Sleep imaging and the neuro-psychological assessment of dreams

Sophie Schwartz and Pierre Maquet

Recent neuroimaging studies show that human rapid-eye-movement (REM) sleep is characterized by a specific pattern of regional brain activity. Although this is usually interpreted in relation to physiological and cellular mechanisms, the specific regional distribution of brain activity during REM sleep might also be linked to specific dream features. Remarkably, several bizarre features of normal dreams have similarities with well-known neuropsychological syndromes after brain damage, such as delusional misidentifications for faces and places. We propose that neuropsychological analysis of dream content might offer new ways of interpreting neuroimaging maps of sleep, and make specific predictions for future neuroimaging studies.

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The study of human sleep has recently benefited from the contribution of functional imaging techniques, such as PET [1–6] and fMRI [7], which provide maps of changes in regional neural activity during distinct sleep stages. Meaningful information is obtained when the neuroimaging data are explained by a model that embodies our current understanding of brain function at various levels of description. Such a model is all the more powerful when it incorporates the knowledge acquired from various sources, including cognitive psychology, neuropsychology, primate brain anatomy and cellular neurophysiology.

Until now, functional neuroimaging of normal human sleep has essentially been interpreted in light of our knowledge of animal sleep, at the cellular and neural network levels. Although, to some extent, this strategy has proven successful, confining the analyses to this kind of interpretation cuts off this research from an interesting source of information, namely the cognitive aspects of sleep. Cognitive processing during sleep can be inferred by using measures of waking performance in behavioral tasks (e.g. pre- and post-sleep memory scores [8]), by presenting external stimuli during sleep (e.g. sounds or words [7]), as well as by analyzing specific dream features. Here we suggest that a thorough understanding of human sleep mechanisms will require an interpretation of functional imaging maps of sleep in terms of their concomitant cognitive processes revealed by dream content (Fig. 1).

In the first part of this article, we briefly summarize the current interpretation of recent functional neuroimaging maps of human sleep, in terms of the underlying cellular activity recorded in animals. (A more comprehensive review can be found in Ref. [9]). In the second part, we propose a new approach for the interpretation of functional maps where explanatory parameters are to be found in the subject's dream reports. In particular, we argue: (1) that some bizarre features reported in dreams present remarkable similarities with specific neuropsychological syndromes observed in brain-damaged patients; and (2) that the lesional topography corresponding to these syndromes might provide useful information to constrain the model of brain organization used to analyze functional imaging data in sleep. The hypothesis is not, of course, that sleep is a pathological process but rather that the isomorphism between certain neuropsychological syndromes and typical dream productions suggests specific commonalities in brain organization. The relevant constraints and limitations inherent to this approach are also reviewed (see Box 1).

The goal of this article is to open up a new perspective in the study of human sleep by integrating two approaches, functional imaging during sleep and neuropsychological analysis of dream reports. We will concentrate here on mentation during rapid-eye-movement (REM) sleep, mainly because REM sleep elicits more abundant, vivid, and phenomenologically detailed dream reports than non-REM sleep [10].

Human sleep brain maps interpreted in terms of cellular activities in animals

Several recent studies used functional neuroimaging techniques to examine brain activity associated with different sleep stages. During REM sleep, significant increases in regional blood flow or glucose metabolism were found in the pontine tegmentum, thalamic nuclei, limbic and paralimbic areas: amygdaloid complexes, hippocampal formation, anterior cingulate cortex [1,3,6] (Fig. 2). Posterior cortices in temporo-occipital areas were also activated [3,11]. By contrast, the dorso-lateral prefrontal and parietal cortices as well as the posterior cingulate cortex and precuneus were the least active brain regions [1,3]. Figure 2 shows the typical pattern of relative activation and deactivation in REM sleep.

These regional distributions of brain activity are in good agreement with what is known about REM sleep generation in animals. In particular, REM sleep is generated by neuronal populations in the meso-pontine reticular formation that activate the thalamic nuclei and in turn the forebrain [12]. The resulting cerebral activation is far from being homogeneous. For example, limbic structures present a characteristic activation during REM sleep in animals, as evidenced by high glucose metabolism in limbic structures found in rats and cats [13–16]. Moreover, hippocampal theta

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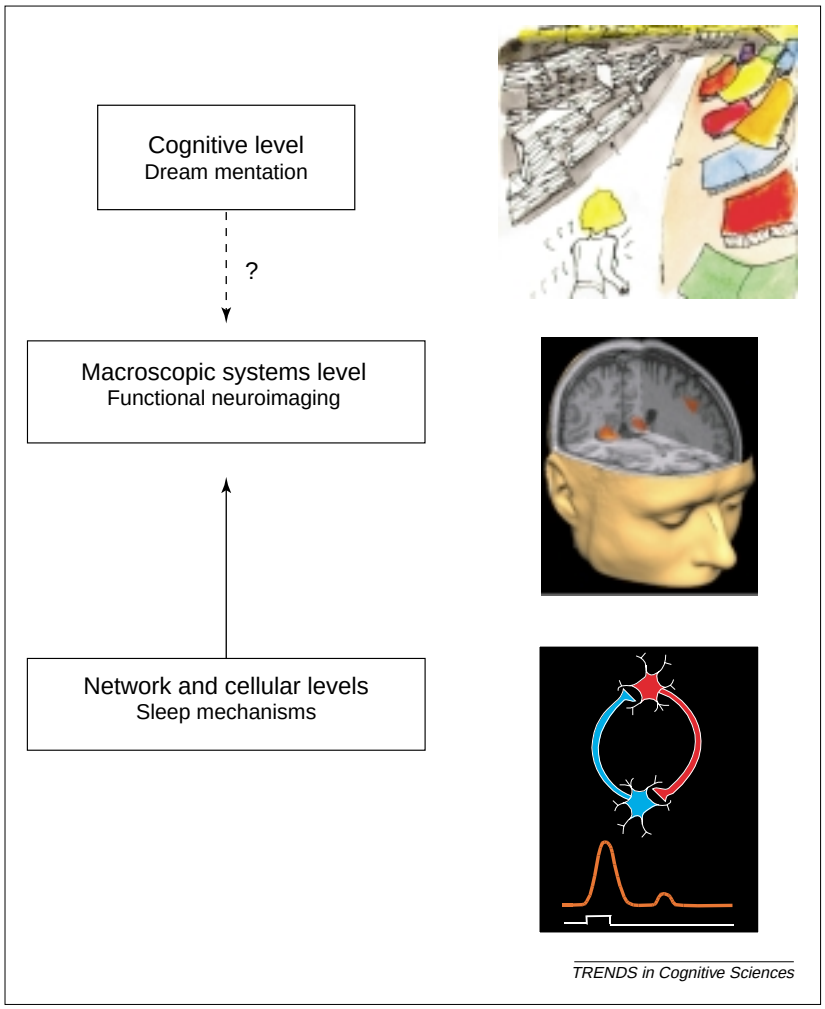

Fig. 1. Schematic representation of two possible ways of interpreting human sleep brain maps. The bottom-up approach relies on findings about the cellular processes involved in sleep to understand brain activity patterns observed at the macroscopic neuroimaging level. The top-down approach relies on a cognitive analysis of dreams and on recent neuropsychological knowledge to predict concomitant patterns of brain activity revealed by functional neuroimaging techniques.

rhythm is a prominent feature of REM sleep in rats, rabbits and cats [17,18]. Functional neuroimaging in humans has established the limbic/paralimbic activation as a main characteristic of REM sleep organization, contrasting with the relative quiescence of associative frontal and parietal cortices [1,3].

Regionally-specific brain activity during sleep also involves motor cortices. During REM sleep, muscular atonia is normally induced through the inhibition of spinal motor neurons by the ponto-bulbar reticular formation [19]. Lesions of the reticular formation in cats suppresses the normal muscular paralysis and the cats show various motor behaviors, ranging from a slight raising of the head, to elaborate displays [20]. These motor behaviors probably imply the activation of motor programs and motor related brain regions. Additional evidence comes from extracellular recordings that have established that both motor cortex and subcortical motor areas are activated during REM sleep [21]. Accordingly, a significant activation of motor and supplementary motor areas has been observed in normal subjects during REM sleep (see control group 3 in Ref. [8]).

A further example of a neurobiological interpretation of functional sleep maps is provided by the generation of eye movements in REM sleep. In animals, the occurrence of rapid eye movements during REM sleep is closely related to the occurrence of phasic neuronal activity, named PGO waves because they are most easily recorded in the pons (P), the lateral geniculate bodies (G) and the occipital cortex (O). Recent PET data lend support to the hypothesis that in humans also, rapid eye movements are generated by mechanisms similar to PGO waves during REM sleep: the brain regions differentially more activated in relation to eye movement density during REM sleep than during wakefulness included the right geniculate body and the occipital cortex [22].

The overall pattern emerging from functional imaging suggests that the distribution of brain activity during REM sleep in humans is compatible with the network and cellular mechanisms underlying sleep in animals.

Human sleep brain maps interpreted in terms of human dream content

The study of cognitive processes during REM sleep assumes that the anatomical segregation of brain functions is preserved during sleep [23,24]. Recent fMRI data show that this assumption holds for the auditory system: sounds presented during non REM sleep are associated with regionally-specific responses broadly similar to those observed during wakefulness [7]. It is most probably true also for the other brain systems and during REM sleep. Dream features can therefore be potentially mapped onto a specific distribution of brain activity. Indeed, quantitative analyses of dream content (see Box 2) have been obtained from various sampling methods, and revealed several frequent and stable features of dream phenomenology which fit remarkably well with the distribution of brain activity during REM sleep [1,9,24].

Dreams are characterized by their perceptual features. The sensory modalities represented in dreams are very consistent across studies: visual events are present in almost all dreams, auditory elements occur in about 60% of dreams, movement and tactile sensations in about 15%, whereas smell and taste appear in less than 5% of the dream reports [25,26]. The abundance of visual aspects in dreams is in good accordance with the activation in associative visual brain areas during REM sleep [11].

Another well-documented regularity in dreaming is the prominence of negative emotions, anxiety and fear [26–29]. Fear-related emotions are significantly more frequent in dream reports than in waking event reports [30]. In addition, the occurrence of fear-related emotions is remarkably stable, as revealed in a dream diary kept over a period of 15 successive months, contrasting with other themes that appeared to vary as a function of current concerns and daily activities (see Box 2). It is sensible to relate this common fear experience in dreams to the activation of the limbic system, in particular the amygdala [1]. In animals and humans, the amygdala mediates responses to threatening stimuli or stressful situations; it is thus in a perfect position for

Box 1. Methodological issues in dream sampling and dream evaluation

Like other domains in the study of consciousness, dream research relies critically on phenomena that are known only via introspection, and not accessible to direct observation. The dreamer alone is witness to his dream. However, the difference between introspective data obtained from report and objective data obtained from behavioral responses is largely overstated. Like introspective data, behavioral measurements in cognitive studies often rely on inspecting mental representations or sensations and making decisions about them [a].

Two radically different sampling methods provide representative and reliable dream material, if their conditions are carefully defined. On the one hand, home-based dream diaries offer rich information about the commonality of dreams spontaneously remembered. They can allow, for example, a comparison 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 long time periods [b]. In order for home-based dream samples to comply with scientific demand, they must follow controlled, systematic and exhaustive recording procedures [b]. On the other hand, dreams can be collected after awakenings in the laboratory under polysomnographic monitoring. This technique permits dream characteristics to be analyzed as a function of sleep stages [c], although with the limitation that their content might be poorer than home-based reports (e.g. fewer emotions) and often incorporates the novelty of the experimental setting [d].

By the very fact that they are produced during sleep and reported while awake, minutes or hours after they occur, dream reports are memory reports that involve both distinct consciousness states and a time lag between the original dream event and its restitution when awake. Dream reports can thus be influenced by several factors, most of which might also affect waking thought reports. Possible biases in reporting subjective experiences and methods to limit these biases are listed below.

Forgetting

Introspective reports, including dream reports, might be incomplete because: (1) forgetting is proportional to the time lag between the experience and the recall; (2) remembering is compromised by interference at the recall stage; (3) encoded information is not accessible to recall. The quantity of dream material reported is increased by a daily practice of reporting dreams, in a context that minimizes interference, immediately after awakening, and by selecting subjects who regularly remember their dreams [c]. Controlled awakenings during the REM-sleep stage can also ease the capture of ongoing dream experience.

Reconstruction mechanisms

Memory reconstruction might involve: (1) reporting more information than really experienced [e]; and (2) reordering the sequence of events [f]. Compared with dream reports, memory reports of real life events are particularly prone to reconstruction errors because they are often part of daily routines (i.e. spatially and temporally organized behavioral sequences) that facilitate recall but also reconstruction processes.

Verbal description difficulties

Subjective experiences can be difficult to describe verbally (e.g. emotions, complex scenes, unreal objects, unusual experiences). This problem can be partially solved by training subjects to talk about such experiences [g]. As dreams are mostly visual, and present frequent bizarre elements, pictorial descriptions such as drawings can offer valuable, complementary information.

Censorship

Embarrassing thoughts, immoral actions, sexual or aggressive fantasies, might remain unreported. This limitation can be overcome by reducing embarrassing mental contents to labeled categories, so that only a category need be reported [h].

Experimental demands

Introspective reports might be voluntarily or involuntarily distorted to agree with the experimental hypotheses. This is a common limitation in behavioral studies which might be assessed by introducing control conditions (e.g. using emotional as well as neutral pre-sleep stimuli when studying the effects of emotional pre-sleep stimuli on dreaming). It can be minimized by adequately informing the participants, by training them in dream reporting before the experiment, and by adding a checklist of dream features that might be under-reported (e.g. emotions [i]).

Lack of independent verification

By definition, there is no ultimate test for the authenticity of introspective reports. However, it is possible to judge whether a report is consistent with other reports provided by the same person, or by other people in similar conditions. In addition, it is possible to check that the report is consistent with our knowledge of the cognitive processes involved.

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organizing emotional processing during sleep, and might favor fearful experience in dreams [31–34].

Other characteristic features of dreams such as the lack of insight, distortion of time perception, and amnesia on awakening have been tentatively attributed to the relative hypoactivation of prefrontal cortex [1,24]. Conversely, lesions to lateral prefrontal cortex do not affect the ability to experience and

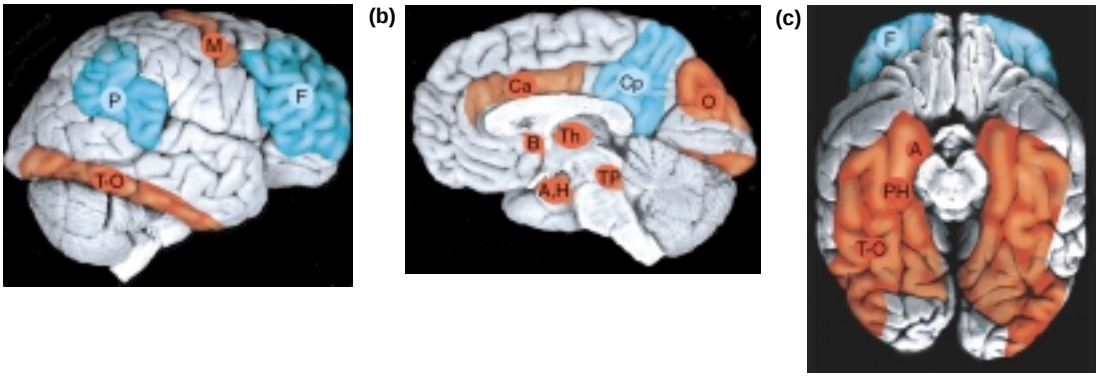

Fig. 2. Schematic representation of the relative increases and decreases in neural activity associated with rapid-eye-movement (REM) sleep. Regions colored in red are those in which regional cerebral blood flow (rCBF) increases during REM sleep; those in blue correspond to rCBF decreases. (a) lateral view; (b) medial view; (c) ventral view. A, H, amygdala and hypothalamus; B, basal forebrain; Ca, anterior cingulate gyrus; Cp, posterior cingulate gyrus and precuneus; F, prefrontal cortex; M, motor cortex; P, parietal supramarginal cortex; PH, parahippocampic gyrus; O, occipital-lateral cortex; Th, thalamus; T-O, temporo-occipital extrastriate cortex; TP, pontine tegmentum. (Adapted from Refs [1,3,6,8].)

report dreams in human patients who suffer stroke or head injuries [35].

These observations provide only a general perspective on the plausible match between global dream characteristics and 'canonical' REM sleep pattern of brain activity. More insight into REM sleep mechanisms would be gained if the content of individual dreams were to be used as an explanatory variable to model neuroimaging data. Unfortunately, in our personal experience, the use of standard scales to parameterize dream content in terms of the motor, perceptual or emotional content has not been successful in describing dream-related brain correlates. In the next section, we propose another approach which might be more fruitful.

Cognitive neuropsychology of dream bizarreness

As just mentioned, the link between functional neuroimaging of sleep and dream data has been confined to rather broad descriptions of both brain activity in sleep and dream phenomenology. However, dreaming is not a random collection of sensations and emotions experienced in a state resembling mental confusion [36]. Dreams have an internal structure which reflects ongoing cognitive processes. Like waking cognition, dreaming experiences depend on a large-scale neural network, subtending distinct neuropsychological domains such as attention, memory, language, mental imagery [37]. From this perspective, dream phenomenology can be examined using a neuropsychological approach and the traditional method of clinical-anatomical correlation (see Box 1 for methodological issues in using introspective reports such as dreams). More specifically, in our proposal, some bizarre features in normal dreaming imply an underlying pattern of regional brain activity not unlike the one imposed by lesions in specific neuropsychological syndromes.

In this section, based on several empirical examples, we suggest that the study of bizarre features in dreams indicates a heterogeneous activation of cerebral regions in the ventral visual stream during REM sleep. This observation allows us to define regionally specific hypotheses that can be used for the interpretation of human functional neuroimaging maps.

Misidentification syndromes

Several bizarre phenomena in dreams resemble typical misidentification syndromes, in which a visual percept (e.g. the face of a character or a geographical location) is mistakenly recognized as a different one.

Misidentification of faces: Frégoli syndrome. Normal identification of faces relies on a large scale network involving occipital, temporal, limbic and prefrontal areas (Box 3). Delusional misidentification or hyper-identification for people corresponds to a well-known neurological disorder, the Frégoli syndrome, whereby an unknown person's face is erroneously recognized as a familiar person despite the lack of any obvious physical resemblance [38–40].

Frégoli syndrome is associated with temporal and frontal lesions (see Box 3). Whereas such misidentifications for people are relatively rare in normal everyday life and usually quickly corrected, it is a common feature of dream experience (Fig. 1a) [41,42]. The following dream reported after awakening from REM sleep illustrates a mismatch between the identity attributed to a character seen in the dream (one of the experimenters) and the physical appearance of the character (a much younger person resembling a familiar childhood friend of the dreamer): '…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…' (Ref. [26], p. 71).

Frégoli-like phenomena in dreams indicate that neuronal processes during sleep can simultaneously and independently engage (1) unimodal visual areas underlying the internal generation of a perceptual representation of an individual's face (e.g. in the fusiform face area [43]), and (2) distinct multimodal associative areas in the temporal lobe responsible for triggering the retrieval of a familiar individual's identity [44] (see Box 3). The absence of supervisory control functions normally exerted by the frontal lobe (markedly hypoactive during REM sleep) would then prevent

Box 2. Quantifying dream content

Different methodologies for reducing and analyzing dream content have been used. Basic dream elements can be coded according to empirically defined scales, the frequency of certain words can be measured, and dream characteristics can be revealed by multidimensional statistical analysis of word distribution in dream reports

Dream scales

Empirical scales have been developed to record basic components of dream phenomenology such as characters, settings, objects, emotions and social interactions, and to measure their frequency in dream reports [a,b]. Tables 1 and 2 present two examples of recent bizarreness scales.

Lexical statistical analysis of dreams

Word count can provide an estimation of dream productivity, as well as the frequency of words related to predefined sensory or cognitive categories (e.g. visual words) [c].

We recently showed that dreams can be automatically categorized on the basis of their word content, without any *a priori* coding of their content. Namely, multidimensional clustering techniques applied to a dream diary of 1770 dream reports resulted in five highly segregated and consistent dream categories (Fig. I). 35% of the dream reports were clustered into two categories related to current concerns of the dreamer (academic and artistic); 15% were characterized by the presence of objects, people and social activities; 30% described prominent visual-spatial experiences; 20% were characterized by fearful emotions and constituted a remarkably stable category during the 15 months of the dream diary (S. Schwartz, Doctoral thesis, University of Lausanne, 1999). A complete discussion of these results is beyond the scope of this article, but these broad categories suggest the existence of distinct functional brain states engaging specific cognitive processing during sleep.

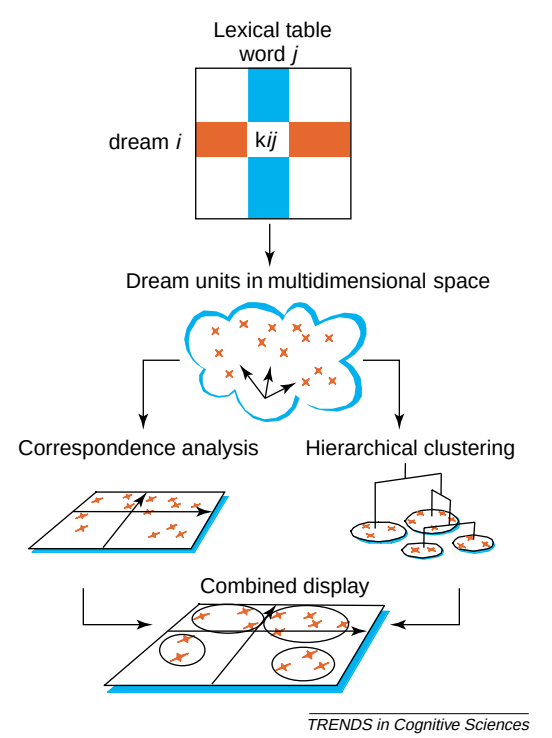

Fig. I. Main steps in performing a multidimensional analysis of dream reports. First, word occurrences in each dream (or dream part) are automatically organized into a single lexical table, in which the case k*ij* represents how many times the word *j* appeared in the dream *i*. Dream reports form a cloud of points (red) in the multidimensional space of the words (blue), where the distances between the points reflect differences in patterns of word content. Correspondence analysis gives a reduced bi-dimensional map of these distances. It can be combined with hierarchical clustering that groups dreams with similar word content together [f]. Finally, the words themselves can be displayed on the map, thus facilitating the interpretation of the clusters of dream reports on the map.

Table 1. Bizarreness scoring system*

Locus of bizarreness
(a) Dream plot (character, action, place, object, time) (b) Thoughts of dreamer or dream characters (c) Emotions/feelings of dreamer
Type of bizarreness
(a) Discontinuity (b) Incongruity (mismatching features) (c) Uncertainty

* Adapted from Ref. [d]

Table 2. Content bizarreness scoring*

1. Non-bizarre element (congruous with waking reality)
2. Incongruous element a. Internally distorted or contextually incongruous elements b. Exotic elements (unlikely to occur in the dreamer's real life) c. Impossible elements 3. Vague element
4. Discontinuous element (suddenly appearing or disappearing or being transformed in the dream)

* Adapted from Ref. [e]

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Box 3. The cognitive neuroanatomy of face recognition

Current cognitive models of face recognition have implicated three main functional components: (1) information representing structural visual encoding of faces; (2) affective responses to faces in relation to familiarity; and (3) stored semantic and biographical information about the seen faces [a,b]. Perceiving and recognizing faces involve a specific network of specialized brain areas: medial temporal lobe structures, in particular the fusiform face area (FFA) for the visual extraction of facial traits [c,d] and the amygdala for detection of emotional significance [e], but also other infero-temporal and prefrontal regions providing semantic information about particular people [f,g]. Furthermore, 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 [h] (Fig. Ia).

Face recognition deficits in neurological patients can be modeled as disturbances in a given functional module or in the integration between modules. Depending on the lesional topography, different neuropsychological syndromes arise:

Prosopagnosia (impaired recognition of known faces): follows damage of the fusiform gyrus, most often in the right hemisphere [i–k] (Fig. Ib).

Capgras delusion (belief that a familiar person has been replaced by an impostor, a robot or an alien with the same traits): has been associated with a variety of cerebral disorders, involving most often frontal and temporal-limbic lesions [l–n]. The delusion might result from a dissociation between intact extraction of face traits in the FFA and abnormal emotional evaluation by the amygdala [a,b] (Fig. Ic).

Frégoli syndrome (delusional hyperidentification – the patient mistakes an unknown individual as being a familiar person, despite the absence of physical resemblance) : available neuropsychological reports have in common lesions of the ventral temporal areas, predominantly in the right hemisphere, and of the prefrontal cortex [o–q]. It has been suggested that Frégoli syndrome is generated by a simultaneous activation of high-order associative areas of the temporal lobes that store information about person 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 [r] (Fig. Id).

Although prosopagnosia and Capgras-like phenomena are only sometimes clearly reported in dreams, Frégoli-like descriptions are more reliably identified in dreams reports because the dreamer spontaneously comments on the mismatch between his/her face perception and the puzzling misidentification.

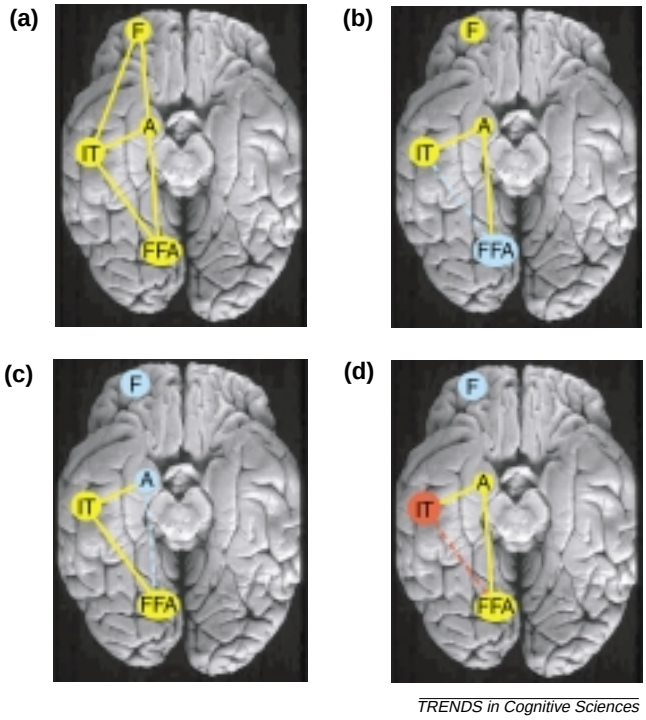

Fig. I. Simplified model of networks involved in face processing. (a) Normal face-processing network involves the fusiform face area (FFA), the amygdala (A), infero-temporal cortex (IT) and prefrontal cortex (F). Supposed modifications to this network are shown for prosopagnosia (b); Capgras delusion (c); and Frégoli syndrome (d). Normal functioning is shown in yellow; disturbances are shown in blue (representing a decrease in neural activity) and red (increase in neural activity). Dashed lines correspond to modifications in the connections between areas.

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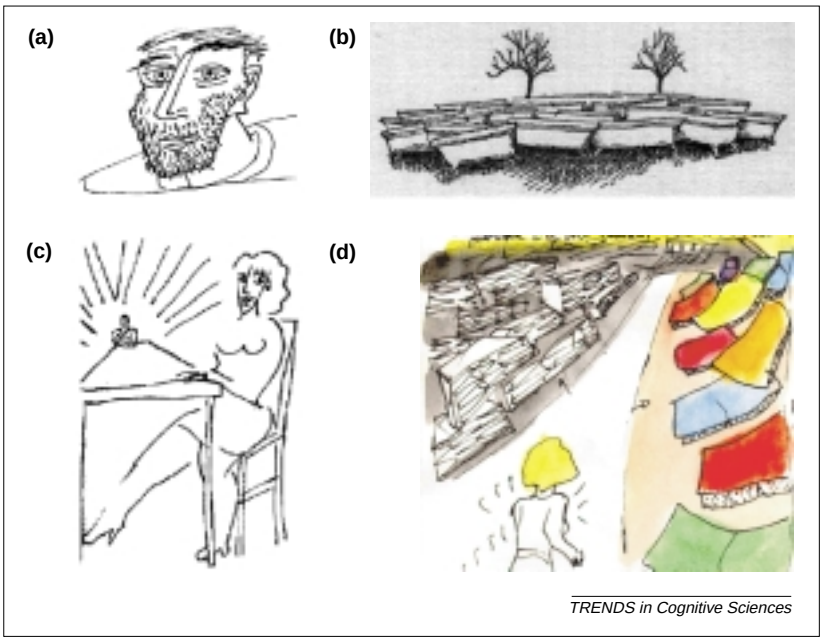

Fig. 3. Some typical dream phenomena show remarkable similarities with neuropsychological syndromes. All but one of the pictorial descriptions presented here are original drawings selected from a dream diary extensively analyzed elsewhere (S. Schwartz, Doctoral thesis). (a) Frégoli syndrome in a dream. The dream description was: 'I recognize A.'s sister (…) I am surprised by her beard, she looks much more like a man than a woman, with a big nose…'. (b) Polyopic images of bathtubs in a dream (Reproduced with permission from Ref. 58). (c) Micropsia in a dream. The woman in front was seen at normal size, but the man at the other end of the table was seen as minuscule. (d) Hemi-achromatopsia in a dream. Color was missing only from the left half of visual space.

the detection and verification of this mismatch between face-identity and face-appearance, hence favoring the delusive quality of Frégoli-like representations in dreams, usually accepted without much surprise by the dreamer.

Misidentification of places: reduplicative paramnesia. Misidentifications in dreams are not limited to faces: there are numerous examples of dreams in which a place is recognized as familiar despite a complete lack of resemblance with the corresponding original place. Functional imaging has shown that an area in parahippocampal cortex (just anterior to the fusiform face area) is selectively activated by passive viewing of spatial scenes and layouts [45]. As for faces, the identification of locations might involve a specific cerebral network. Again, this dream phenomenon is reminiscent of delusional misidentification syndromes or 'reduplicative paramnesia' for places in neurological patients with brain lesions [46–49]. As in Frégoli syndrome, brain lesions usually combine temporal and prefrontal lesions [50,51]. The disorder is likely to result from abnormal integration of environmental cues and semantic information about place identity.

Other visual distortions

Deficits in spatio-temporal integration leading to the multiplication of a visual percept in time ('palinopsia') or in space ('polyopia') are observed in patients with lesions in visual associative areas [52,53]. Similarly 'macropsia' and 'micropsia' (seeing things as too big or too small, respectively) can occur after right occipital damage [54]. Dream reports present many instances of these visual distortions (Fig. 3b and 3c), which again suggest a regionally-specific hypoactivation within visual areas. A defect in working memory could aggravate the symptoms by disturbing spatio-temporal integration [37].

Heterogeneous activation in visual cortices during sleep is further suggested by the frequent loss of color saturation, or achromatopsia, in dream imagery [55]. In neurological patients, achromatopsia is caused by occipital lesions in lingual and fusiform gyri [56], which are regarded as the human equivalent of the color area V4 in monkeys. After unilateral occipital lesions, the deficit in color perception is limited to one hemifield (hemi-achromatopsia). Hemi-achromatopsia in dreams, although less frequent than achromatopsia, suggests a selective unilateral hypoactivation of an occipital color area [56] (Fig. 3d). Finally, reports of colorless dreams are unlikely to be due to memory failure because this characteristic is usually actively reported by the dreamer as departing from his/her usual waking experience. Moreover, a forgetting process would not convincingly account for dreams in which the lack of color occurs only in one visual hemifield, as in Fig. 3d.

Predictions

The neuropsychological interpretation of normal dreams suggests that activation within the visual ventral stream is regionally variable across dreams during REM sleep. This could in part explain why the activation of temporo-occipital areas is not systematically reported in functional neuroimaging [1,3]. In this context, the neuropsychological assessment of dream content would provide hypotheses about the distribution of regional activity in these areas. The categorization of dream reports based on the presence of specific bizarre features in dreams might thus offer new constraints to the analysis of REM sleep data that would be acquired immediately before the dream reports.

For example, we predict that the activation of V4 will be lower in scans that are followed by dream reports containing achromatopsia than those without. Likewise, the correlation in activity between the fusiform face area and infero-temporal cortex should be weaker in REM sleep scans that are followed by dream reports in subjects with Frégoli syndrome than in those without. Although the patterns of regional (de-)activation underlying some specific categories of visual distortions still remain incompletely studied and present some degree of inter-individual variability, these limitations can be overcome by appropriate neuroimaging procedures during the waking state that would allow the neuroanatomical localization of relevant cognitive components on an individual basis (e.g. presenting subjects with a face-recognition task when studying misidentification for faces in dreams). Overall, this approach of dream analysis might reveal, for the first time, genuine cerebral correlates of dreaming activity.

Acknowledgements
Personal work reported here is supported by the Swiss National Science Foundation (grant 8210-061240) for S.S., and by the FNRS (Belgium), by the University of Liège and by the Queen Elisabeth Medical Foundation for P.M. The authors thank Patrik Vuilleumier for his thoughtful advice and Chris Frith for reviewing an earlier version of the manuscript.

Implications for models of brain organization during REM sleep

We have shown that bizarre phenomena in dreams have much in common with clearly defined 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 ventral stream areas, and possibly all sensory cortices, are heterogeneously activated during different REM-sleep episodes. Functional neuroimaging in sleep might benefit from this new, neuropsychological, approach to human dream experience. Future research should objectively characterize these region- and episode-specific patterns of activation and help specify the hypothesized mechanisms that might explain them, such as PGO activity or experience-dependent cortico–limbic interplay [21,57]. In this respect, this new approach might lead to a more comprehensive model of human brain function during REM sleep.

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