Brain Reactivity Differentiates Subjects with High and Low Dream Recall Frequencies during Both Sleep and Wakefulness

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The neurophysiological correlates of dreaming remain unclear. According to the “arousal-retrieval” model, dream encoding depends on intrasleep wakefulness. Consistent with this model, subjects with high and low dream recall frequency (DRF) report differences in intrasleep awakenings. This suggests a possible neurophysiological trait difference between the 2 groups. To test this hypothesis, we compared the brain reactivity (evoked potentials) of subjects with high (HR, \(N = 18\)) and low (LR, \(N = 18\)) DRF during wakefulness and sleep. 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. Brain responses to first names dramatically differed between the 2 groups during both sleep and wakefulness. During wakefulness, the attention-orienting brain response (P3a) and a late parietal response were larger in HR than in LR. During sleep, we also observed between-group differences at the latency of the P3a during N2 and at later latencies during all sleep stages. Our results demonstrate differences in the brain reactivity of HR and LR during both sleep and wakefulness. These results suggest that the ability to recall dreaming is associated with a particular cerebral functional organization, regardless of the state of vigilance.

Keywords: auditory P3a, automatic attention orienting, dreaming, electrophysiology, event-related potentials, functional brain organization, NREM, REM sleep

Introduction


In the 1950s, rapid eye movement (REM) sleep was considered as the neurophysiological state underlying dreaming (Aserinsky and Kleitman 1953; Dement and Kleitman 1957; Sastre and Jouvet 1979). Following this hypothesis, some scientists restricted their investigation of the cerebral correlates of dreaming to the investigation of REM sleep (e.g., Maquet et al. 1996; Braun et al. 1998). However, the REM sleep hypothesis of dreaming has been challenged. First, according to several studies, REM sleep is not necessary for dreams to be reported. A significant amount of awakenings in non-REM (NREM) sleep are followed by a dream report (mean 43%, range 0–75%, for a review, see Nielsen 2000), even if no REM sleep occurred before the NREM episode (e.g., Palagini et al. 2004; Noreika et al. 2009). Second, some studies have shown that REM sleep is not sufficient for dreams to be reported. Ten to 20% of awakenings from REM sleep are not followed by a dream report (Nielsen 2000), and several neuropsychological studies have shown that lesions in the temporoparietal junction and medial prefrontal cortex are associated with a cessation of dream report but not with REM sleep disturbance (Murri et al. 1985; Solms 1997; Bischof and Bassetti 2004). Based on these findings, Solms (2000) argued that dreaming and REM sleep are dissociable states and that dreaming can occur in any sleep stage. According to this hypothesis, investigating brain activity only during REM sleep is not sufficient to characterize the cerebral correlates of dreaming. Electrophysiologists have investigated the electroencephalogram (EEG) power of both REM and NREM sleep in the few minutes preceding a dream report (Takeuchi et al. 2003; Esposito et al. 2004; Chellappa et al. 2011; Marzano et al. 2011); however, the results proved to be heterogeneous. These results might have been blurred by the difficulties in determining precisely when the reported dreams occurred during sleep (REM or NREM).

Noteworthy, in the 1970s, with the “arousal-retrieval” model, Koulack and Goodenough (1976) proposed another mechanism than sleep stages to explain the formation of dream reports. It is currently well accepted that sleep is involved in memory consolidation (e.g., Diekelmann and Born 2010); however, there is no clear evidence of long-term memory encoding during sleep (e.g., Walker et al. 2002; 2003; Wamsley, Perry, et al. 2010). The Koulack and Goodenough model is based on the assumption that the sleeping brain is unable to encode new information in long-term memory. These authors argued that an effective transfer of a dream to long-term memory is possible if, and only if, an awakening occurs during the life of the short-term memory trace of the dream. In other words, these authors postulated that dream encoding in memory (and thus dream recall at awakening in the morning) depends on intrasleep arousals/awakenings. Some studies using questionnaires supported this hypothesis by demonstrating that subjects with high dream recall frequency (DRF) report more intrasleep awakenings than subjects with low DRF (Cory and Ormiston 1975; Schredl et al. 2003). These data suggest the possibility that neurophysiological trait-related differences between subjects with high and low DRF are associated with differences in intrasleep awakening.

To test this hypothesis, we compared the sleep characteristics and brain activity of subjects with high and low DRF (High-recallers and Low-recallers; Goodenough et al. 1959; Lewis et al. 1966) using polysomnographic recordings and auditory event-related potentials (ERPs). Complex sounds (the subject’s first name and an unfamiliar first name) were presented randomly and rarely among repeated pure tones (Eichenlaub et al. 2012). This novelty oddball paradigm...
allowed us to investigate the various steps of auditory information processing associated with perception (the frontocentral N1 component evoked by any sound ∼100 ms; Näätänen and Picton 1987), attention orienting (the frontocentral novelty P3 or P3a component evoked by unexpected sounds ∼250 ms; Friedman et al. 2001; Polich 2007), and higher level cognitive processing (parietal components evoked by complex sounds after 300-ms poststimulus; Holeckova et al. 2006; Eichenlaub et al. 2012). We acquired electromyogram (EMG), electrooculogram (EOG), and EEG data using 21 scalp electrodes in 18 High-recallers (>3 dream reports per week) and 18 Low-recallers (<2 dream reports per month, Supplementary Table S1) presented with the oddball paradigm described above while they watched a silent movie with subtitles during wakefulness and while sleeping at night (Fig. 1).

Materials and Methods

Subjects
A total of 1000 persons interested in participating in this study filled out a questionnaire concerning sleep and dream habits (the subjects were unaware that DRF was a criterion for subject selection). Subsequently, the subjects were contacted by telephone and selected as High-recallers upon confirming dream recall on >3 mornings per week (the question asked, "on average, how many mornings per week do you wake up with a dream in mind?"). A dream was previously defined as a long and bizarre story, an image that vanishes rapidly, or a feeling of having dreamt. Subjects were selected as Low-recallers upon confirming dream recall on <2 mornings per month. Eighteen High-recallers and 18 Low-recallers were selected. The following parameters did not differ between the groups: gender, age, habitual sleep duration, habitual sleep time, education level and the size of the place of residence (Schredl 2008; Schredl and Reinhard 2008) (Table 1). The local ethics committee (Centre Leon Bérard, Lyon) approved this study, and subjects provided written, informed consent in conformity with the Declaration of Helsinki. The subjects were paid for their participation.

Stimuli
The auditory stimuli comprised spectrally rich tones (standard and deviant tones) with a main frequency of 800 Hz and 2 harmonic partial frequencies (1600 and 3200 Hz), which included the first name of the subject (novel 1) and an unfamiliar first name (novel 2). The first names were digitally recorded in a neutral masculine voice using Adobe Audition 1.5 (Adobe software). After recording, the maximum amplitudes of all stimuli were normalized. The mean duration of novel 1 (581 ± 86 ms) and novel 2 (598 ± 78 ms) were not significantly different (Eichenlaub et al. 2012).

Experimental Design
The 4 types of auditory stimuli were presented in accordance with the rules of a novelty oddball paradigm. Tones lasting 75 and 30 ms (including 5-ms rise/fall times) were used as standards (P = 0.82) and deviants (P = 0.14), respectively. Novel 1 and Novel 2 were presented with a probability of occurrence of 0.02 each. The stimuli were presented in a pseudorandomized order: 1) each deviant followed at least 2 standards and 2) each novel sound followed at least 10 standards and/or deviants. The stimulus onset asynchrony was set at 650 ms, except for the standard following a novel stimulus, which appeared at 1260 ms after the onset of the novel stimulus, regardless of the duration of the novel stimulus (Eichenlaub et al. 2012).

Procedure
The subjects arrived in the laboratory at 7.00 PM, after they had eaten. During approximately one and a half hours, electrodes were
EMG data were continuously recorded using a BrainAmp system scalp (the extended International 10–20 System). EEG, EOG, and EMG data were recorded from 21 Ag/AgCl electrodes placed on the scalp (Fig. 1).

The subjects reported their dreams "Do you have anything in mind?" and subsequently asked, "Did you dream that night?" or "Do you have anything in mind?". The subjects reported their dreams freely and answered a questionnaire concerning their dream content.

EEG Recording
EEG data were recorded from 21-Ag/AgCl electrodes placed on the scalp (the extended International 10–20 System). EEG, EOG, and EMG data were continuously recorded using a BrainAmp system (Brain Products GmbH, Germany) with an amplification gain of 12 500, a high-pass filter of 0.1 Hz, and a sampling rate of 1000 Hz.

### Table 1
Subject information

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Mean HR 4.42 22.7 473 11.50 PM 2.7 300 000
SEM HR 0.25 0.6 17 8 min 0.4 54 212
T-test *** ns ns ns *** ns ns
Mean LR 0.25 22.4 449 11.58 PM 2.6 270 000
SEM LR 0.02 0.9 11 11 min 0.5 49 497

Habitual DRF: habitual dream recall frequency (the number of awakenings per week with a dream in mind). Gender: subject’s gender (F, female; M, male). Age: subject’s age (years). Habitual sleep duration: habitual sleep duration during the week (min). Habitual sleep time: habitual sleep time from Monday to Friday. Occupation: occupation of the subject at the time of the experiment. Domain: domain of occupation or education. Education level: number of years of education. Size of place of residence: number of inhabitants in the subject’s city of residence. Age, habitual sleep duration and time, education level, and size of the place of residence were not significantly different between high- and low-recallers, however, the DRF was significantly larger in high-recallers than in low-recallers.

Sleep Stage Scoring
The sleep stages were visually scored offline according to standard criteria (Silber et al. 2007) and automatically scored using ASEEQA software (Berthomier et al. 2007) (http://aseegaonline.com/pub/index.html) to derive hypnograms based on 30-s epochs and to determine the vigilance state (wake, REM, N1, N2, or N3) occurring for every stimulus delivered during sleep. Only sleep periods for which the JBE and ASEEGA scores were consistent were considered for analysis. The percentage of consistency between the JBE and ASEEGA scoring was 82.9% with a kappa coefficient of 0.762 (epoch-by-epoch comparison; epochs scored as artifacts were excluded from the statistical analysis).

Event-Related Potentials Analysis
ERPs were analyzed using Elan Pack software (Agoura et al. 2011) (http://elan.lyon.inserm.fr) and Matlab (Mathworks). The ERPs were averaged over an epoch of 1300 ms, including a prestimulus period of 100 ms in each of the vigilance states. Trials were automatically excluded from averaging if the overall electrophysiological signal...
amplitude exceeded 150 µV during wakefulness, 125 µV in REM sleep, and 400 µV in N2 and N3. The baseline was corrected according to the mean value of the signal during the 100 ms prior to the stimulus onset. A 30-Hz low-pass digital filter was applied (bidirectional Butterworth, fourth order) to individual averaged responses.

The components elicited by novel sounds during wakefulness (N1, P3a, and the late positive parietal component, PP) were identified in the grand average of all subjects. The amplitudes and latencies were measured in individual tracings at electrodes showing the largest amplitude in the grand average of all subjects.

For group comparison, we made no assumption regarding the possible ERP correlates of the DRF. In each vigilance state, we performed sample-by-sample between-group tests at each electrode in the whole post-stimulus period (for ERPs to novels and for the difference between ERPs to deviants and ERPs to standards). A between-group difference was considered only if >15 consecutive samples (15 ms) were significantly different (Guthrie and Buchwald 1991; Rugg et al. 1995; Thorpe et al. 1996; Fort et al. 2002; Caclin et al. 2008; Eichenlaub et al. 2012). Scalp potential maps were generated using a spherical surface spline interpolation algorithm (Perrin et al. 1989).

**Statistical Analysis**

Between-group comparisons of the sleep characteristics were achieved using t-tests (level of significance, P < 0.05). Between-group comparisons of the evoked potentials were achieved using Kruskal-Wallis sample-by-sample tests (level of significance, P < 0.05). Correlations across groups between event-related responses and sleep characteristics were computed using a Spearman rank-order correlation test (level of significance, P < 0.05).

**Results**

**Behavioral Results**

Despite the uncomfortable nature of the experimental setup, sleep quality was generally preserved. For both groups, all sleep parameters evaluated were in the normal range (see Table 2 and Fig. 2). The sleep parameters did not differ between the 2 groups with the exception of the duration of intrasleep wakefulness (computed through the number of epochs scored as wakefulness during the sleep period; this measure did not include arousals or microarousals lasting <15 s). High-recallers demonstrated longer intrasleep wakefulness than Low-recallers (~15 min 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 (HR, 17.5 ± 8.7; LR, 12.1 ± 11.9; t-test, P = 0.14), but the mean duration of the awakenings was (HR, 1.90 ± 0.91 min; LR, 0.95 ± 0.40 min; t-test, P < 0.005).

The dream reports obtained immediately after awakening in the morning confirmed a large DRF difference between the 2 groups. Although the subjects were in most cases awakened during REM sleep, only 33% of Low-recallers reported a dream while 94% of High-recallers did (χ² = 14.6, df = 1, P < 0.001; see also Table 3) (Goodenough et al. 1959; Lewis et al. 1966).

**ERPs During Wakefulness**

The mean number (±standard deviation) of accepted novel sounds per subject during wakefulness was 73 ± 18 (61% of the presented trials ±15). Grand averaged responses to novels in HR and LR during wakefulness are displayed in Figure 3 and Supplementary Figure S3. As already detailed in a previous study (Eichenlaub et al. 2012), the typical response to novels includes an N1 component at ~150 ms immediately followed by a central component (novelty P3 or P3a) ~260 ms and at later latencies (~550 ms) a PP component. Mean amplitudes and latencies of these components in the 2 populations (HR and LR) are shown in Supplementary Table S1. The significant differences in ERPs between HR and LR are highlighted in Figure 4 and in Supplementary Figure S3. No difference was observed at the latency of the sensory N1 (Fig. 4) and N1s showed similar topographies in the 2 populations (Supplementary Fig. S1). Around the latency of...
the novelty P3, 
High-recallers showed significantly larger potentials than Low-recallers in a large right-central area (see sample-by-sample test at each electrode in Fig. 4 and topography at 235 ms in Fig. 3). At the latency of the PP, High-recallers showed significantly larger potentials than Low-recallers in a large centro-parieto-occipital area (see sample-by-sample test at each electrode in Fig. 4 and topography at 530 ms in Fig. 3). Finally, ~1000 ms, High-recallers responses were more positive than Low-recallers responses (see sample-by-sample test at each electrode in Fig. 4 and topography at 980 ms in Fig. 3).

Concerning the responses to simple tones, N1s to standards showed no difference between High-recallers and Low-recallers. In the specific ERP response to deviance, larger potentials were found in High-recallers than in Low-recallers in a central window around the latency of P3a (see topography of the difference between the 2 groups at 225 ms in Supplementary Fig. S2).

ERPs During Sleep

The mean number (±standard deviation) of accepted novel sounds per subjects was 92 ± 35 in REM (73% ±12 of the presented trials), 200 ±61 in N2 (95% ±7), and 137 ± 35 in N3 (96% ±4). Grand averaged responses in HR and LR during the 3 sleep stages are displayed, respectively, in Supplementary Figure S4 for REM sleep, in Supplementary Figure S5 for N2 and in Supplementary Figure S6 for N3. The significant differences in ERPs between HR and LR in all sleep stages can be seen in Figure 4.

During N2, the positive wave that was elicited in response to novel sounds at a latency of the P3a component (P3a-like) (Bastuji et al. 1995; Ruby et al. 2008) showed significantly larger amplitudes in HR than in LR at F3 (see significant sample-by-sample differences in Fig. 4 and the topography of the difference between the 2 groups at 290 ms in Fig. 3). During REM sleep, HR responses were larger than LR responses at electrodes F4 and C4 ~480 ms (see significant sample-by-sample differences in Fig. 4 and the topography of the difference at 480 ms in Fig. 3).

At later latencies, the novel sounds elicited large and slow negative waves in all sleep stages (see Fig. 3 and Supplementary Figs S4–6). In the latest part of these negative waves, the responses showed a wide window with potentials that were less negative (or more positive) in HR than in LR with different topographies depending on the sleep stage considered (frontal in N2 and N3 and occipital during REM sleep, see significant sample-by-sample differences in Fig. 4 and the topography of the difference at 480 ms in Fig. 3).

During REM and N3, the specific ERP response to deviance showed potentials significantly more positive for HR than for LR, namely, around the P3a at CP1, CP2, P3, and Pz in REM sleep (see the topography of the difference between the 2 groups at 285 ms in Supplementary Fig. S2), and ~320 ms at Fz in N3 (see Supplementary Fig. S2).

The Brain-Orienting Response and Intrasleep Wakefulness

The amplitude of the P3a during wakefulness (the mean amplitude in the 240–290-ms time window averaged over Fz, FC1, FC2, and Cz) was positively correlated with the percentage of intrasleep wakefulness, independent of the scorer.
Subjects with High and Low DRF · Eichenlaub et al.

(A Spearman rank-order correlations: JBE, $r = 0.41, P < 0.05$; ASEEGA, $r = 0.36, P < 0.05$; Fig. 5), and also with the number of awakenings during sleep calculated for scorer JBE ($P < 0.1, r = 0.31, P = 0.059$). No significant correlation was observed between the amplitude of P3a-like responses in N2 and the total amount of intrasleep wakefulness or the amount of intra-N2 wakefulness.

The mean delay between the onset of a page scored as awakening and the previous novel stimulus was shorter in HR than in LR (HR, $9.4 \pm 3.0$ s; LR, $13.3 \pm 3.8$ s; Mann–Whitney $U$-test, $P = 0.054$), suggesting that novel sounds elicited more easily/rapidly awakenings in HR than in LR.

**Discussion**

In the present study, we tested whether differences in sleep and/or neurophysiological characteristics could be observed between subjects with high and low DRF. We acquired polysomnographic data and investigated the ERPs that arise in response to auditory stimuli (first names presented randomly and rarely among pure tones) in 18 High-recallers and 18 Low-recallers during wakefulness and sleep.

### Intrasleep Wakefulness in High-Recallers and Low-Recallers

No sleep differences were observed between HR and LR, except for intrasleep wakefulness. HR showed double the amount of intrasleep wakefulness compared with LR, although values remained in the normal range in both groups. This is the first study to provide an objective measurement of intra-sleep wakefulness associated with DRF in healthy subjects.

As a consequence, our results provide a strong experimental argument in favor of the arousal-retrieval model.

### Brain Reactivity in High-Recallers and Low-Recallers

The absence of between-group differences in N1s either to standard tones or to standard tones or to standard tones or to standard tones in 18 High-recallers and 18 Low-recallers during wakefulness and sleep.

---

**Table 3**

Awakening and dream characteristics on the morning of the experiment

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Stage before awakening: the sleep stage from which the subject awakened. Vigilance state end: the subject’s state of vigilance when the experimenter entered the bedroom. Wake length before end: time elapsed between awakening and the experimenter’s entrance into the bedroom (min). REM length before awakening: time elapsed in REM sleep before experimental awakening (min). Dream: the response to the question “Did you have a dream during the night?” Type: the type of content of the dream report (story, thoughts, or sensation). Clarity: the clarity of the dream content (1, very blurred; 4, very clear). Emotional intensity: the intensity of the emotions experienced in the dream (1, not very intense; 4, very intense; Ø, no answer). Emotional valence: the valence of emotions experienced in the dream (+, positive; –, neutral; –, negative; Ø, no answer). The duration of the last REM period and the clarity and emotional intensity of the dream content did not differ between the 2 groups ($t$-test, $P < 0.05$), ns, not significant; W, wakefulness; N1, N2, and N3: sleep stages N1, N2, and N3, respectively; REM, REM sleep. The mean and standard error of the mean (SEM) are presented for High- and Low-recallers (last lines). Note that 7 of the 38 subjects were awakened in sleep stage N2 or N3 because these subjects did not experience a REM sleep episode between 7 and 8 AM.
Figure 3. Brain responses to novel sounds in the different vigilance states for High-recallers (HR) and Low-recallers (LR). Upper panel: ERPs at electrodes Fz, Cz, Pz, and O1 in response to novel sounds averaged over 18 HR (red) and 18 LR (black) during wakefulness, REM sleep, N2 and N3. The difference curves between the responses of HR and LR are also presented (blue). The blue horizontal bars highlight significant between-group differences (sample-by-sample Kruskal-Wallis test, \( P < 0.05 \) for >15 ms). Lower panel: Scalp potential maps showing significant between-group differences during wakefulness, REM sleep, N2 and N3. Maps for High-recallers (first row), Low-recallers (second row), and the difference between the 2 groups (third row) are presented. PP, positive parietal component.

Figure 4. Statistical significance of sample-by-sample Kruskal–Wallis between-group test (\( P < 0.05 \)) performed at 15 electrodes in the poststimulus period (High-recallers vs. Low-recallers) during wakefulness (black), N2 (light gray), N3 (medium gray), and REM sleep (gray stripes).
During REM sleep. According to our results, this may also be the case

induce cognitive processing that are more complex in HR
suggested randomly to nonattentive subjects during wakefulness

interpretations, our results could indicate that

et al. 2009; Eichenlaub et al. 2012). According to these

al processing (Curran 2004; Holeckova et al. 2006; Kissler

components, such as familiarity, episodic memory, and emotion-

ness, have previously been associated with complex cognitive

processes, such as the component observed during wakeful-

During wakefulness, the unexpected first names and the
deviant stimuli elicited a P3a component ~260 ms, and the
amplitude was greater in HR than in LR. During sleep, a
P3a-like component (Bastuji et al. 1995; Ruby et al. 2008) eli-
cited by novel sounds in N2 and by deviant tones in REM
sleep was larger in HR than in LR. Attention directed to
sounds is a factor known to enhance the P3a component
(Polich 2007), and it is considered that the larger the P3a the
stronger the orientation of attention (Escera et al. 2003;
Dominguez-Borras et al. 2008; Lv et al. 2010). According to
this hypothesis, the results we obtained during wakefulness
suggest that the unexpected stimuli oriented the attention
more strongly in HR than in LR, as if HR were more reactive
to the external world than LR. During sleep, taken together,
our results suggest that the brains of HR were more reactive
to external stimuli than those of LR, as during wakefulness.

At later latencies during wakefulness, the novel sounds
elicited a larger parietal component in HR than in LR. Interest-
ingly, during REM sleep novel sounds also elicited larger
positive potentials in HR than in LR ~500 ms. Similar PP com-
ponents, such as the component observed during wakeful-
ness, have previously been associated with complex cognitive
processes, such as familiarity, episodic memory, and emotion-
al processing (Curran 2004; Holeckova et al. 2006; Kissler
et al. 2009; Eichenlaub et al. 2012). According to these
interpretations, our results could indicate that first names pre-
sented randomly to nonattentive subjects during wakefulness
induce cognitive processing that are more complex in HR
than in LR. According to our results, this may also be the case
during REM sleep.

Finally, at the latest latencies (~1000 ms), novel sounds elic-
cited a more positive response in HR than in LR in all vigil-
ance state. These group differences showed a frontal
topography during wakefulness, N2 and N3, and an occipital
topography in REM sleep. As a whole, our results suggest
that, during sleep, HR and LR show different cognitive proces-
sing in response to auditory stimuli.

Thus, our results show that randomly presented sounds
elicit different brain responses in High- and Low-recallers
during both wakefulness and sleep. These results suggest that
the cerebral functional organization of High-recallers is intrin-
siclinaly different from that of Low-recallers, which might facili-
tate either the production or encoding of a dream. Interestingly, at the psychological level, High-recallers and
Low-recallers also differ in cognitive abilities and personality
traits (Schredl et al. 2003). Such differences could represent
psychological correlates of the differences in the global cer-
bral functional organization observed in our study between
the 2 groups. Future studies are required to address this issue.

**Brain Reactivity and Dream Recall**

As hypothesized, we found that the differences in intrasleep
wakefulness between HR and LR were associated with neuro-
physiological differences between the 2 groups. Further
studies are required to obtain an improved understanding of
the mechanism linking increased brain reactivity with in-
creased intrasleep wakefulness and increased DRF. Neverthe-
less, consider the following potential hypotheses to explain
these results:

One possible interpretation is that large neurophysiological
responses that occur in HR during both sleep and wakeful-
ness reflect high brain reactivity, which would facilitate
awakening during sleep. Consistent with this hypothesis,
Bastuji et al. (2008) showed that during sleep (N2 and
REM), an increased amplitude of the P3-like wave that was
recorded in response to painful stimulation was strongly
associated with subsequent arousal and awakening reac-
tions. The authors concluded that laser-evoked responses

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**Figure 5.** Scatter plots (dots) and best linear fits (black line) of the data illustrating the percentage of wakefulness during the sleep session (scored by JBE on the left and the ASEEGA software on the right) versus the amplitude of the P3a component in response to novel sounds during wakefulness (the mean amplitude in the 240–790-ms time window averaged over Fz, FC1, FC2, and Cz). The P3a amplitude during wakefulness was positively correlated with the percentage of intrasleep wakefulness (Spearman’s rank-order correlations: JBE, $r = 0.41, P < 0.05$; ASEEGA, $r = 0.36, P < 0.05$). Gray circles, High-recallers; black diamonds, Low-recallers.
to painful stimulation during sleep predict subsequent arousal. We did not observe a significant correlation between the mean amplitude of the P3a-like response in N2 and the percentage of total (or N2-related) intrasleep wakefulness (this negative result may be explained by a poor signal-to-noise ratio during sleep), but we did observe a significant correlation between the amplitude of P3a during wakefulness and the percentage of total intrasleep wakefulness. In addition, we observed that the delay between the pages scored as intrasleep wakefulness and the last preceding novel sound was shorter in HR than in LR. Importantly, this delay was <15 s in both groups. Indeed, an awakening is considered stimulus-related if it occurs within 15 s after stimulus onset (Bastuji et al. 2008; Arzi et al. 2012). This result suggests that novel sounds (which elicit greater responses in HR than in LR) are more arousing in HR than in LR. Taken together, our results suggest the possibility of a causal link between the amplitude of the ERPs to auditory stimuli during sleep and intrasleep awakenings. In this case, the higher brain reactivity in HR during both wakefulness and sleep would contribute to their higher frequency of dream report, by increasing intrasleep wakefulness (which would in turn facilitate the encoding of dreams in memory according to the arousal-retrieval model). According to this interpretation, our results extend the arousal-retrieval model proposing an explanation for the difference in intrasleep wakefulness between High- and Low-recallers through differences in brain reactivity.

Another possible interpretation derives from Freud’s hypothesis suggesting that “dreams are the guardian of sleep” (Freud 1899). Freud postulated that dreaming tends to prevent the sleeper from awakening, notably incorporating external and arousing stimuli into the dream. According to this hypothesis, a possible interpretation of our results is that the sleep of HR would be disrupted by internal causes, inducing long intrasleep awakenings possibly due to high brain reactivity. Such disruptions would trigger an increase of dreaming in an attempt to protect sleep.

Conclusion

We demonstrated that late (later than 200-ms poststimulus) brain responses to unexpected auditory stimuli dramatically differ between subjects with high versus low dream report frequencies, not only during all sleep stages (N2, N3, and REM sleep), but also during wakefulness. These results open a new realm for scientific investigation of dreaming suggesting that the ability to recall dreams is associated with a particular and global functional organization of the brain that is not related to one specific vigilance state. Further investigations of High-recallers and Low-recallers during wakefulness and sleep are thus promising and should provide new insights into brain mechanisms and functions of dreaming.

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Notes

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Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/


