corresponding to these syndromes would provide useful information about likely changes in brain functions during normal sleep.

Neuropsychology of dream disorders

Recent brain-imaging studies in healthy subjects have provided detailed maps of regional cerebral activity across sleep stages, but any attempt to relate these maps to dream processes still remains mostly hypothetical and needs further experimentation (see Dang-Vu et al. in this issue). In the

meantime, we can rely on another instructive source of information about the dreaming brain. Namely, studying patients with focal brain damage can facilitate the identification of brain regions whose integrity is necessary for normal dreaming.

However, clinical investigations of dreaming face several challenges. First, the absence of direct and immediate access to dream experiences imposes important methodological limitations to the assessment of dream functions. Moreover, many people may perceive questions about their dreams as relatively intrusive upon their private life, even in the context of a clinical examination, and may therefore censure or bias their own reports thus providing incomplete or conformable descriptions (see [5], Box 1). In addition, other neuropsychological or psychiatric impairments affecting the patients' waking behaviour are usually diagnosed first because they often engender more discomfort than potential disorders of dreaming which might in turn remain undetected. Finally, a comprehensive brain-based theory of dreaming is required to promote dream data as useful or clinically sound. Despite all these limitations, dream disorders in brain-damaged patients have been reported occasionally for more than 100 years. In 1883 Charcot described the famous case of "Monsieur X" who was no longer able to represent visible objects, neither while awake nor in his dreams: "I dream simply of speech, whereas I formerly possessed a visual perception in my dreams" (quoted in [7], p. 5). The limited series of mostly incidental neuropsychological reports of dream disorders has recently been augmented by an investigation conducted on a large sample of neurological patients that we review in some details below [7].

In this section, we will also question the overstated assumption that dreaming equates to the physiological state known as REM sleep (rapid-eye-movement sleep). Undeniably, linking dream phenomenology to REM sleep neurophysiology provided a valuable framework for the scientific study of dream processes. However, we will argue that a meaningful theory of sleep and dreaming should contribute to a general model of human consciousness and that future work might need to go beyond the original equation "dreaming = REM sleep".

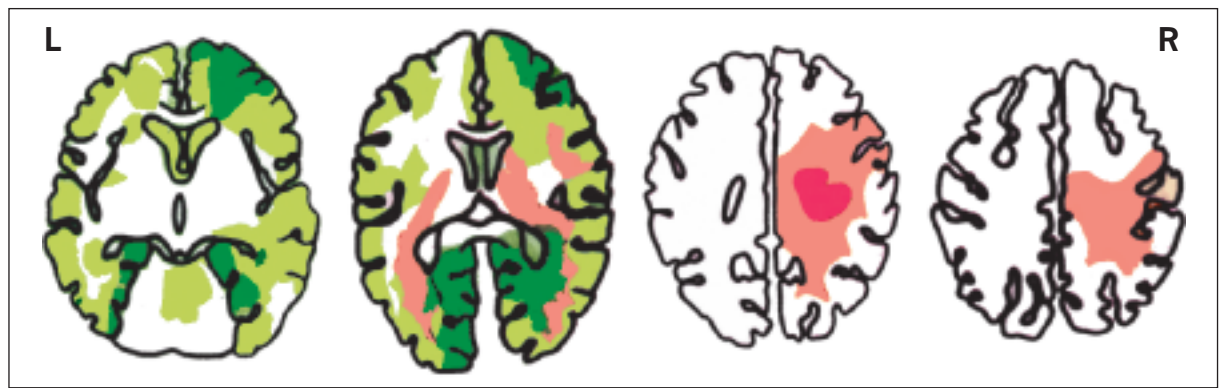
Dream disorders in brain-damaged patients

The first brief reviews focusing on dreaming in brain-damaged patients appeared in the 1970s and 1980s. At that time, laterality of dreaming was debated with questions such as: do dreaming dis-

orders occur more frequently after lesions affecting the right or the left hemisphere [9–11], or does each hemisphere contribute to different dream features [12]? In 1992, Doricchi and Violani [8] published a pioneering meta-analysis of the lesions' sites producing cessation, alteration or maintenance of dreaming following cerebral damage. They used a simplified anatomy that indexed lesions according to the affected lobes (frontal, parietal, occipitotemporal) and hemispheres (right, left, bilateral), thus going beyond previous dichotomic laterality approaches. They found that (a) damage to the frontal lobes is not systematically associated with loss of dreaming (many patients with frontal lobe lesions show maintenance of dream experience), (b) lesions in the parietal lobes and lesion associated with disconnective syndromes can cause loss of dreaming without notable hemispheric asymmetry, and (c) dream cessation after unilateral left or right damage is as frequent as after bilateral (and larger) damage (see contrasting results in [13]).

Five years after Doricchi and Violani's article, Mark Solms [7] established the first nosology of dream disorders with neuropathological significance based on an extensive review of previously published clinical descriptions as well as on his own investigation of 361 neurological and neurosurgical patients. Such a systematic investigation represented a significant advancement surpassing previous sampling biases. Solms asked his patients to freely describe any change in dreaming since the onset of their illness. Their first spontaneous description was followed by detailed dream interviews addressing sleep quality, dreaming experience and dream recall (patients may have the impression that they still experience dreams while being no longer able to report any content in the morning; cf. "blank dreams"; cf. [14]). Finally, specific dimensions of dream experience were assessed including narrative complexity or bizarreness, emotional intensity, presence of recurring nightmares, frequency of dreaming, visual imagery and its vivacity, dream-reality distinction, dream duration and memory sources of dream content. From the 332 cases with confirmed cerebral lesions, Solms could distinguish between four major disorders of dreaming based on the uniformity of their manifestation and their associated neuropsychological deficits at wake, as well as on their association with specific sites or types of lesions (CT scans). Solms' classification of dream disorder first defines the *syndrome of "nonvisual dreaming" (or visual anoneira)* as a loss of visual imagery or an alteration in one aspect of visual imagery (e.g. face, colour or kinematic perception). This syndrome was found to

Figure 1



Lesion map associated with reduction or cessation of visual dreaming (schematic axial brain sections from lower to upper brain slices). Reduction of dream-imagery vividness occurred in 21 cases with preponderant medial occipito-temporal-limbic lesions (green); note that visible right frontal lesions did not discriminate between patients with and without reduced vivacity of dream imagery. Cessation of visual dreaming was found in one case with right parietal arterio-venous malformation and bilateral oedema (red). Adapted from [7].

be concomitant of occipito-temporal lesions and to co-occur with similar impairments of visual processing at wake (fig. 1).

Then a second, major disorder of dreaming, the *syndrome of "global cessation of dreaming"* (or *global anoneira*), is characterised by a total, but sometimes transitory, loss of dreaming. Global cessation of dreaming occurs after either parietal and posterior temporo-occipital lesions (right or left hemisphere) or deep bifrontal lesions (fig. 2a); it is associated respectively with visuospatial memory deficits or with adynamia, disinhibition and perseveration (see [15] for a compelling case report of global cessation of dreaming after occipital lesions). Global cessation of dreaming was also observed in patients with hydrocephalus. The third disorder of dreaming identified by Solms is the *symptom complex of "dream-reality confusion"* (or *anoneirognosis*) in which the patients are impaired at distinguishing internally generated experiences such as their dreams from externally driven percepts. This dream-reality confusion is often accompanied by a quantitative increase in dream frequency. It occurs with frontal-limbic lesions and is associated with defective reality monitoring, as well as with executive and affective disorders, and sometimes with cortical blindness. The fourth category of dream disorder is the *syndrome of "recurring nightmares"*, defined by frequent nightmares with a repetitive theme. Recurring nightmares often occur in the context of temporal-limbic seizure activity, with stereotyped nightmares accompanying complex-partial seizures in some cases [16–19].

Solms' investigation also provides a description of the anatomical correlates of normal (or mostly unchanged) dreaming from a large population of brain-damaged patients. Normal dreaming occurred in 24 of the patients' series, with a clear preponderance of lesions in the dorsolateral pre-

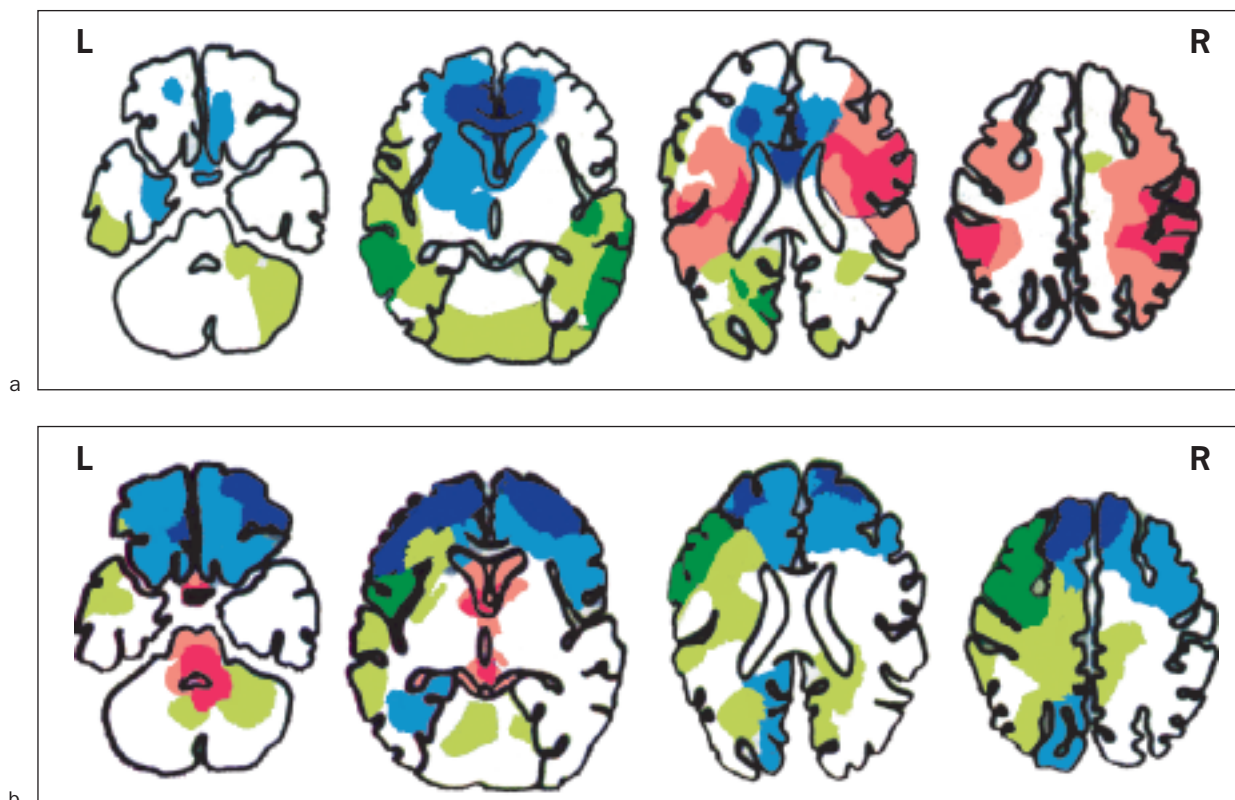
frontal cortex (predominantly in the left hemisphere; fig. 2b), and was sometimes associated with aphasia, problem-solving deficits and perseveration. This result obtained with an improved anatomical resolution elucidates Doricchi and Violani's (1992) perplexing finding that frontal lobe lesions were not systematically associated with loss of dreaming. The resulting lesional map is also truly impressive when confronted with the neuroimaging results from healthy subjects showing reduced activity in the dorsolateral prefrontal cortex during normal sleep [2, 20] (results published after Solms had finished his manuscript). Finally, preserved dreaming was also observed after brainstem lesions, suggesting that dreaming may be at least partly independent of REM sleep processes generated in brainstem regions (fig. 2b).

Taken together, these clinical investigations suggest that neurological diseases result in specific alterations of dreaming experience. Like other neuropsychological impairments affecting the waking behaviour of the patients, dream disorders can also inform about their underlying neuropathological processes. Dreaming deficits therefore provide valuable diagnostic and/or prognostic indications (see Bassetti et al. in this issue) and should thus be included in standard neuropsychological investigations.

Is REM sleep necessary for dreaming?

Electroencephalograms (EEG) of sleep had been taken since the late 1920s, but it was not until 1953 that electrooculograms (EOG) were recorded along with the sleep EEG, leading to the discovery of REM sleep ([21]; see also [22, 23]). REM sleep is characterised by low voltage "activated" EEG (resembling certain waking patterns),

Figure 2



Lesion maps associated with cessation vs preservation of dreaming. (a) Global cessation of dreaming is illustrated by: 6 cases with parietal lobe lesions (inferior lobule and supramarginal gyrus; red), 9 cases with deep frontal lesions (blue), and 8 cases with posterior lesions, close to parietal lobes (green). (b) Preserved dreaming processes were found in: 15 cases (entirely unchanged dreaming) with left hemispheric and frontal convexity lesions (green), 14 cases with bifrontal lesions (cortical convexity, blue), and 17 cases with brainstem lesions (red). Adapted from [7].

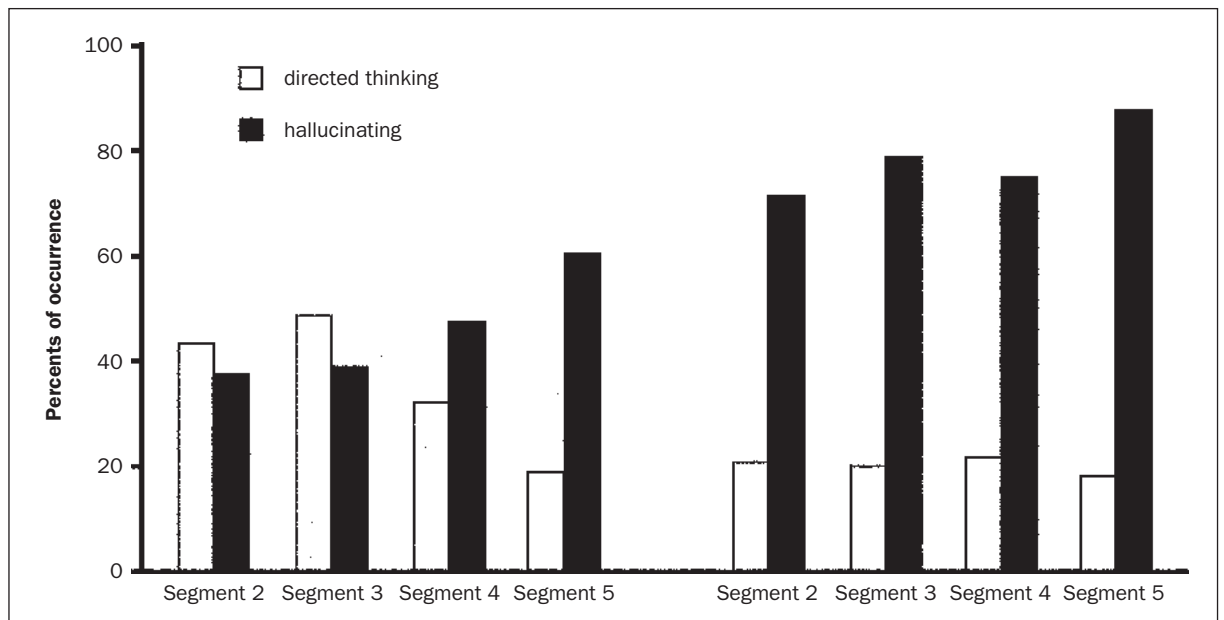
intermittent bursts of rapid eye movements and profound motor inhibition, consuming about 20% of the total sleep duration and distributed across 4–5 periods getting longer as the night progresses. REM sleep might thus reflect periods during which the sleeper's mind is intensely active and possibly produces dreams. To test this hypothesis, Aserinsky and Kleitman [21] conducted awakenings during REM and NREM phases, inquiring whether a dream occurred just prior to the awakening. Twenty of 27 REM awakenings yielded detailed dream reports, while only 2 out of 23 NREM awakenings did. Since then, it has been confirmed repeatedly and with different methods that REM awakenings produce more vivid dream reports and more frequently when compared to NREM awakenings [24–28]. It therefore became conventional belief that we dream during REM sleep.

The equation “REM sleep = dreaming” is historically significant because it gave credit to a scientific approach to dreaming, a topic previously relegated to the realm of untrustworthy anecdotes, dubious popular beliefs (e.g. oniromancy) and psychoanalytical interpretations. In particular, this equation partitioned sleep into a dream-present brain state (REM) and a dream-absent brain state (NREM) thus reducing the characterisation of the

neural correlates of dreaming to a comparison between REM sleep and waking or NREM sleep. However, ever since the discovery of REM sleep, the question of whether dreaming exclusively relates to REM physiology has been and still remains highly controversial [29–31].

One fundamental problem with the original equation “REM sleep = dreaming” is that neither dreaming nor REM sleep are stable, homogeneous and unique states. Instead of relying exclusively on REM sleep mechanisms, 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 [26, 32] (see fig. 3). Nielsen has recently proposed that contradictory results about REM vs NREM quantitative and qualitative differences might be best explained by the existence of “covert” REM sleep processes during NREM sleep ([33]; but see [34] for opposing results), as well as by a combination of chronobiological oscillations modulating the dream production system. Such chronobiological oscillations can include 90-minute ultradian oscillations, circadian oscillations, and 12-hour circasemidian rhythms, up to 7-day rhythms and 28-day rhythms (in women) [35]. Nielsen's view favours a two-generator model,

Figure 3



Reciprocal changes in directed thinking and hallucinating in NREM and REM over the night, showing increasing hallucinatory content and decreasing thinking in NREM dreams as the night progresses. By contrast, high levels of hallucinations and low levels of directed thoughts remain unchanged across successive REM episodes (adapted from [39]).

in which qualitatively different generators produce cognitive activity during the two main sleep states. Other studies suggested that sleep is associated with a reciprocal relationship between thoughts and hallucinations that is shifted toward more dreamlike hallucinations and fewer directed thoughts both by REM and by time spent in sleep, thus explaining why NREM dreams start resembling REM dreams as the night progresses (fig. 3; [32, 36–39]).

Based on these findings, we think that an inclusive acceptance of dreaming equivalent to that of sleep mentation should be favoured, i.e. “the occurrence of any subjectively experienced cognitive events during sleep” (as in defined in [35], p. 404). Such a definition will allow future dream research to fulfil its main objective: to account for all facets and varieties of sleep mentation and to provide the most useful data for an integrative model of human sleep. Thus, REM sleep is not a necessary, but a facilitating condition for dreaming to occur. Conversely, there is little doubt that dreaming was a necessary condition for REM sleep to become famous.

Limitations to the study of dream in brain-damaged patients

To conclude this section, we point out some limitations to the dream examination in neurological patients that future research should address. First

of all, the ability to recall dreams presents considerable individual variability due to many different factors such as age [40–43], attitude towards dreams [44, 45], personality [46, 47], creative and visual abilities [48, 49], and environmental variables including cultural, professional or affective current concerns [50–54]. Furthermore, some rare individuals might not experience dreaming as they cannot report any dream even when awakened during polysomnographically defined sleep and in the absence of any neurological disease or damage [55], suggesting that dreaming might not be as ubiquitous as generally accepted. Secondly, consistent changes in dreaming can be difficult to assess because of the lack of premorbid dream data which have to be evaluated retrospectively by the patients and are thus likely to be subjected to memory distortions or social biases [5]. Thirdly, patients reporting a sudden reduction or a loss of dreaming might still experience dreams without being able to remember them on the next day. Moreover, brain damages may also alter sleep parameters [56, 57], which in turn could influence the dreaming processes [58, 59]. Therefore, future investigations of dreaming abilities in brain-damaged patients should be complemented by polysomnographic recordings to detect any associated sleep disorder and should also include awakenings during sleep to collect dream data with no time delay (e.g. [15, 60, 61]). Finally, dreaming changes in neurological patients may also be attributed to neurochemical disturbances and/or

pharmacological treatments that must be carefully examined and might provide additional information about neurophysiological mechanisms underlying dreaming [62–65].

Phenomenology of normal dreaming

Genetics, molecular biology, electrophysiology, clinical observations, as well as brain-imaging studies have considerably augmented our knowledge of human sleep by illuminating sleep mechanisms at distinct levels of biological organisation. This contrasts with the limited number of investigations addressing sleep functions at the cognitive level. The difficulty to obtain measurable and reliable data about cognitive processes during sleep constitutes the main cause for this apparent negligence and thus represents a major challenge for a successful integration of cognition with more basic, physiological levels of investigation in sleep research. However, the resistance of dreaming to experimental control does not dictate that this natural source of information about cognitive processes at work during sleep cannot be studied at all. Methods have been developed to measure distinct features of dream content, including scales, scoring systems, as well as automated lexical statistical analyses that will be presented below.

We and others have proposed that dream reports contain valuable information about the cognitive processes that participate in their generation and that cognition during sleep can be inferred from typical or common features in dream reports, independent of their specific meaning for a given dreamer [4, 5, 31]. For example, vivid visual imagery, emotional intensification and illusion of reality represent some of the defining features of common dream experiences (e.g. [66–70]). It is our claim that frequent cognitive features in dream reports might also inform about underlying brain functions during dreaming, thus allowing the integration of dream data into a unified model of human sleep.

Methods to collect reliable dream data

Like other manifestations of conscious processes, dreaming poses the following methodological problem: how can we study a phenomenon that is not directly and objectively observable, but mediated by introspection? Yet, introspection constitutes a fundamental dimension of our everyday mental experience as the famous American psychologist William James wrote: “Introspective

observation is what we have to rely on first and foremost and always” ([71], p. 185). Introspection implies that we first look into our own mind and then report any thought, feeling and sensation that we could discern. Thus, introspection into our waking or dreaming mind always relies on memory (and might thus best be referred to as “retrospection”). It is noteworthy that the difference between introspective data and objective data derived from “overt” behavioural responses is often exaggerated as dedicated studies showed that verbal reports provide reliable data about mental processes [72, 73]. Like other memory data, dream reports can be influenced by several factors such as forgetting, reconstruction mechanisms, verbal description difficulties, censorship, experimental demands and lack of independent verification that can be alleviated using appropriate strategies (see [5], Box 1).

Different methods can be used to collect representative and reliable dream material. Home-based dream diaries are the most frequent source of dream data in current research. This method provides rich information about the commonality of dreams spontaneously remembered, allowing for example comparisons between specific groups of individuals (e.g. people with normal sight vs blind people), as well as a unique access to longitudinal properties of dream activity over several months or years [44]. A second method consists in administering dream questionnaires (as in Solms’s study) to investigate selective features of dream experience [74, 75]. A third method is to collect dreams in a sleep laboratory by waking subjects during polysomnographically defined sleep stages and interrogating them about the content of their minds just prior to the awakening. This allows dream characteristics to be analysed as a function of sleep stages [40], but the content of “laboratory dreams” is often poorer than home-based reports (e.g. fewer emotions) and may incorporate elements of the sleep laboratory and experimental setting [76]. An attractive alternative to polysomnographic recordings in the sleep laboratory is the use of portable sleep monitoring devices that the subjects can use at home [32, 38, 39, 77]. Finally, it has been proposed that asking people to write down the most recent dream they can remember, whether it was “last night, last week, or last month” (“most recent dream” method; [44]), can provide informative data to characterise a given population or group of individuals. The reliable sample size for such studies as for studies using home-based dream reports has been approximated to about a hundred reports ([44]; see also [78]).

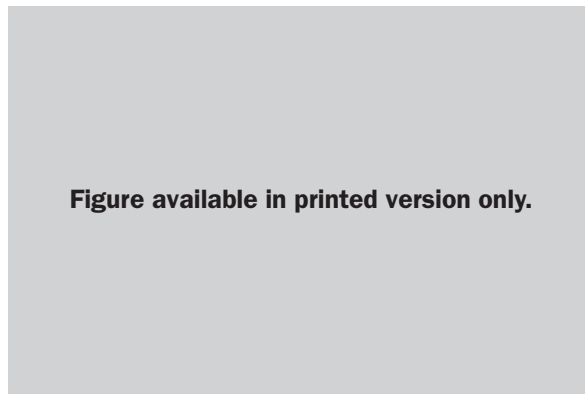
In 1893, Mary Calkins published one of the first statistical studies of dream content [79]. She identified and quantified more than 10 parameters in 375 dream reports from two individuals. Calkins found a clear predominance of visual experiences in dreams (57%), followed by auditory experiences (37%) and then by gustatory and olfactory experiences (1%) (see [40] for similar results). By programming awakenings at different times in the night, she could also observe that more dreams occurred during the late part of the night (between 4 and 8 a.m.) and that these late dreams were more vivid (see also previous section). More recently, almost contemporarily to the discovery of REM sleep, Hall and Van De Castle published an extensive manual for coding of the content of dream reports [80]. This classification system was first 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.). It provided normative values for the different scales proposed in the manual that have since then been used to study many different dream samples (e.g. [44, 81]).

In recent dream research, scales and coding systems have become standard tools to quantify empirical as well as theoretical categories of dream features (e.g. [40, 44, 66, 80, 82]). This classification approach is very efficient when assessing specific categories of interest, such as the different types of emotions or bizarre features, in the dreams of healthy or patient populations (e.g. [59, 83]), or when testing theoretically driven hypotheses (e.g. [80, 84]). However, manually coding dream content is time consuming, especially when analysing large amounts of data. It also requires the delimitation of *a priori* categories to be quantified and may therefore miss important information hidden in the data. To overcome these limitations, we proposed to use lexical statistical methods on large samples of dreams ([5]; see [4] for details about the method). Such methods allowed us to identify recurrent patterns of dream content based on the distribution of words in the dream reports, without any *a priori* coding of the dreams.

We have recently 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 of a total of 1000 dreams from 50 male and 50 female students (dataset available: www.dreambank.net; [4, 80]). Our results revealed well-segregated and consistent cognitive dimensions in the dreams from different individuals, thus un-

covering selective cognitive processes that contributed to distinct dream episodes. This supports a neuropsychological approach to dreaming according to which functional brain modules can be identified by studying distinct cognitive functions that participate in dream experience in an independent or dissociated manner. Like circumscribed neuropsychological impairments after focal brain damages, functional dissociations in the sleeping mind can reveal cognitive “modules” that would otherwise remain undetected since they are normally integrated during wakefulness to form our coherent everyday-life experiences.

For example, we found a first dissociation between verbal and motor activities implying that brain circuits subtending the ability to manipulate language or communicate verbally may be activated during sleep independently of those involved in motor behaviour, and vice versa. In normal healthy subjects motor and premotor cortices were found to be active during REM sleep [85], suggesting that dreamed movements may exploit the same cortical circuits as the ones underlying motor behaviour while awake (while actual execution of the movements are suppressed by the system controlling muscle atonia during REM sleep). Further dissociations were found in the visual domains including fine visual judgments, colour vision, motion perception, landscapes or outdoor representations, and dreams containing familiar people. The dissociation between these visual properties is consistent with well-known functional specialisations in the human brain, including colour vision in V4 [86], motion processing in MT/V5 [87, 88], layouts and landscapes in the parahippocampal place area (PPA) [89], and face processing in the face fusiform area (FFA) [90]. The predominance of visual aspects in dreams is in good accordance with the widespread activation in associative visual areas observed with PET during REM sleep [20, 85, 91], but our analyses of dream features suggest a temporally and spatially more detailed mapping of the visual dimensions than that provided by available PET studies. Finally, emotions such as fearful experiences represented a highly consistent feature in all dreams' samples. Since limbic circuits, in particular the amygdala, contribute to threat-related emotions and memory processing [92–96], amygdala activation during sleep [2, 20, 97–99] might thus provide a permissive condition for emotionally relevant elements of memory to be selectively reprocessed in sleep in animals and humans [100–106] or contribute to the rehearsal of genetically programmed or “primitive” behavioural responses to threatening stimuli [107, 108]. This would result in an



René Magritte, *Ceci n'est pas une pipe*, 1928/29 (© 2005, ProLitteris, Zurich).

overrepresentation of frightening dream episodes as well as numerous incorporations of affective and working concerns from waking life ([40, 69, 70, 79, 109–111], see [112]), and suggests that different varieties of memory functions may operate during sleep.

Functional dissociations in dream experiences might implicate distinct and heterogeneous, but reproducible patterns of activation, thus corroborating the idea that the anatomical segregation of brain functions is mostly preserved during sleep. Identifying well-delimited cognitive dimensions in dreams will certainly guide future brain-imaging studies that will disclose transient patterns of regional cerebral activity during sleep (e.g. fMRI).

Neuropsychological approach to normal dreaming

The analyses reported in the previous section demonstrated that cardinal features in large dream samples can be identified using statistical methods and that these features effectively match current descriptions of brain activity during sleep. These analyses were entirely based on the frequency of occurrence and degree of uniformity of dream contents. Although the source of our dreams pertains to memory, dream experiences do not fulfil a simple memory reactivation agenda [109, 113]. Indeed, when compared to usual experiences of our normal, waking lives, dreams present innumerable anomalies [66, 82, 84, 114, 115]. It is precisely because dreaming dislocates, distorts and reinvents a world of experience (“a virtual reality realized in the brain” [116], p. 55) that it represented the most inspiring model of creativity for the surrealists (fig. 4; [117]).

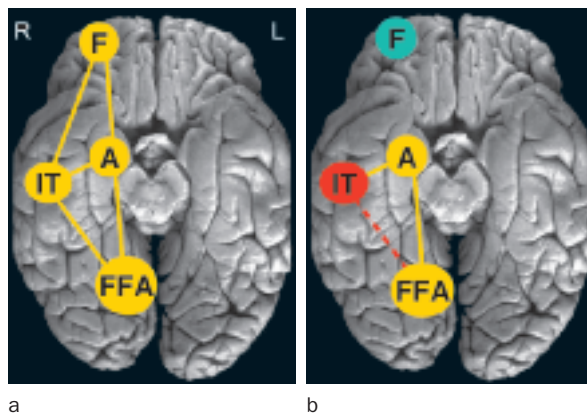
In this section, we show that bizarre features in the dreams may reflect specific functional states of the sleeping brain. More specifically, in our pro-

posal, some bizarre features in normal dreaming are underpinned by a pattern of regional brain activity not unlike the one imposed by lesions in specific neuropsychological syndromes. The neuropsychological approach to normal dreams goes as follows: (a) some bizarre features reported in dreams present remarkable similarities with specific neuropsychological syndromes observed in brain-damaged patients, and (b) the lesional topography corresponding to these syndromes might provide useful information about brain regions activated during normal sleep. The existence of striking similarities between certain neuropsychological syndromes and typical dream productions suggests specific commonalities in their underlying brain organisation, but this does not imply that sleep or dreaming is a pathological state. Thus, dream data could be used to guide the analysis and interpretation of functional imaging data collected during sleep [5]. Some of these predictions are already confirmed while others still await experimental investigation and shape future paradigms for dedicated functional neuroimaging studies. We describe below a few examples of these parallels between dreams and neurological syndromes.

Neuropsychology of dream bizarreness

One common bizarre feature in dreams is the disruption in visual recognition, whereby a dreamed character or object is clearly recognised although its physical appearance is drastically modified in the dream [5, 118]. The painting from Magritte (fig. 4) exemplifies the possible dissociation between the appearance of an object (a pipe) and its meaning in the mind of the observer (this is not a pipe). In dreams, similar dissociations 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 ...” ([40], p. 71). Normal identification of faces relies on a specific network of specialised brain areas including medial temporal lobe structures, especially the FFA for the visual extraction of facial traits [90] and the amygdala for detection of emotional significance [95, 119], but also infero-temporal and prefrontal regions that provide semantic information about particular people (fig. 5; [120, 121]). Delusional misidentification or hyperidentification for people corresponds to a well-known

Figure 5 Brain network for face processing. (a) Normal face processing. Face recognition involves three main functional components: the visual extraction of facial traits in medial temporal lobe structures, in particular the fusiform face area (FFA); affective responses to faces in relation to familiarity in limbic circuits (amygdala; A); and stored semantic and biographical information about the seen faces in infero-temporal regions (IT) and prefrontal regions (F). Both the perception of real faces and mental imagery of faces (in the absence of an external stimulus) rely on the same network of brain areas. (b) Frégoli syndrome in dreams. Patients with Frégoli usually mistake an unknown individual as being a familiar person despite the lack of physical resemblance. This syndrome involves lesions in the right ventral temporal areas and prefrontal regions. Frégoli-like phenomena in dreams could thus be generated by a simultaneous activation of high-order associative areas of the temporal lobes storing information about persons' identities and the FFA responsible for the processing of visual facial features, in the absence of monitoring from the prefrontal area (adapted from [5]).



neurological condition, called Frégoli syndrome, whereby an unknown person's face is erroneously recognised as a familiar person, despite the lack of any obvious physical resemblance [122–124]). Common lesions are located in the ventral temporal areas, predominantly in the right hemisphere, and in the prefrontal cortex [125, 126]. This syndrome may result from a simultaneous activation of high-order associative areas in the temporal lobes (storing information about persons' identities) and the FFA (responsible for the processing of visual facial features), in the absence of selective reciprocal constraints and monitoring from the prefrontal area [127]. As illustrated by the dream excerpt above, the Frégoli-like phenomenon is also a common feature of dream experience [118, 128], 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 (that are deactivated during human sleep as revealed by PET studies), accompanied by an activation of the amygdala providing a feeling of familiarity (fig. 5; [2, 20]).

Misidentifications of places are also extremely frequent in dream reports, in which places can be recognised as familiar in the absence of any appa-

rent similitude to the corresponding original places. In the following dream from a 30-year-old man (laboratory recording, REM sleep), the spatial environment was changed in two ways as the bedroom was actually located on the ground floor, not the third floor, and there was no physician's office in the building: "I found myself in this test situation. I got up and turned off the microphone. But the room was upstairs, on the third floor, and I stepped into the physician's office, where something was running." ([40], p. 108) The processing of places and layouts involves the PPA (just anterior to the fusiform face area; [89]), and delusional misidentification syndromes or "reduplicative paramnesia" for places can occur after temporal and prefrontal lesions, with right hemisphere predominance [129–134]. Therefore, like misidentifications of faces, misidentifications of places in dreams likely result from a deficient integration between perceptive and semantic information about places, suggesting that sleep may provide a favourable condition for the modular architecture of brain functions to be expressed and consolidated.

Other examples of visual distortions include the multiplication of a visual percept in time ("palinopsia") or space ("polyopia"), which is observed in patients with lesions in visual associative areas [135, 136], and deficit of visual size perception with apparent reduction ("micropsia") or increase ("macropsia") of the size of objects, previously reported after right occipital damage [137]. A typical example of macropsia is offered in the following excerpt from a dream of a 23-year-old woman (laboratory recording, 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." ([40], p. 147) These distortions are present in a significant fraction of dream reports, suggesting a regionally specific hypoactivation within these visual areas or a functional disconnection from other higher-level areas during this type of dreaming experience [5]. The loss of colour saturation in visual perception ("achromatopsia") found in patients with occipital lesions in lingual and fusiform gyri [138] is also frequently found in dream imagery [68, 139] and suggests a hypoactivation of occipital colour areas [86] or a disconnection between colour regions and other visual or parietal regions subtending multimodal integration.

Together, the examples provided above suggest a regionally variable activation within visual ventral stream generating heterogeneous dreaming experiences during sleep. This also points to a

possible explanation for why activation of temporo-occipital areas is not systematically reported in functional neuroimaging studies (cf. [2, 20]). The analysis of specific bizarre features in dreams might thus offer new constraints to the analysis of sleep data acquired just before dream reports and might help refine the genuine cerebral correlates of dreaming activity [5]. Future neuroimaging studies will be able to test the predictions raised by these similarities between dream features and neuropsychological syndromes.

Conclusions and perspectives

"Dreams are true when they last. Can we, at the best, say more about life?" (H. Ellis 1922, p. 281 [127])

In this review, we first showed that selective disorders of dreaming can be assessed clinically and that they result from regionally specific brain damage. We suggested that the neuropsychological examination of dream deficits in brain-damaged patients is clinically useful and should be complemented with polysomnographic recordings whenever possible. We then reported results from statistical analyses of dreams' reports from neurologically healthy individuals. These analyses identified clearly separable cognitive categories in the dreams strongly supporting the idea that brain activity during sleep might involve the regular engagement of distinct specialised brain subsystems. Finally, we demonstrated that some bizarre but common features in normal dreams present striking similarities with neuropsychological symptoms observed in brain-damaged patients while awake. We proposed that such similarities reflect specific commonalities in brain organisation that might serve as useful information to constrain analyses of functional imaging data in sleep. In conclusion, convergent data from a neuropsychological approach to dreaming provide specific hypotheses about the distribution of regional brain activity during dream episodes and therefore constitute the primary source of information for future attempts at unravelling the cerebral correlates of dreaming.

Altogether, these data confirm that dreaming is a pervasive but distinctive faculty of the human mind. However, it is still unclear how dream experiences will integrate current models of brain organisation because dreams do not seem to fulfil any useful function. A neurocognitive function of sleep and dreaming possibly relates to memory consolidation or reprocessing [140–142]. Yet, our dream experiences often challenge our working model of the real world, displaying irrational behaviours and impossible facts. It is fortunate that

we do not memorise our dreams as if they were real events of our waking lives as we would certainly get confused [143, 144]. Further theoretical work is thus required to achieve a comprehensive model of brain states that would integrate both our waking and sleeping worlds of experience.

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