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The cerebral correlates of dream recall frequency

**Jury**

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*À Isabelle et Alain*

*« J’ai rêvé tant et plus, mais je n’y entends note. »*

François Rabelais*, Pantagruel,* 1532

*« Je croyais entendre,*

*Une vague harmonie enchanter mon sommeil,*

*Et près de moi s'épandre un murmure pareil,*

*Aux chants entrecoupés d'une voix triste et tendre. »*

Charles Brugnot, *Les Deux Génies*, 1833

RÉSUMÉ

ABSTRACT

Since the dawn of time, men and women have been fascinated by their dreams, and have sought to understand their nature and meaning. However, despite millennia of philosophical speculation and more than a century of scientific exploration, several questions regarding dreams remain pending. This is mainly due because dreaming is solely accessible by recollection of the dreamer after awakening, and therefore cannot be observed directly.

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**\*** The authors contributed equally to this work

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GENERAL INTRODUCTION



Jean-Jacques Grandville. *Second rêve –Une promenade dans le ciel*, 1847

1. The science of sleep and dreams

« Dream science holds an intermediate position between history and biology. It is a science of observation, because observation is an essential part of it, but it is also an historical science in the sense that the elapsed dream can never be reenacted and is therefore investigated, not directly, but through memory. »

Yves Delage. Le rêve. Etude psychologique, philosophique et littéraire. 1920

# Dreams

## Modern definition

According to the Cambridge Dictionary, a dream is a *“series of events or images that happen in the mind when one is sleeping”*. This vague definition illustrates quite clearly how little we know about dreams, despite more than a century of experimental research and millennia of religious and philosophical speculation on their nature and meaning. The main reason for this lack of a clear and consensual definition (Pagel et al. 2001) is due to the fact that dreaming is, by nature, elusive, or, to say it in other words, *“a phenomenon that we can observe only during its absence”* (Paul Valery, *Analecta*, 1926). Indeed, we still do not know precisely when dreaming occurs during sleep, and the dreamer alone is witness to his or her dream. For that reason, the study of dreaming relies critically on the introspective recall, or *“retrospection”* (Schwartz et al. 2005), of the dreamer.

## Scientific conceptualization

This observation led Guénolé to distinguish three successive forms of the dreaming phenomenon, intertwined like nesting dolls (Guénolé 2009). The primordial state is the dream-experience, which occurs during sleep, and of which very little is known because the dreamer has no means to communicate in real-time his or her oneiric travels to the external world. With the notable exception of lucid dreaming, the dream-experience is unobservable to the waking consciousness, be it that of an external observer, but also that of the dreamer him- or herself. The second form is the memory of the dream-experience as we recall it after awakening. Importantly, the dream recall occur in a consciousness state different from the one in which the dream was experienced. As a memory object, dream recall is therefore likely to be influenced by several mechanisms such as forgetting, reconstruction, verbal description difficulties and censorships (Schwartz and Maquet 2002; Schwartz et al. 2005). The third and last element of the model is the verbal report of the dream memory, using words or pictures. The dream report is the only one that can actually be communicated to others and therefore the only one eligible to empirical investigation. As a consequence, most of the dream research has in fact focused on dream reports.

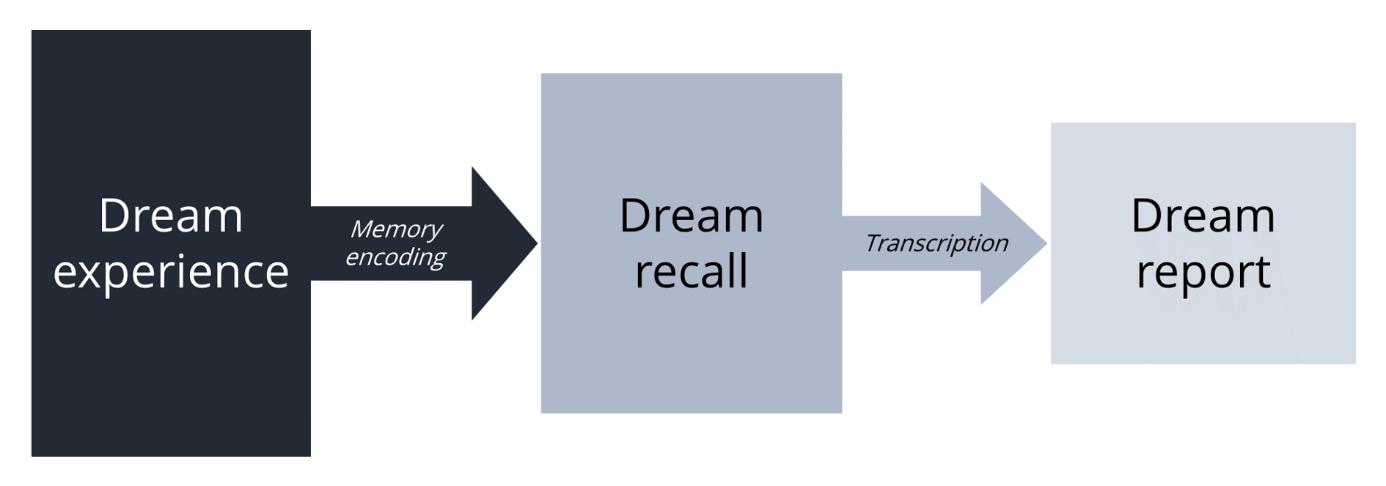


Figure : Guénolé’s model of dreaming (Guénolé, 2009)

Because of this inherent constraint, dreaming still remains one of the great mystery of the human cognition. Several questions on its nature and meaning are still not answered: do we dream every nights? For how long? Why do we sometimes recall our dreams and sometimes not? Are dream reports accurate and exhaustive transcriptions of the dream experience? What is, or what are, the function(s) of dreaming? What are the neurophysiological correlates of dreaming?

The aim of the present thesis is to offer a modest contribution to the ongoing effort to solve these questions. Our first research axis concerned the neurophysiological correlates of dream recall frequency.

# Sleep

## Definition

Sleep is a normal physiological and periodic state characterized by vigilance suspension, which generally occurs during night time in humans. Sleep is a vital need that allows restoration of the immune, nervous, skeletal and muscular systems, leading some authors to postulate that *“sleep is the price we pay for being alive”* (Tononi and Cirelli 2014). Long regarded as an idle state, it is becoming increasingly evident that sleep is *“first and foremost a brain process”* (Hirshkowitz 2004) in which the brain is “*hard at work and helps makes something of the world”,* to borrow the words of Heraclitus’s famous aphorism (for an exhaustive review of the cognitive processes occurring during sleep, see (Andrillon 2016).

## Polysomnographic recordings

The invention of electro-encephalography (EEG) by Hans Berger in 1928 has paved the way for the scientific study of sleep. It was indeed soon after that discovery that Alfred Loomis first described a global slowing down of the brain rhythm during sleep, associated with the apparition of several grapho-elements such as K-complexes. Since then, sleep researchers have used EEG to monitor brain waves, electrooculography (EOG) to monitor eye movements and electromyography (EMG) to measure skeletal muscle activity. The simultaneous collection of these measurements is called polysomnography (PSG) and provides sufficient information to identify sleep stages according to standard international established guidelines. PSG is the gold standard in modern sleep science and is used in both clinical and research settings.

## Sleep stages

A first set of rules were published by Rechtschaffen and Kales (R&K) in 1968 (Kales and Rechtschaffen 1968) and proposed to divide sleep into 5 stages with distinct electrophysiological properties, named rapid-eye movement (REM) and non-REM (NREM) stages 1, 2, 3, 4. This nomenclature was updated in 2007 by the American Academy of Sleep Medicine (Iber 2007) and sleep stage 3 and 4 have been merged into stage N3. In humans, a normal night of sleep consists of a repetition of four or five cycles in which sleep stages tend to follow each other in a particular order. Sleep staging is generally done visually by inspecting consecutive polysomnographic segments of 30 seconds. It results in a hypnogram which represents the succession of sleep stages across time. Below are summarized EEG-EOG-EMG characteristics for wakefulness and the different sleep stages (see alsoFigure 2).

### Wakefulness

Before diving into sleep, we first need to define the state of wakefulness. Eyes-closed quiet wakefulness is accompanied by an EEG rhythm predominantly in the alpha range (8-12 Hz). Opening the eyes or engaging in a significant mental task (for example mental calculation) reduces or blocks the alpha activity. Fairly high muscle activity can be present and slow or rapid eye movements may occur.

### N1 sleep

Stage N1 corresponds to the transitional period between wakefulness and sleep. The brain rhythm progressively decreases from alpha to theta (5 – 7 Hz), and the EOG is characterized by slow, rolling eye movements. N1 sleep represents approximatively 5% of a normal night of sleep.

### N2 sleep

Each night, we spend more than half the night’s sleep in N2 sleep. The EEG activity during this stage is characterized by a predominance of theta waves, recurrently interrupted by two grapho-elements, the spindles and K-complexes, which are the landmarks of this sleep stage. K-complexes are defined as sharp negative waves followed by a positive component, prominent over frontal scalp electrodes and lasting more than 0.5 seconds. Spindles refer to burst of 12 to 14 Hz waves predominant over central scalp electrodes and lasting between 0.5 and 2 seconds. Beyond that, N2 sleep is characterized by an absence of eye movements as well as decreased muscle tone and brain metabolism.

### N3 sleep

N3 sleep, also referred to as deep sleep or slow-wave sleep, is the deepest sleep stage. It is characterized by a predominance (> 20 % of the epoch) of high amplitude (> 75 µV) delta waves (0.5 – 4 Hz). Eye motility, muscle tone and brain metabolism are even more decreased than in N2 sleep. N3 sleep represents approximatively 20% of a normal night of sleep.

### REM sleep (or paradoxical sleep)

As its name suggests, rapid eye movements (REM) sleep is characterized by rapid eye movements easily observable on the EOG channels. They consist of conjugate, irregular and sharply peaked eye movements, similar to some extent to those exhibited during wakefulness. Another fundamental aspect of REM sleep is its muscle atonia, as revealed by a low EMG activity. However, some transient muscle activity or muscle twitching (MTs) can also be observed. These short irregular bursts of EMG activity are superimposed on the background of low EMG activity. Brain metabolism is similar to that of wakefulness, and the EEG is marked by mixed low-amplitude waves predominantly in the theta band (saw-tooth waves), as well as a complete absence of delta rhythms. Other physiologic activities accompany REM sleep including middle ear muscle activity, periorbital integrated potentials, and sleep-related erections. REM sleep constitutes approximatively 20% of a normal night of sleep.

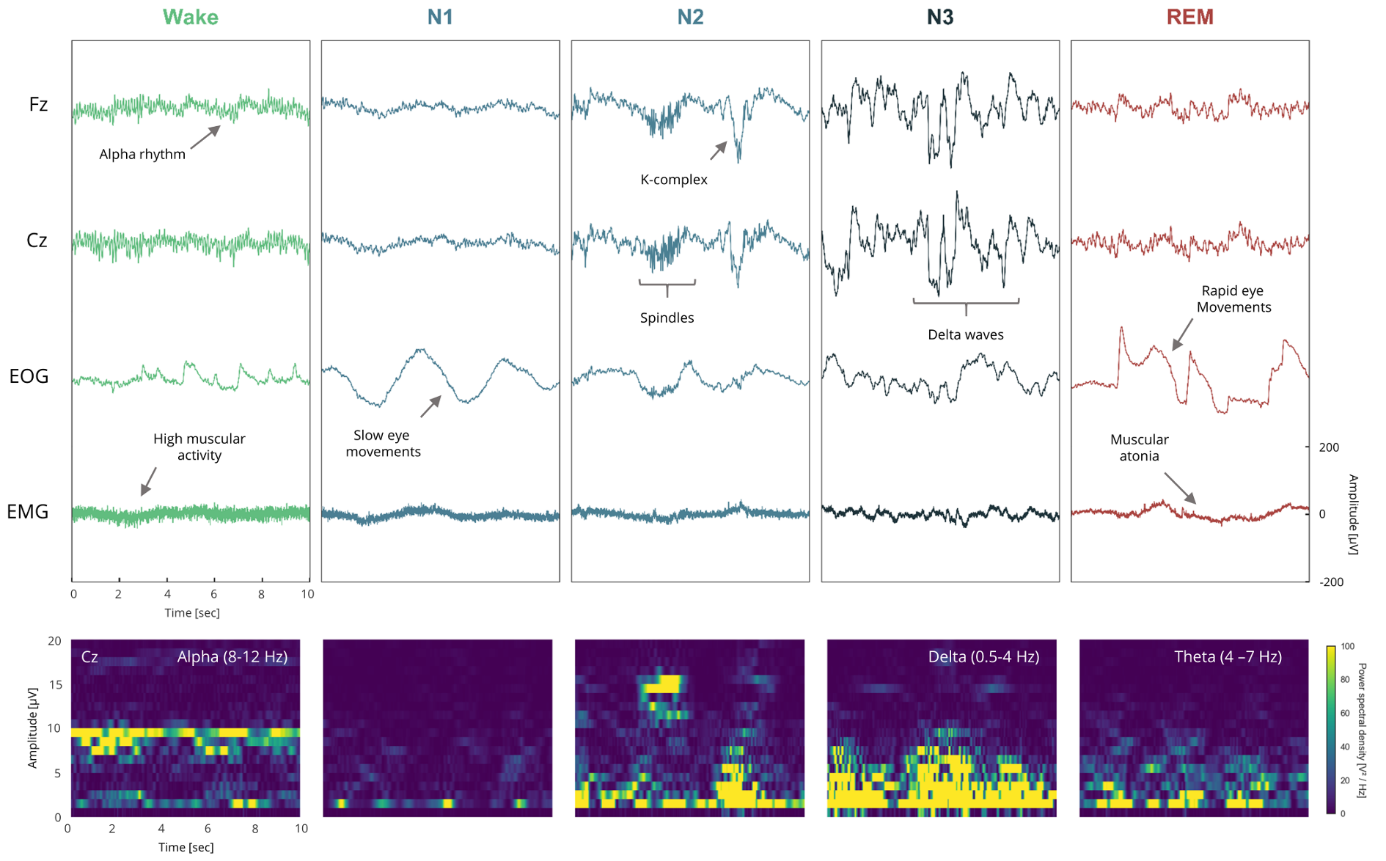


Figure : Polysomnographic recordings across sleep and wakefulness. Top: Scalp EEG, EOG and EMG performed in one healthy young adult during wakefulness, N1, N2, N3 and REM sleep. The main features of each vigilance state are described. Bottom: Spectral properties of each stage obtained by computing the spectrogram of the Cz EEG signal atop.

## Sleep architecture

Modern research has revealed that sleep is not a unitary, single block, but rather a cyclical succession of different brain states, which are all associated with specific functional roles. A normal night of sleep consists of a repetition of four or five 90 to 110 minutes long cycles in which sleep stages tend to follow each other in a particular order. The cycle properties evolve with each cycle reoccurrence. In his overview of the human sleep, Hirshkowitz described five generalizations about normal sleep architecture (Hirshkowitz 2004):

1. Sleep is entered through non-REM sleep
2. Non-REM and REM sleep alternate approximately every 90 to 120
3. Minutes
4. N3 sleep predominates in the first third of the night
5. REM sleep predominates in the last half of the night
6. REM sleep occurs in four to six discrete episodes each night with episodes generally lengthening as sleep period progresses

# Link between dreaming and sleep stages

## The REM sleep hypothesis of dreaming

In the early fifties, Nathaniel Kleitman and his doctoral student Eugene Aserinsky, discovered in humans the existence of periods of sleep with an EEG similar to wakefulness (low voltage and fast frequencies), rapid eye movements and neurovegetative responses (Aserinsky and Kleitman 1953). This discovery had a strong and persistent impact on dream and sleep research. The authors have indeed proposed that the rapid eye movements corresponded to the scanning of dream images. They reached this conclusion by comparing the proportion of dream reports obtained upon awakening in periods of eye motility and outside these periods, respectively 75% and 11% in their 1953’s study, and 80% and 7% in their 1957’s study (Dement and Kleitman 1957). They concluded that their newly-discovered REM sleep stage was the neurophysiological basis of dreaming. A few years later, the French neurophysiologist Michel Jouvet, who had started working on sleep in cats, found that REM sleep was associated with muscular atonia (Jouvet, Michel, and Courjon 1959), a finding that was soon after replicated in humans (Berger 1961). Pursuing his research on REM sleep, or “paradoxical sleep” as he named it, Jouvet had the idea to suppress the muscular atonia by injuring the brain stem of cats. To his astonishment, he found that the injured cats were performing, only during REM sleep, complex motor sequences, that he named “oneiric behavior” (Sastre and Jouvet 1979). For him and the scientific community at the time, it was clear that these motors sequences were directly related to the cat’s dreams, and this experiment provided a significant evidence in favor of the REM sleep hypothesis of dreaming.

## The new hypothesis: a continuum of mentation during sleep?

Even though equating dreaming with REM sleep provided a useful way to explore, with a scientific approach, the secrets of dreams, it soon became apparent that dreaming was not exclusively present during REM sleep but also during all the other sleep stages. Few years after the initial discovery of REM sleep, several researchers reported a much higher proportion of dream report in non-REM sleep than what was expected based on the findings of the Kleitman’s team (Goodenough et al. 1959; Foulkes 1962). Comparing the recall rate of people who never remembered their dreams with people who frequently recalled them, Goodenough and colleagues found respectively 34% and 54% of dream reports outside of REM sleep. The recall rate went up to 54% in Foulkes’s study which comprised 200 awakenings. Since then, numerous studies have replicated the finding of mentation outside of REM sleep (Nielsen 2000), even in the periods of non-REM sleep located before the first nocturnal episode of REM sleep (Noreika et al. 2009). As a counterpoint, it has become apparent that a significant proportion (~15%) of REM sleep awakenings were not followed by a dream report. There results show that REM sleep is not a necessary condition for dream report to occur.

Another strong evidence against the REM sleep hypothesis of dreaming comes from neuropsychology. Traditionally, the pons region of the brain stem, has been described as one generator of REM sleep. From this postulate, Solms conducted in his landmark work an exhaustive review, in humans, of studies reporting brain lesion and the associated symptomatology within this area (Solms 1997). He found that out of 26 case reports of REM sleep loss or alteration following a lesion in the pons area, 25 were not associated with subsequent alterations in dream reporting. Similarly, he reported that lesions in the temporo-parietal junction (TPJ) and the white matter of the medial prefrontal cortex (MPFC) were associated with a complete or partial cessation of dream reports, without any subsequent REM sleep disturbances. This double dissociation provides a clear argument that not only dreaming can occur outside of REM sleep, but it is also not dependent of the brain generators of REM sleep. Rather, Solms put forward the fore-brain hypothesis of dreaming, which proposes that dreaming is controlled through forebrain mechanisms involving at least TPJ and MPFC.

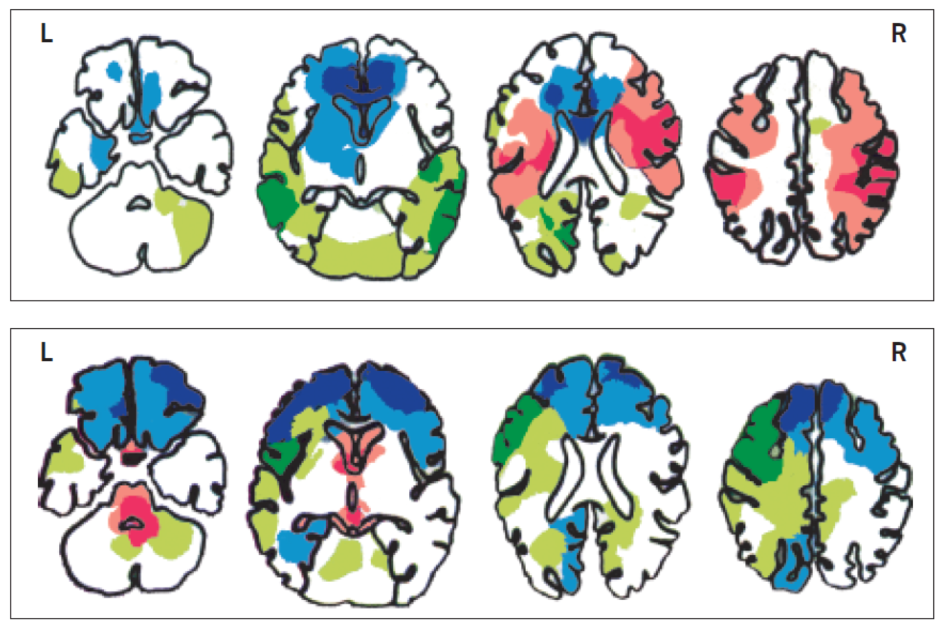


Figure : Lesion maps associated with cessation vs preservation of dreaming. Top: Global cessation of dreaming was found following parietal lobe lesions (6 cases, inferior lobule and supramarginal gyrus; red), medial frontal lesions (9 cases; blue), and posterior lesions (8 cases; green). Bottom: Preserved dreaming was found following left hemispheric and frontal convexity lesions (15 cases; green), bifrontal lesions (14 cases; blue), and brainstem lesions (17 cases; red). Reproduced from Schwartz et al. 2005.

Based on these findings, some authors have postulated that instead of relying on REM sleep mechanisms, dreaming might be best described along a “continuum” of mentation during sleep, ranging from the hypnagogic reveries typical of sleep onset to florid and vivid dreamlike experiences typical during REM sleep (Schwartz et al. 2005). A brief description of this continuum of mental activities during sleep is reported in Table 1.

Table : A brief description of sleep mentation in their typical order of placement during the sleep cycle. Modified from De Koninck 2012.

|  |  |  |  |
| --- | --- | --- | --- |
| **Name** | **Description** | **Sleep stage** | **Recall rate** |
| Hypnagogic reverie | Simple images | Sleep onset mentation (N1 or early N2 sleep) | ~80% |
| Reflections | Thoughts with no hallucinatory content | N2 sleep | 40-50% |
| Vivid dreams | Vivid imagery and sequences, presence of characters, interactions and emotions | REM and NREM sleep | Up to 80% in REM sleep |
| Lucid dreams | The dreamer is conscious of dreaming and can sometimes controls the dream scenario | REM sleep | - |
| Nightmares and bad dreams | Unpleasant and highly anxiogenic dream. The content of nightmare actually awakens the dreamer | REM sleep | - |
| Hypnopompic reverie | Characterized by elaborate imagery | Sleep offset mentation (REM or NREM sleep) | - |

# Neurophysiological correlates of dreaming

Thanks to the recent advances in neuroimaging techniques, we have the means to measure, with unprecedented spatial and temporal accuracy, what is happening in the brain at a specific moment in time (see Box neuroimaging). Yet, since it is now well-accepted that dreaming is not time-locked to a specific sleep stage, but can occur anytime during the night, we are currently unable to localize when a dream occurs during the night. This conceptual issue has not prevented sleep and dream researchers to try to investigate the cerebral correlates of dreaming. The main methods and findings are summarized in the following paragraphs.

## Brain activity during REM sleep

On the basis of the REM sleep hypothesis of dreaming, which was predominant during the nineties, researchers used functional neuroimaging techniques such as positron emission tomography (PET) to investigate the brain activity during REM sleep. They reported that, despite strong similarities between the wake and REM sleep electrophysiological scalp signals, the brain metabolism in these two vigilance states was disparate (Braun et al. 1997; Maquet et al. 1996). Among the most notable findings, the regional cerebral blood flow (rCBF) was decreased in several brain regions including the dorsolateral prefrontal cortex (DLPFC), and was increased in other regions (occipital, temporal, and superior parietal cortices, hippocampal formation, anterior cingulate and the pons). Following these works, researchers postulated that these changes in the brain functional organization could explain the phenomenological characteristics of dream reports (Nir and Tononi 2010; Ruby 2011; Hobson, Pace-Schott, and Stickgold 2000). For instance, increased occipital cortex activity during REM sleep could explain the clear predominance of visual modality in dream reports, a phenomenon that Vincent van Gogh had already noticed when he wrote: *“I often think that the night is more alive and more richly colored than the day”* (Vincent van Gogh, 1888). Second, the increased activity during REM sleep in the hippocampal formation, a region well-known for its role in memory encoding and retrieval, could account for the presence of known images and characters in dreams. Finally, the decreased activity in the dorsolateral prefrontal cortex, a region involved in executive function, cognitive control and working memory, could account for the lack of consistency, voluntary control and logical reasoning over the dream story. This is consistent with studies on lucid dreaming which showed a partial reactivation of this area in lucid dreams compared to non-lucid dreams. We will return to these correspondences between the phenomenology of dreams and brain activity in the chapter on the default mode network.

## Brain activity during lucid dreaming

Long considered as a fantasy, lucid dreaming - the ability to become self-aware of dreaming during a dream, and in some cases, to control the dream scenario – has recently gained considerable interest among researchers and the public. The scientific study of lucid dreaming started in the nineteenth century when Hervey de Saint Denys, a learned oneirologist, published his landmark book “*Dreams and the Ways to Direct Them: Practical Observations”,* in which he described his own lucid dream experiences. More than a century later, more objective methods such as EEG and functional magnetic resonance imaging (fMRI) have become the technique of choice for understanding lucid dreams. Using a pre-determined ocular signal, Dresler was remarkably able to measure, in real-time, the brain activity during lucid REM sleep and non-lucid REM sleep (though only one subject out of four had lucid dreams of sufficient length; Dresler et al. 2012). Lucid REM sleep was associated with a reactivation of areas that are normally deactivated during REM sleep, such as bilateral precuneous, parietal lobules and prefrontal and occipito-temporal cortices. Phenomenologically, these regions are either involved in self-awareness and executive functions, and their reactivation during lucid dreaming could account for the resurgence of a certain level of self-awareness and voluntary control. Even more recently, Voss was able to induce self-reflective awareness during dream using fronto-temporal transcranial alternating current stimulation (Voss et al. 2014). They reported that lucid dreams were most prominent during stimulation in the lower gamma band (58% of lucid dreams following a stimulation at 25 Hz and 77% of lucid dreams following a stimulation at 40 Hz). However, the lucidity was not assessed directly by the dreamer but assumed a posteriori if the subjects reported elevated ratings on a lucidity scale. In conclusion, lucid dreaming provides an appealing and elegant way to study, in real time, the cerebral correlates of dreaming. Yet, the inherent problem with this method lies precisely in the fact that lucid dreams are, by nature, different from non-lucid dreams. As exciting as the results are, it would be however difficult to generalize them to the research on non-lucid dreams.

## Brain activity in the minutes preceding a dream report

Another line of research consists in comparing the EEG power in various frequency bands in the minutes preceding a morning awakening associated, or not, with a dream recall. This paradigm has been used in several studies over the last decades, the findings of which are summarized as follows.

In 2004, Esposito reported that in both REM and N2 sleep, dream recall was associated with a lower alpha and delta power in the 3 minutes preceding awakening. According to the authors, the alpha effect may reflect increased cognitive elaboration and visual imagery as well as increased attention and memory processes. A few years later, Marzano found that dream recall after morning awakening from REM sleep was associated with a higher frontal 5–7 Hz (theta) activity in the 5 minutes preceding awakening (Marzano et al. 2011). In N2 sleep, dream recall was associated with a decrease in alpha power, an observation consistent with Esposito’s results. The same year, another study reported a lower delta power for the dream recall condition following awakening from N2 sleep, and a higher alpha and beta power in occipital derivations for REM sleep (Chellappa et al. 2011). Finally, a recent study, inaccurately entitled *“the cerebral correlates of dreaming”*, reported that in both N2 and REM sleep, reports of dream experience were associated with local decreases in delta power in posterior cortical regions in the 2 minutes preceding awakening. The authors were able to predict whether an individual reported dreaming or the absence of dream experiences after awakening from N2 sleep by monitoring this posterior ‘hot zone’ in real time.

The results from these studies are heterogeneous and sometimes contradictory. Moreover, despite this paradigm may seem attractive at first, the problem still remains that we can never be sure whether the dream actually took place in the minutes just before awakening or several tens of minutes before.

## Dreaming as a subsystem of the default mode network

The past few years have witnessed the emergence of a new conceptual framework of dreaming, centered on the idea that dreaming is a unique form of mind-wandering, which cerebral correlates are a subsystem of the default mode network (DMN; see Box 1; Domhoff 2011; Domhoff and Fox 2015; Christoff et al. 2016). Based on the fact that dreaming and waking spontaneous thought share many features (i.e. predominance of the audiovisual modalities, centered on one’s current goals and concerns, draw heavily on semantic and episodic memory in constructing simulations and future plans, presence of a wide range of affect), some authors have postulated that dreaming is a *“type of spontaneous thought that is highly unconstrained, hyper-associative and highly immersive”* (Christoff et al. 2016). Using the results of lesion and REM sleep neuroimaging studies, they argued that dreaming should be accompanied, at the neural level, by a strong recruitment of the default mode network medial temporal lobe (MTL)-centered subsystem and strong deactivations in frontoparietal control network regions (such as the DLPFC). Activation of the former areas could be related to the generation of spontaneous thoughts, during both wake and sleep, while the deactivation of the latter areas could explain the high volatility and variability of dream content over time.

**BOX 1: FUNCTIONAL CONNECTIVITY & DEFAULT MODE NETWORK**

The basis of functional connectivity is to measure the correlations between brain regions of spontaneous low-frequency (>0.1 Hz) BOLD fluctuations (Buckner, Krienen, and Yeo 2013), preferentially when the subject is not performing an explicit task (resting-state, Fox and Raichle 2007). Thanks to this method, several large-scale distributed functional networks have been identified (Fox et al. 2005; Yeo et al. 2011), among which the default mode network (DMN) has been one of the most investigated. The DMN is comprised of several brain areas that are highly correlated when the subject is not focused on a task but rather engaged in a variety of internal cognitive processes, such as self-reflection, spontaneous cognition, autobiographical memory and future event simulation (Raichle et al. 2001; Buckner, Andrews-Hanna, and Schacter 2008).

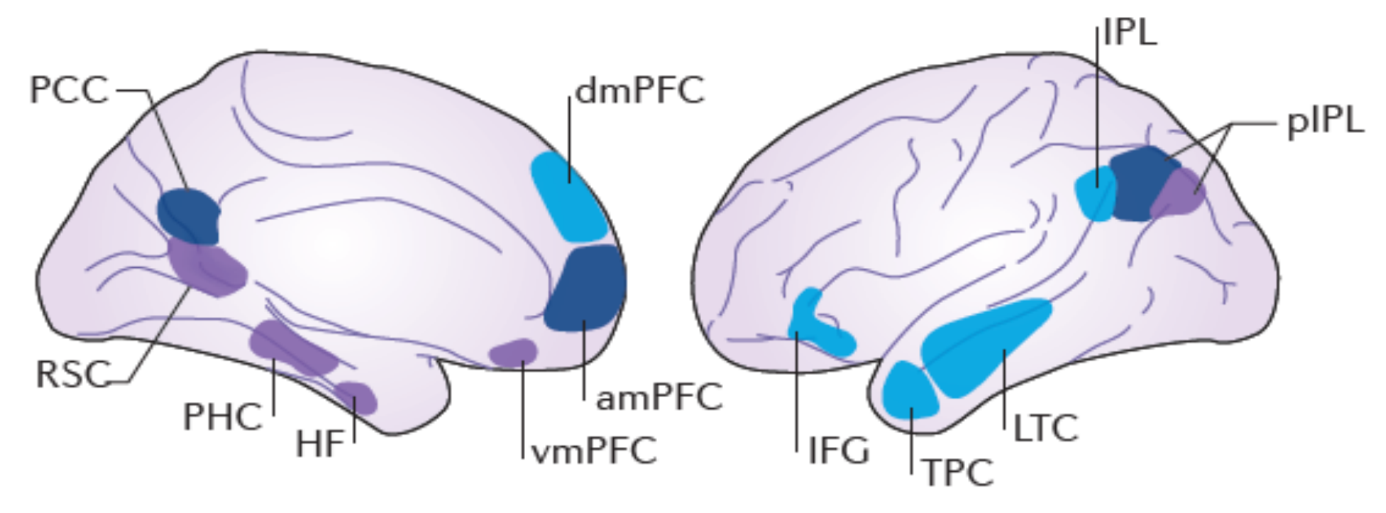


Figure 4: The default mode network and its subcomponents. The DMN is centered on the medial prefrontal cortex (MPFC), the medial parietal cortex and the lateral parietal cortex, and extends into the temporal lobe and lateral prefrontal cortex. Three subcomponents within the DMN have been identified. The first, the core DMN subsystem (deep blue) includes the MPFC, posterior cingulate cortex (PCC) and posterior inferior parietal lobule (pIPL). It is characterized by its hub-like properties and its contributions to internally oriented cognition. The second subcomponent (purple), which is known for its roles in memory and mental simulation, is centered on the medial temporal lobe (MTL), and includes as well the hippocampal formation (HF) and parahippocampal cortex (PHC). The third subcomponent (cyan) extends more dorsally and includes the dorsomedial prefrontal cortex (dmPFC), the lateral temporal cortex (LTC), the temporopolar cortex (TPC) and parts of the inferior frontal gyrus (IFG). It seems to be linked to a wide range of functions, including mentalizing, conceptual processing and emotional processing. Adapted from Christoff et al. 2016.

1. Dream recall frequency

« We must also inquire what the dream is, and from what cause sleepers sometimes dream, and sometimes do not; or whether the truth is that sleepers always dream but do not always remember (their dream); and if this occurs, what its explanation is. »

Aristotle. On dreams. 350 B.C.



# Measuring dream recall frequency

As Aristotle had rightly pointed out, we do not always remember our dreams. More than two thousand years after, modern research has confirmed that the dream recall frequency (DRF) – i.e. the number of dream reports over a given period of time - is indeed highly variable both within individuals over the life course, but also between individuals (Schredl et al. 2003; Ruby 2011).

There is no gold standard for measuring DRF, and each method has its pros and cons. In research settings, three methods are commonly applied: questionnaire scales, dream diaries, and laboratory awakenings (Schredl 1999). The former consists in simply asking the participants to estimate their dream recall frequency over the last few weeks or months. This method has the advantage of being fast, inexpensive, and unaffected by the measurement, however, the DRF could be over- or under-estimated due to erroneous or incomplete recollection. Regarding dream diaries, the participants are asked to report each morning whether they have recalled a dream or not. This method minimizes the bias of retrospective estimation, but has the disadvantages of potentially increasing drastically the dream recall frequency, especially in persons who usually almost never recall their dreams (Schredl 2002). Finally, laboratory awakenings consist in awakening the participants in the sleep lab and asking them whether they recall a dream or not. While this method has the clear advantage that the experimenters can measure physiological parameters (EEG, EOG, ECG, respiration and heart rate) prior, during and after the awakening, it is also time-consuming and expensive. Moreover, as for dream diaries, laboratory awakenings are associated with a dramatic increase in DRF, especially for low dream recallers.

# DRF in the general population

## Average DRF

Measured by questionnaire, the average weekly DRF was 2.58 ± 2.03 in 444 German students (Schredl et al. 2003) and 0.83 ± 1.57 in a representative German sample of 931 participants (Schredl 2008). Using dream diaries, the average weekly DRF was 3.1 ± 1.5 in 70 Finnish children (Valli et al. 2005) and 3.9 ± 2.5 in a sample of 196 German student (Schredl and Fulda 2005). In lights of these results, we can conclude that the average weekly DRF in the general population lies between 1 and 3 dream reports per week.

## Intra-individuals variability

Daily experience suggest that our ability to recall dream fluctuate over time. Investigating this issue using the diary technique in 169 participants, Schredl reported that the stability of DRF was very high over a period of one month (Schredl and Fulda 2005). Similarly, he reported high DRF stability coefficients in a sample of older adults who had been interviewed weekly about their dream life over a period of 26 weeks (Schredl et al. 2001). However, to our knowledge, there are no studies evaluating the stability of DRF in the same individuals over an extended period of time.

## Inter-individuals variability

DRF vary drastically between individuals: some persons almost never recall a dream, whereas others can relate one or several dreams every morning. In an Austrian sample of 1000 persons, Stepansky et al. (1998) reported that 31% of the participants reported 10 dreams or more per month, 37% reported between one and nine dreams per month, and 32% reported less than one dream per month. In a sample of 285 German students, Schredl (2002) found that 44% reported dreams four or more times per weeks, 44% reported a dream one time per week and 12% reported a dream less than one time per month. This variability allows to differentiate behavioral profiles of DRF: high dream recallers (HR), who can relate a dream almost every morning (e.g. more than 5 times a week, Schredl and Fulda 2005) and low dream recallers (LR), who almost never recall a dream (e.g. less than one dream per month, Goodenough et al. 1959). Importantly, the frequency of HR is higher in the general population, and even more in young and/or student sample (Schredl and Fulda 2005).

# Parameters correlated with DRF

The identification of factors co-varying with - and thus influencing - DRF both in frequency and quality has been studied extensively in both the laboratory and the home environment. The main factors are as follows (reviewed in Ruby 2011; Blagrove and Pace-Schott 2010).

## Psychological factors

First, increased professional or personal stress is positively associated with DRF (Schredl 1999). Similarly, an interest in dreams, or a positive attitude towards dreams in general is clearly associated with DRF, as is frequent day-dreaming and rich fantasy life (Schredl et al. 2003). DRF decreases with age and tends to be higher in women, who are also typically more interested in dreams (Schredl and Reinhard 2008; Schredl 2008). Regarding personality dimensions, studies have found positive correlations between DRF and thin boundaries, anxiety, and openness to experience. However, most of the correlations between DRF and personality traits are low and explain only a small percentage of the total variance. Regarding cognitive abilities, several studies have consistently reported that DRF is positively correlated with creativity. A simple explanation of why individuals differ in their ability to remember dreams could be because they differ in some more general memory abilities (verbal, visual, short and long term). However, the literature yielded contradictory results, with some support for a positive association between DRF and visual memory, but also evidence against it for verbal and visual material and short-or long-term story narrative recall (Ruby 2011; Blagrove and Pace-Schott 2010).

## Sleep parameters

First, DRF varies according to the sleep stage preceding awakening (Nielsen (2000) for a review). More dream reports are obtained after an awakening during REM sleep than after an awakening during NREM sleep. These results inspired the REM sleep hypothesis of dreaming discussed earlier in this thesis. However, when a dream is not reported on awakening, there is no method of establishing whether it did not happen or was forgotten. This idea was rightly pointed out by Conduit: “*An ongoing assumption made by sleep scientists is that since dreams are more often recalled on awakening from REM sleep, dreams must occur more often during this sleep stage. An alternative hypothesis is that cognition occurs throughout sleep, but the recall of mentation differs on awakenings”* (Conduit, Crewther, and Coleman 2004).

This idea that DRF variability is not a matter of dream production during sleep, but of dream recall during awakening, is the core of several models of dream recall (detailed later in the section on dream recall theories), among which the arousal-retrieval model is one of the most significant. In its simplest form, it claims that a period of wakefulness must occur just after dreaming so that the dream content can be transferred from short term to long term memory (Koulack and Goodenough 1976).

Several studies support this model. First, using retrospective evaluation, Schredl et al. (2003) found a positive correlation between the number of nocturnal awakenings and DRF. Second, De Gennaro et al. (2010) reported that recovery sleep following a full night of sleep deprivation was characterized by an almost complete abolition of dream recall, paralleled with a lower number of nocturnal awakenings, which could, according to them, have *“reduced the contents available in memory as possible cues for retrieval of dream experiences at morning”.* Finally, these results were recently reinforced by a full-night PSG study in 36 subjects (18 HR and 18 LR; Eichenlaub et al. 2014; Figure 5). HR showed in average longer intra-sleep wakefulness than LR (~15min more on average). The number of awakenings (the number of phases composed of consecutive pages of awakening) was not significantly different between the 2 groups, but the mean duration of the awakenings was (HR, 1.90 ± 0.91 min; LR, 0.95 ± 0.40 min).

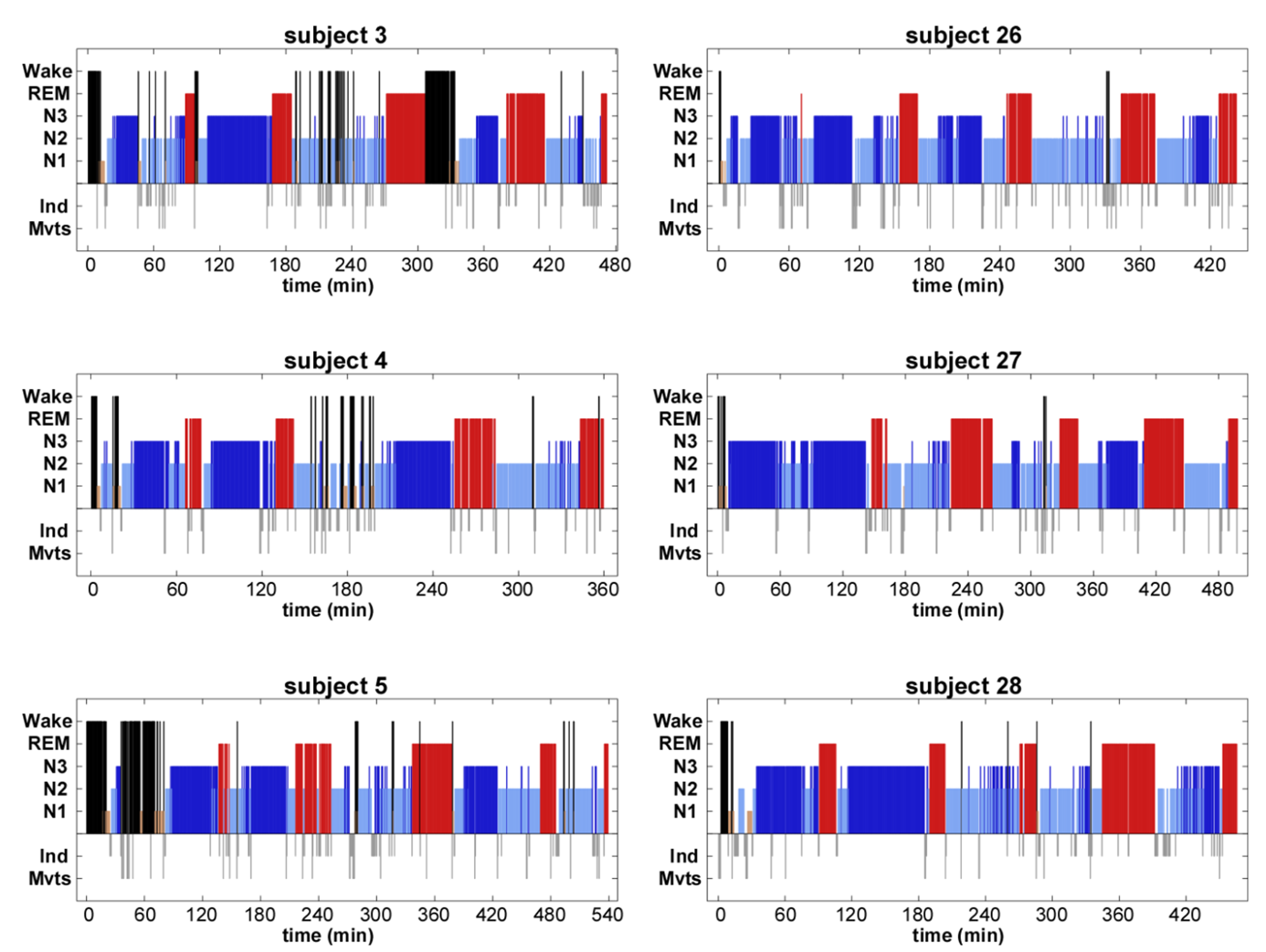


Figure : Hypnograms of three representative HR (left) and three representative LR (right). Full night PSG recordings were acquired in the sleep lab in 18 HRs and 18 LRs. Wake: wakefulness (black); N1, N2, and N3: sleep stages N1 (very light gray), N2 (light gray), and N3 (dark gray), respectively; REM: REM sleep (medium gray); Ind: pages for which the dominant sleep stage could not be determined; Mvts: movements. From these 6 examples, it can be observed that the wakefulness periods during the sleep period time are longer in HR than in LR. Adapted from Eichenlaub et al. (2014)

## Neurophysiological parameters

The neurophysiological parameters that covary with DRF had never been investigated until the doctoral work of Jean-Baptiste Eichenlaub, conducted with Perrine Ruby a few years ago. The present study follows on from this work, in which they compared the brain activity of HR and LR during both sleep and wakefulness and using several neuroimaging techniques such as auditory evoked potentials (AEP) and positron emission tomography (PET). The main findings from his Eichenlaub’s doctoral thesis are summarized in Figure 6.

First, they conducted a sleep lab study in which they compared the brain reactivity (AEP) of 18 HRs (DRF = 4.4 ± 1.0 dream reports per week) and 18 LRs (0.25 ± 0.1) during sleep and wakefulness. During data acquisition, the subjects were presented with sounds to be ignored (first names randomly presented among pure tones) while they were watching a silent movie or sleeping. They found that brain responses to first names dramatically differed between the 2 groups during both sleep and wakefulness (Figure 6A). During wakefulness, the attention-orienting brain response (P3a) and a late parietal response were larger in HR than in LR. During sleep, there were between-group differences at the latency of the P3a during N2 sleep and at later latencies during all sleep stages.

Second, they used PET to compare the resting state cerebral blood flow of 21 HRs (DRF = 5.2 ± 1.4 dream reports per week) and 20 LRs (DRF = 0.5 ± 0.3 dream reports per week) during sleep and wakefulness. Compared with LRs, HRs showed higher rCBF in the TPJ during REM sleep, N3, and wakefulness, and in the MPFC during REM sleep and wakefulness (Figure 6B).

Altogether, these findings show that HR and LR have different neurophysiological traits: spontaneous and evoked brain activity of HR and LR differ during wakefulness and sleep. They argued that HR’s neurophysiological profile could promote mental imagery during sleep and the encoding or retrieval of the dream memory during wakefulness. Notably, increased attention-orienting responses during sleep in HR could increase the proportion of intra-sleep awakenings, which in turn would facilitate the encoding of dreams according to the arousal-retrieval model, and finally result in a higher likelihood of dream recall in the morning after awakening.

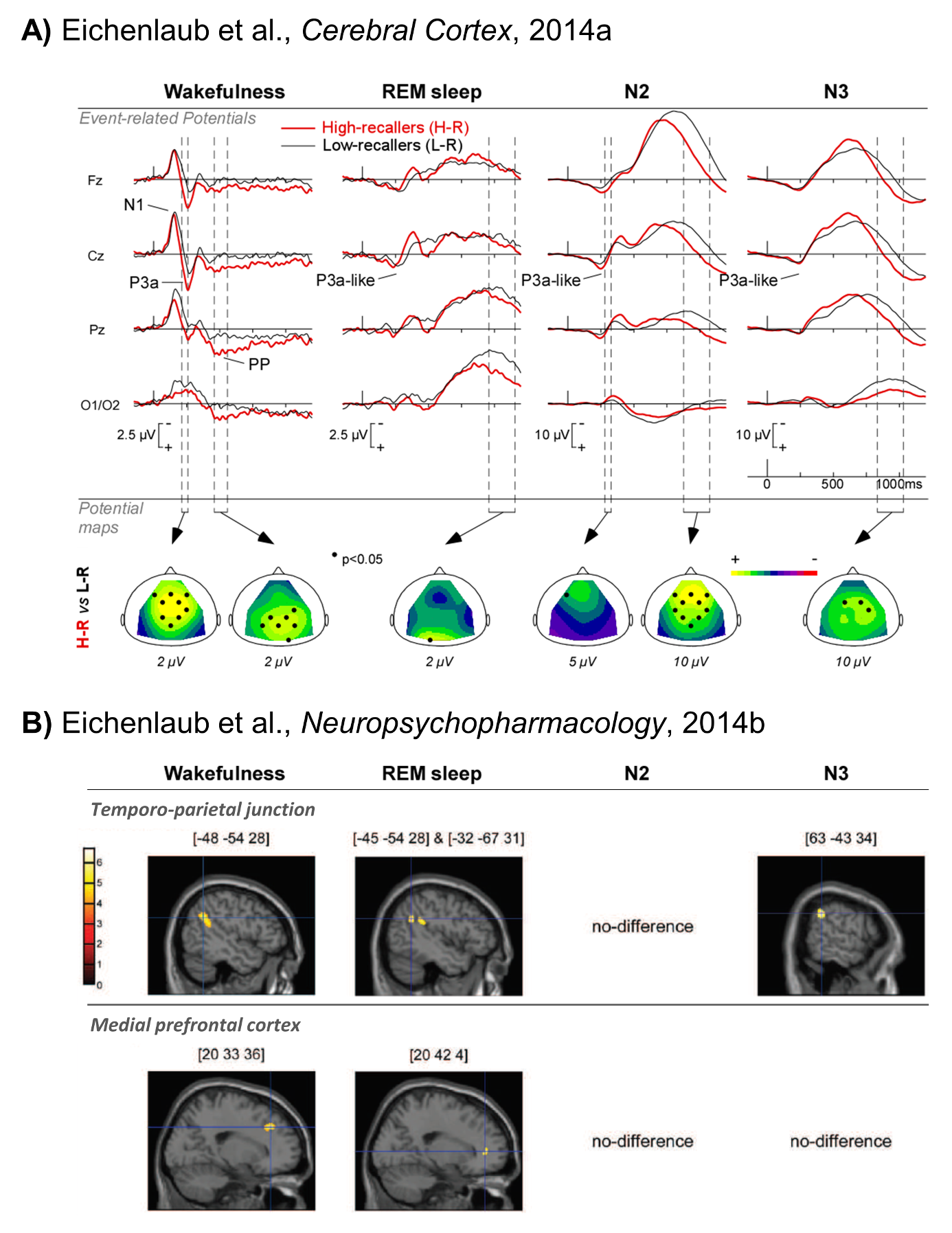


Figure : Summary of the results obtained in Eichenlaub's PhD thesis

## Link between neurophysiological and psychological traits

In conclusion, we have seen that many parameters covary with DRF. The ability to recall dreams seems to be associated with psychological and personality factors on one hand, and neurophysiological trait factors on the other hand. These results should be regarded as complementary rather than contradictory. For instance, the fact that HRs demonstrate higher rCBF during sleep and wakefulness in the TPJ and MPFC, two regions of the DMN, is consistent with the DMN hypothesis of dreaming, and is well in line with the finding that HRs are more often absorbed in their inner worlds (i.e. day-dreaming, fantasy) and more anxious. Indeed, studies have reported a positive correlation between the activity of the MPFC during wakefulness and scores of openness to experience (Sutin et al. 2009) and neuroticism (Zald, Mattson, and Pardo 2002).

# Theories on dream recall

How do we explain such variability in dream recall? Several theories attempted to address this issue. They are summarized as follows.

## Freud’s repression hypothesis

Freud believed that the function of dreams is to preserve sleep by representing as fulfilled wishes that would otherwise awaken the dreamer. According to him, “*the forgetting of the dream is in a large measure the work of the resistance”* (Freud 1900), which means that dreams that are not sufficiently disguised to pass the censor will be entirely repressed and therefore forgotten. However, as highlighted by Schredl (1999), it is impossible to test this hypothesis because we cannot measure the non-recalled dreams in order to compare them to the recalled ones.

## Life-style hypothesis

Schonbar was one of the first to investigate the psychological correlates of differential DRF. She proposed that DRF can be better explained as part of a general life-style and personality traits (Schonbar 1965). According to her work, high dream recallers are characterized by an ‘inner-acceptant’ life-style, which involves higher creativity, introspection, fantasy proneness and openness to experience. This hypothesis has been corroborated by several experimental studies that reported a positive association between DRF on one hand and openness to experience, absorption and creativity on the other hand (see section II. 3. A).

## Salience hypothesis

Based on the idea that the principles of waking memory apply to dream recall, Cohen developed in the seventies the interference hypothesis (Cohen and Wolfe 1973) followed by the salience hypothesis (Cohen and MacNeilage 1974). The interference hypothesis postulates that the dream memory trace remains so long as there is no distraction or interference. Otherwise, dreams are forgotten in order to maximize the memory capacity for the day ahead. This echoes French philosopher Roger Caillois’s idea on dream forgetting: *“Dreams are quickly forgotten because they have no consequences on waking life and there is only benefits in forgetting them.”* (Roger Caillois, *L’incertitude qui vient des rêves*, 1956). In more practical terms, the central idea of this theory is that the dreamer must voluntary pay attention to the dream immediately after awakening. In this respect, it overlaps the life-style hypothesis since high dream recallers are expected to be more interested in their dreams and therefore put more attention on them upon awakening.

Cohen further extended his model in the salience hypothesis, which emphasizes dream content and states that the more salient a dream (e.g. a vivid, bizarre, and highly emotional dream), and the less interferences there are during the recall process, the more likely the dream is to be recalled. Several findings are in favor of this hypothesis. For example, it has been shown that bizarreness (Cipolli et al. 1993) and emotionality (Schredl and Doll 1998) enhance recall of dream content (an observation that was however not replicated when taking the effect of dream length into account; Schredl 2000). More recently, Parke and Horton (2009) have studied the combined effect of interference and salience processes on dream recall. The findings suggest that a link is present, as the more interference experienced has tended to reduce the length of the dream recall in turn reducing the reported salience.

## Arousal-retrieval model

Koulack and Goodenough (1976) proposed in their so-called arousal-retrieval model that a short period of wakefulness (arousal) must occur immediately after dreaming in order to transfer the dream content from short-term memory to long term memory. Furthermore, they drew on Cohen’s work to propose that the salience of dream content and lack of interferences during the recall process were critical for a successful recall of the stored dream (retrieval). Importantly, the arousal-retrieval model has received great support from the literature, reviewed earlier in section II. 3. B.

## State-shift hypothesis

Extending these arousal-based ideas, Koukkou and Lehmann (1983) proposed the state-shift hypothesis which emphasizes the state dependent effects of dream recall rather than short-term memory effects. According to them, *“forgetting of dreams is a function of the magnitude of the difference between states during encoding and recall.”* (Koukkou and Lehmann 1983). Consequently, the closer two functional states are, the better is the transference of information. This could explain higher rates of dream recall following REM sleep (which is functionally close to wakefulness) than NREM sleep (and especially N3 sleep in which cortical activity is very different from wakefulness).

## Sleep inertia

In 2004, Conduit and colleagues demonstrated that the performance during or shortly after awakening is of importance for the process of dream recall. The design of their study is as follows. Participants were instructed to produce an eye movement signal whenever they heard a tone, presented at increasing volume during N2 and REM sleep until an eye movement signal verification was observed. Ninety seconds after signal verification, participants were awakened and asked if they remembered hearing the tone or responding with the EM signal. Such recollection of signal verified tone presentations was significantly less after Stage 2 sleep (65%) compared to REM sleep (100%) presentations. Furthermore, signal verified tone recall was significantly correlated with reported dream recall frequency. They concluded that *“quite possibly, brain functioning underlying the reporting and non-reporting of dreams does not exist within the pre-sleeping period at all, but within the period just after awakening, when cognitive resources are in demand to recall and/or consolidate events which have just occurred within the previous sleeping period”* (Conduit, Crewther, and Coleman 2004).

Echoing these findings, Schredl et al. (2003) noted that cognitive functioning in the period just after awakening is often severely impaired (an effect referred to as sleep inertia; Tassi and Muzet 2000; Trotti 2016), and that it would be in consequence *“promising to correlate interindividual differences regarding the sleep inertia with DRF”*. This issue will form a large part of the doctoral work hereby presented and we will return to this in the problematic and hypothesis section.

## Towards a unifying theory of dream recall

This brief overview leads to the initial observation that there is a broad spectrum of dream recall theories, ranging from relating to the content of the dream (Freud’s repression and Cohen’s salience hypotheses) to accounting for the psychological (life-style hypothesis), cognitive and physiological processes (arousal-retrieval, state-shift hypothesis, sleep inertia). The empirical data are hitherto in favor of the arousal-retrieval model and the life-style hypothesis. A comprehensive, unified theory of dream recall should combine these two models, for example using the arousal-retrieval model to account for day-to-day variability in DRF (state factors), and the life-style hypothesis to account for the large interindividual DRF variability (traits factors). Moreover, there is a currently a lack of evidence for the state-shift hypothesis (due to the difficulty of deriving valid quantitative measures for the closeness of functional states; Schredl 1999) and the sleep inertia theory, which both insist on brain functioning within the period just after awakening.

1. Dream content and dream function

Schopenhauer

# Dream content

## Methodology: basic principles of dream content analysis

## Experimental results

## The memory sources of dreams

# The function(s) of dreams

## Historical perspective

Voir bouquin De Koninck

Plato: dreams express hidden desires and are dominated by negative emotions (in tune with Freud, see De Koninck).

Aristotle

## Emotional regulation

## Memory processing

## Others hypotheses

1. Hypothesis and objectives

# Unresolved issues

## Differences between HR and LR at awakening

## Differences in the micro-structure of HR and LR

## What are the memory sources of dreaming?

EXPERIMENTAL RESULTS

METHODOLOGICAL DEVELOPMENT

GENERAL DISCUSSION

Reprendre les theories dream recall:

Salience hypothesis (blagrove pace schott)

ANNEXES

REFERENCES