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ORIGINAL ARTICLE

Brain functional connectivity upon awakening from sleep predicts interindividual differences in dream recall frequency

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Abstract

Why do some individuals recall dreams every day while others hardly ever recall one? We hypothesized that sleep inertia—the transient period following awakening associated with brain and cognitive alterations—could be a key mechanism to explain interindividual differences in dream recall at awakening. To test this hypothesis, we measured the brain functional connectivity (combined electroencephalography–functional magnetic resonance imaging) and cognition (memory and mental calculation) of high dream recallers (HR, $n = 20$) and low dream recallers (LR, $n = 18$) in the minutes following awakening from an early-afternoon nap. Resting-state scans were acquired just after or before a 2 min mental calculation task, before the nap, 5 min after awakening from the nap, and 25 min after awakening. A comic was presented to the participants before the nap with no explicit instructions to memorize it. Dream(s) and comic recall were collected after the first post-awakening scan. As expected, between-group contrasts of the functional connectivity at 5 min post-awakening revealed a pattern of enhanced connectivity in HR within the default mode network (DMN) and between regions of the DMN and regions involved in memory processes. At the behavioral level, a between-group difference was observed in dream recall, but not comic recall. Our results provide the first evidence that brain functional connectivity right after awakening is associated with interindividual trait differences in dream recall and suggest that the brain connectivity of HR at awakening facilitates the maintenance of the short-term memory of the dream during the sleep–wake transition.

Statement of Significance

Why do some individuals recall their dreams every day while others hardly ever recall one? In this article, we present evidence that the answer to this question lies in part in the functional state of the brain immediately upon awakening from sleep. Using a combined electroencephalography–functional magnetic resonance imaging design, we compared the brain functional connectivity of individuals with a high and low dream recall frequency (HR and LR, respectively) before and after awakening from an early afternoon nap. Our results show a pattern of enhanced connectivity in HR within the default mode network (DMN) and between the DMN and regions associated with memory processes, therefore suggesting that trait differences in dream recall are associated with a specific brain functioning during the sleep–wake transition.

Key words: dream recall; dreaming; sleep inertia; awakening; EEG–fMRI; functional connectivity; default mode network

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Introduction

Dreaming is a universal and still intriguing experience that one may (or may not) recall upon awakening from sleep. Several aspects of dreaming are still poorly understood, one of which is the interindividual differences in dream recall frequency (DRF), that is, why some individuals recall dreams every morning while some hardly ever recall one.

Previous research identified several state and trait factors that participate in intra- and interindividual variability in dream recall, respectively [1, 2]. The main state factors identified are the sleep stage and the amount of sleep preceding awakening [3], circadian and ultradian rhythms [4], psychotropic drug intake [5], and the method of awakening [6]. Regarding trait factors, some personality dimensions such as creativity and openness to experience as well as anxiety and interest in dreams have been consistently correlated with interindividual variability in DRF [7]. Intra-sleep awakening—which is both a state and a trait factor—was also hypothesized to promote dream recall [7, 8], a hypothesis that was recently confirmed using objective sleep measurements. In two studies [9, 10], we used full-night polysomnography to compare the sleep architecture and microstructure of high dream recallers (HR, ≥ 5 dream recalls per week) and low dream recallers (LR, ≤ 2 dream recalls per month). Results showed more intra-sleep wakefulness in HR than in LR (with no differences in other sleep parameters), which is coherent with the idea that periods of wakefulness during sleep are necessary to encode dream content into long-term memory [8].

Remarkably, LR still recall significantly fewer dreams than HR regardless of the sleep stage in which they are awakened, even when the number of awakenings is increased and experimentally controlled during a night in the lab [9, 11–13], showing that state factors cannot completely compensate for trait factors.

We propose here that the functional state of the brain in the first minutes after awakening from sleep could explain, at least in part, the trait variability in DRF. The wake period immediately following awakening from sleep is indeed marked by sleep inertia, a transient state of impaired vigilance and cognition that usually dissipates within the first 30 min after awakening [14–16]. Because sleep inertia can largely vary both within and between individuals, it represents a good candidate to explain both state and trait variability in dream recall [7, 17, 18]. Previous observations argue in favor of this hypothesis. For instance, Morel and colleagues [18] reported that “the findings do not support the hypothesis linking increased recall ability to increases in cortical activation prior to awakening. However, the recall groups depicted a different pattern of arousal in their transition from sleep to wakefulness.” Similarly, Rochlen et al. [19] noted that “healthy controls showed a large shift in delta amplitude in the sleep–wake transition during successful recall but not during recall failure.”

According to this hypothesis, one could expect that LR would show more sleep inertia (as measured by cognitive and brain functional connectivity disturbances [16]) after awakening than HR. This hypothesis is supported by previous results showing trait brain differences between HR and LR during both wakefulness and sleep, either while performing a task, or at rest (task: auditory oddball during wake and sleep, method: electroencephalography (EEG) [9]; task: rest during wake and sleep, method: positron emission tomography [PET] [13]). Noteworthy, we found that HR have an increased regional cerebral blood flow in the

medial prefrontal cortex (MPFC) and temporoparietal junction (TPJ) at rest (during wake and sleep), as well as an increased white matter density in the MPFC [20]. The MPFC and TPJ are known to be involved in dream production and/or recall. Indeed, lesions of one or both regions induce cessation of dream reports [21, 22], and therefore, the proper functioning of these regions upon awakening could mediate the retrieval of dream content upon awakening. Specifically, the proper functional connectivity of the network that encompasses these two regions, the so-called default mode network (DMN), could be a necessary condition for successful dream recall upon awakening. Indeed, the DMN is a set of functionally coupled brain areas [23, 24] involved in mind-wandering and episodic memory retrieval [25], and several authors have postulated that the DMN might be the neural correlate of dreaming [26, 27]. Coherent with this, it is noteworthy that the DMN is typically hyperconnected during rapid eye movement (REM) sleep, the sleep stage associated with the highest rate of successful dream recall, and hypoconnected during N3 sleep, the sleep stage associated with the lowest rate of successful dream recall [28–31]. However, it is still unknown if the DMN is implicated in the production of dream experience while asleep, the recall of dream content while awake, or both.

The present study aimed therefore at comparing the brain and cognitive functioning of HR and LR during the sleep inertia period following awakening from sleep. This has surprisingly never been experimentally tested before, despite several studies mentioning the brain and cognitive functioning during sleep inertia as a potential explaining factor of DRF variability [7, 32]. We designed a functional magnetic resonance imaging (fMRI) study to compare the brain functional connectivity of HR and LR in the minutes following awakening from a 45 min early afternoon nap. Resting-state scans were acquired before the nap, 5 min and 25 min after awakening to investigate the dynamics of brain functional reorganization during the first half hour following awakening, and each scan was associated with a mental calculation task to measure the cognitive impairment associated with sleep inertia. We predicted that HR would show (1) more dream recall following awakening from sleep, (2) higher functional connectivity within the DMN and between the DMN and regions involved in memory retrieval, and (3) less cognitive performance impairments, suggesting a faster recovery of normal cognitive functioning upon awakening.

Methods

This study is a reanalysis of previously published data [16] to specifically investigate group differences between HR and LR participants.

Participants

Behavioral and neurophysiological data were acquired from 55 healthy participants (28 males, mean \pm SD age = 22.55 \pm 2.41 years, range = 19–29 years) having normal sleep characteristics and BMI (habitual sleep time per night, 7.7 \pm 0.9 h; BMI, 22.1 \pm 2.6 kg/m²). The subjects were informed of the study through an announcement sent to the mailing list of Lyon University, which briefly described the study and included a link to a questionnaire concerning sleep and dream habits [33]. Subjects were selected if they reported and subsequently confirmed during a

phone interview: (1) having a high or low DRF, that is, a DRF superior to 5 dream recalls per week for HR and inferior to 2 dream recalls per month for LR, as well as having (2) a regular sleep-wake schedule, no difficulty to fall asleep, being occasional or frequent nappers and having preferentially already done an MRI brain scan in the past few years (we assumed that participants who are already familiar to the MR environment might be less anxious and therefore more prone to fall asleep).

Among the 55 participants, 28 of them were HR (mean DRF = 6.6 ± 0.7 dream reports per week) and 27 were LR (mean DRF = 0.2 ± 0.1 dream report per week). Apart from the DRF ($p < 0.001$), the two groups did not differ in other assessed parameters, including age, BMI, habitual sleep duration, or education level (all p 's ≥ 0.25). They had no history of neurological and psychiatric disorders and had no sleep disturbances. They provided written informed consent according to the Declaration of Helsinki and received monetary compensation for their participation. The study was approved by the local ethics committee (CCPPRB, Centre Leon Berard, Lyon, France).

Procedure

The paradigm and procedure are presented in Figure 1.

Evening and night

To facilitate sleep in the MRI environment and maximize sleep inertia upon awakening from the nap, participants underwent a partial sleep deprivation on the night before the experiment (3 h of sleep allowed). They arrived in the sleep unit of the hospital Le Vinatier (Lyon, France) at 8:00 pm. From 8:00 pm to 10:00 pm, they underwent several personality and cognitive tests administered by RV (results will be presented elsewhere). They were then instructed to stay awake until 5:00 am (the possible activities were reading, making puzzles, and watching movies), at which point they could sleep for 3 h until 8:00 am in a bed in the sleep unit. Energy drinks or physical activity were prohibited during the partial sleep deprivation, and nurses regularly checked that the subject did not fall asleep. Activity was monitored via wrist actigraphy (Actigraph, Pensacola, USA) during the whole night. At 8:00 am, participants were awakened by the experimenter, and immediately asked to report their dreams, if any. They were then offered breakfast and a shower and occupied themselves

(reading or internet) under the experimenters' supervision until the MRI session.

Day

After lunch at 11:30 am, participants were conducted to the neuroimaging center (CERMEP). During the first half hour, experimenters installed on the participant's head an MRI compatible EEG cap (EASYCAP). Participants were then installed in the MRI scanner at about 1:20 pm ($1:17 \text{ pm} \pm 13 \text{ min}$). They read a 5 min comic strip during the calibration of the eye-tracking camera. The subjects were led to believe that the only purpose of the comic strip was to calibrate the eye-tracking system, and therefore were not given any explicit instructions to memorize it. Next, they performed the descending subtraction task (DST) for 2 min and the first resting-state scan was subsequently acquired, with the instructions to remain awake and look at a central fixation cross on the screen. At the end of the scan, participants were informed that they could close their eyes and sleep (at $1:39 \text{ pm} \pm 14 \text{ min}$ on average) during the next 45 min. At the end of the nap slot, participants were awakened, if they were sleeping, by calling their first name and the second resting-state scan was acquired as close to the awakening as possible. At the end of the scan, the second DST was performed. During the following 10 min, subjects were asked to recall the dream(s) they had during the nap if any, to comment on the quality of their sleep in the scanner and to recall the comic that they had read during the calibration of the eye-tracking camera. The third resting-state scan and DST were finally performed about 25 min after awakening, and were immediately followed by an 8-min T1 anatomical scan.

Behavioral tests

In the evening at the sleep unit, participants trained on the DST (six blocks of 2 min each), which was used to evaluate cognitive performances during the MRI session on the following day, to avoid a practice effect over the first trials [34]. The DST has been previously used to evidence performance deficit and normalization in the first 30 min post awakening [34–36]. Subjects were presented with a three-digit number. They were instructed to subtract 9, saying the operation and the result aloud, and then continue by subtracting 8 from the remainder, then 7, and so on

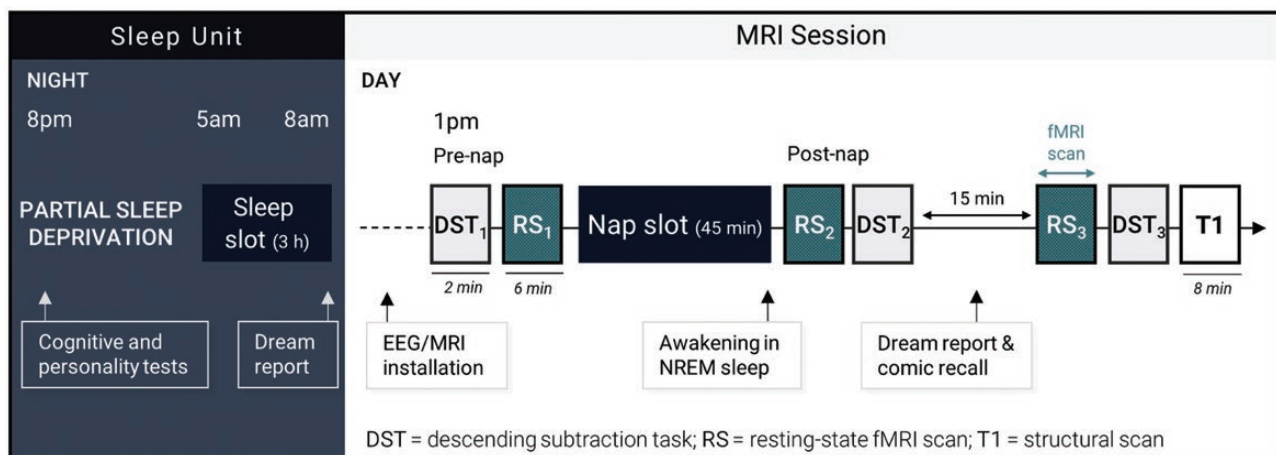


Figure 1. Experimental design.

until they had to subtract 1. At this point, they were to start the cycle of descending subtractions again. Participants were asked to do the task for two minutes and were instructed to be as fast and accurate as possible.

In the scanner, between the second and the third scan, participants were asked to recall and describe any dream(s) they had while napping. Second, they were asked about their sleep in the scanner. Third, they were asked to recall the comic strip that they read just before the nap slot. They were first told to recall the story freely and then answered pre-determined questions about the content of the story.

Data collection

EEG and eye movement recordings

Polysomnography data were recorded using a 15 channels MR-compatible cap (EasyCap, Brain Products GmbH, Gilching, Germany) designed for sleep studies, with a layout designed according to the American Academy of Sleep Medicine Guidelines 2007. It comprised nine EEG electrodes placed according to the international standard 10/20 system (O1, O2, C3, C4, F3, F4, M1, M2, Cz, FCz was used as reference and AFz as ground), two EOG electrodes, three EMG electrodes, and an electrocardiogram electrode placed on the back of the participant. The sampling rate was 5,000 Hz and an analog band-pass filter (0.016–250 Hz) was applied before data digitalization to prevent saturation and reduce the gradient artifact amplitude [37]. The EEG was synchronized with the MR scanner's clock using BrainProducts' SyncBox. A real-time pulse-artifact correction was performed using the BrainVision Recorder (Version 1.2) and BrainVision RecView (Version 1.4) software (Brain Products) to allow for on-line sleep scoring during the fMRI session.

To ensure that the participants were not closing their eyes during the resting state scans, eye movements were monitored during the experiment using an EyeLink 1000 fMRI eye-tracking system (SR Research Ontario, Canada). The position of eyes was calibrated at the beginning of the experiment and monitored throughout the whole MRI session.

MRI acquisition

MRI scans were obtained from a MAGNETOM Prisma 3.0 T scanner (Siemens Healthcare, Erlangen, Germany) at the Primage neuroimaging platform (CERMEP). Structural MRI was acquired with a T1-weighted (0.9-mm isotropic resolution) MPRAGE sequence and functional MRI data with a T2*-weighted 2D gradient echo-planar imaging sequence with 180 volumes (TR/TE: 2,000/25 ms; flip angle: 80°; voxel size: 2.68 × 2.68 × 3 mm; slices: 40, duration: 6 min). Functional and anatomical scans were performed using a 20-channel head coil. The coil was foam-padded to improve subject comfort and restrict head motion.

Data analysis

Electroencephalography

Artifacts related to gradient switching and cardiac pulse (cardio-ballistic artifact) were removed using standard routines available in BrainVision Analyzer version 2.0 software (Brain Products). Polysomnographic data were downsampled to 500 Hz and band-pass filtered between 0.1 and 40 Hz. Offline sleep stage scoring was done in epochs of 30 s following standard AASM rules [38, 39] by the first author (R.V.) using the SLEEP software [40].

Functional magnetic resonance imaging

Preprocessing and quality check were performed using a standard routine in SPM12 software (Wellcome Department of Imaging Neuroscience) and the CONN toolbox, version 17f (<http://www.conn-toolbox.org>) [41]. Preprocessing included functional realignment, slice-time correction, coregistration to structural scan, spatial normalization, and spatial smoothing using a 6 mm full-width at half-maximum isotropic Gaussian kernel filter. No field map correction was applied. Individual T1 images were segmented into gray matter, white matter, and cerebrospinal fluid tissue maps. Functional and structural images were then normalized to MNI152 space (Montreal Neurological Institute). Functional images underwent artifact and motion regression in the Artifact Detection Toolbox (https://www.nitrc.org/projects/artifact_detect/) using the following criteria to define outliers: global signal intensity changes greater than 9 standard deviations and movement exceeding 2 mm. SPM motions parameters and outliers were subsequently included as covariates in connectivity analyses.

Connectivity analyses were performed using the CONN toolbox version 17f. First, we performed a denoising step including a regression of the six motion correction parameters and their corresponding first-order temporal derivatives, as well as a component-based strategy (aCompCor [42]) to identify and remove physiological confounds that are unlikely to be related to neural activity. The resulting BOLD time series were band-pass filtered (0.008–0.09 Hz) to further reduce noise and increase sensitivity [43].

Having done so, we performed seed-based analyses on the core regions of the DMN. As per our hypotheses, we focused on the default mode since it has been suggested to be involved in dream recall and/or production [13, 20–22]. Specifically, we used the MPFC (center of mass in MNI coordinates = 1, 55, –3, 1,346 voxels in 2 mm space), the posterior cingulate cortex (PCC, 1, –61, 38, 4,833 voxels) and the lateral parietal cortices (LP, right = 47, –67, 29, 1,326 voxels; left = –39, –77, 33, 1,041 voxels). Since the LPs are bilateral, functional connectivity contrasts were estimated using the main effect of both hemispheres. These anatomical regions of interest are included in the CONN toolbox default atlas and were extracted using an ICA approach on 497 subjects from the Human Connectome Project.

Statistics

For the DST, between-group comparisons were achieved using a two-way mixed ANOVA with a group factor (between-subject factor with two levels: HR and LR) and a time factor (within-subject factor with three levels: Pre-sleep, 5 min p-a, 25 min p-a). Post hoc two-sided t-tests were used in case of significance. All statistical tests were performed using the Pingouin package [44] for Python (<https://pingouin-stats.org/>). Seed-based functional connectivity analyses were performed using a cluster-defining voxel-wise height threshold of $p < 0.01$ (uncorrected, two-sided) and a whole-brain family-wise error (FWE) corrected extent threshold of $p < 0.05$.

Results

Sleep parameters

As expected and due to the inherent discomfort of the MRI environment, several participants were not able to reach and maintain N2 and N3 sleep during the 45 min nap slot. Note that here we

used a more liberal threshold than in our previous article [16] to determine whether to include or not a participant in further analysis. This decision was mainly motivated by considerations of statistical power and sample size in our HR versus LR comparison. Specifically, in our previous article, inclusion of the participants in either one of the N2 or N3 groups was based on the two following rules: (1) presence of N2/3 sleep during the nap, (2) awakening in N2/3 sleep. In the current article, inclusion of the participants in subsequent analyses was based on the three following rules: (1) presence of N2/3 sleep during the nap, (2) awakening in N1, N2, or N3 sleep, (3) more than 80% of epochs in the 10 min prior to awakening by experimenter are scored as sleep (N1 included).

One subject out of the 39 remaining was discarded because of a technical failure during data acquisition, leading thus to a total of 38 participants included in the final analysis (20 HR and 18 LR). The two groups differed in DRF (HR = 6.5 ± 0.7 dream reports per week, LR = 0 ± 0 dream report per week, $p < 0.001$), but did not differ for all the other variables including age (HR = 22.5 ± 2.5 years, LR = 22.7 ± 2.4 years, $p = 0.86$), BMI (HR = 22.9 ± 2.6 kg/m², LR = 21.8 ± 2.2 kg/m², $p = 0.15$), education (HR = 3.8 ± 2.5 years of higher education, LR = 3.6 ± 1.3 years of higher education, $p = 0.83$), habitual sleep duration (HR = 7.7 ± 0.9 h, LR = 7.6 ± 1.0 h, $p = 0.73$), and sex ratio (HR = 0.81, LR = 1, $p = 0.99$). Means of the main sleep parameters during the nap in the two groups are presented in Table 1. Importantly, there was no significant group difference for any of the sleep parameters considered or in the latency between the awakening and the two post-awakening resting-state scans.

Behavioral results

Descending subtraction task

DST performances are reported in Figure 2. A two-way ANOVA revealed a significant effect of time in the number of responses

($F(2, 72) = 6.04$, $p = 0.004$) and percentage of correct responses ($F(2, 72) = 4.29$, $p = 0.017$). Specifically, the total number of responses and the percentage of correct responses were reduced at 5 min p-a compared to pre-nap and 25 min p-a (all p 's < 0.05). There was no main effect of time in the percentage of mistakes, a finding in line with the generally held view that speed is more impaired than accuracy during sleep inertia [15]. Contrary to our hypothesis, there was no significant main effect of group or interaction between group and time for the DST performance.

Dream recall

After awakening from the partial sleep deprivation in the sleep unit, significantly more HR reported dreams than did LR (65% of HR and 22% of LR reported a full or a white [contentless] dream; $X^2 = 7.0$, $p = 0.008$). A similar effect was observed after awakening from the 45 min nap inside the MRI (75% of HR vs. 33% of LR, $X^2 = 6.7$, $p = 0.010$; see Table 2). The between-group difference in dream recall after the nap was significant for participants that were awakened in N2 sleep (75% of HR and 17% of LR, $X^2 = 4.6$, $p = 0.03$), but not for participants that were awakened in N3 sleep (Table 2). Lastly, when combining participants from both groups, we did not find a significant between-stage difference in dream recall after awakening from the nap. That is, dream recall was not significantly different after awakening from N2 or N3 sleep ($X^2 = 0.08$, $p = 0.78$).

Memory recall

For the recall of the comic, no significant group difference was found in the final memory score to the questionnaire about the story content (on a scale from 0 to 10: HR = 5.6 ± 2.0 ; LR = 4.7 ± 2.7 ; $p = 0.26$). However, there was a tendency for a significantly higher number of words during free recall in HR than LR (HR = 223.8 ± 113 words; LR = 156.1 ± 98 words; $p = 0.056$).

Functional connectivity

We found significant interaction effects between group and time for all three seeds, which are reported in Supplementary Table S1. Planned contrasts evaluating group differences at each of the three resting-state scans are presented in Table 3 and Figure 3, and summarized in the paragraph below. Importantly, there was no group difference in motion parameters at any of the three resting-state scans, as indexed by the framewise displacement [45] and the number of scans that were defined as outliers by the Artifact Detection Toolbox (all p 's > 0.4).

First, we did not find any significant group differences in the functional connectivity of any of the three seeds during the pre-nap resting-state scan. In other words, the two groups did not differ in the DMN functional connectivity before the nap. Similarly, there were almost no group differences during the 25-min post-awakening resting-state scan, except increased connectivity between the MPFC and the putamen in HR. The larger group effect was observed at 5 min post-awakening. The functional connectivity of MPFC, PCC, and LP was increased in HR as compared to LR, specifically between the MPFC and the precuneus, the PCC and the right PFC, the PCC and the superior frontal gyrus (SFG), the LP and the SFG, and the LP and the right angular gyrus (AG).

Table 1. Mean sleep parameters of the HR ($n = 20$) and LR ($n = 18$) groups

Sleep parameters	HR	LR	P-value
TST (min)	36.4 ± 7.5	38.1 ± 4.6	0.42
SE (%)	87.7 ± 7.8	87.3 ± 7.7	0.89
Wake (min)	8.4 ± 3.3	9.8 ± 4.2	0.32
N1 (min)	13 ± 7.9	10.3 ± 6.4	0.28
N2 (min)	17.2 ± 5.3	20.4 ± 6.4	0.11
N3 (min)	6.6 ± 6.3	7.7 ± 5.7	0.59
REM (min)	0 ± 0	0 ± 0	–
Longest N2 (min)	12.1 ± 5.1	13.6 ± 4.4	0.34
Longest N3 (min)	6.2 ± 6.1	7.3 ± 5.3	0.57
Stage prior to awakening	2.3 ± 0.7	2.6 ± 0.6	0.25
LAS1 (min)	3.4 ± 1	5.2 ± 4.1	0.10
LAS2 (min)	24.4 ± 4.1	24 ± 3.8	0.73

TST, total sleep time; SE, sleep efficiency in percentage; Wake (W), N1, N2, and N3, total duration of each sleep stage in minutes. Stage of awakening, sleep stage prior to awakening, where Wake was encoded as 0, N1 as 1, N2 as 2, and N3 as 3. Therefore, higher value represents higher sleep depth prior to awakening. Longest N2, longest period of uninterrupted N2 sleep, in minutes. Longest N3, longest period of uninterrupted N3-sleep, in minutes. LAS1, latency between the awakening and the start of the first post-awakening resting-state scan, in minutes. LAS2, latency between the awakening and the start of the second post-awakening resting-state scan, in minutes. p -Values were obtained using two-sided independent t -tests.

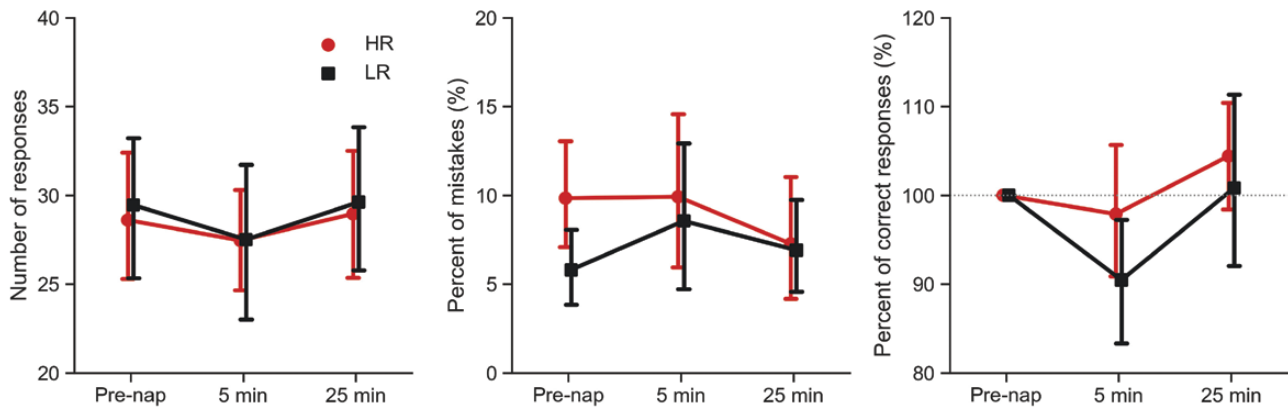


Figure 2. Group performances at the DST. Red lines, HR ($n = 20$), black lines, LR ($n = 18$). Left, total number of responses (index of speed). Middle, percentage of mistakes (marker of accuracy). Right, percentage of correct responses relative to pre-nap performances (marker of both speed and accuracy). Error bars represent the 95% confidence intervals. A significant main effect of time was found for the number of responses and the percentage of correct responses, but no significant group differences or interactions between group and time were observed for any of the three outcomes.

Table 2. Dream recall after the nap in the MR scanner

Stage prior to awakening	HR	LR	All	P-value
N1 sleep	3/3 (100%)	0/1 (0%)	3/4 (75%)	–
N2 sleep	6/8 (75%)	1/6 (17%)	7/14 (50%)	0.031
N3 sleep	6/9 (67%)	5/11 (45%)	11/20 (55%)	0.343
All	15/20 (75%)	6/18 (33%)	21/38 (55%)	0.010

Count and percentage of successful dream recall in HR and LR after awakening from the nap in the MR scanner, stratified by the sleep stage prior to awakening. p -values were calculated using a Pearson chi-squared test, with the exception of N1 sleep for which the observed frequencies were too small (< 5) to estimate reliable p -values.

Discussion

This study is the first one to compare the brain functional connectivity and cognitive performance of high and LR in the minutes following awakening from sleep, in an effort to understand the basis for interindividual differences in dream recall.

In line with our predictions, we have found a group difference in dream recall after awakening from the nap between the two groups despite no significant difference in the recall of a comic strip that was presented to the participants just before the nap. The group difference in dream recall was stage-specific, such that significantly more HR than LR recalled a dream after being awakened from N2 sleep, but not from N3 sleep. Second, contrary to our hypothesis, we did not find a significant group difference in the behavioral impairment caused by sleep inertia (as measured by a mental calculation task, Figure 2). Third, we found several differences in brain functional connectivity between the two groups at 5 min post-awakening (Figure 3). Compared to LR, HR showed increased functional connectivity between regions of the DMN and several regions known to be involved in memory processes at 5 min post-awakening, and between the MPFC and the right putamen at 25 min post-awakening. Importantly, no group differences in functional connectivity were found during the pre-nap scan, therefore suggesting that these changes were specific to the post-awakening period.

Between-group contrasts of the functional connectivity at 5 min post-awakening revealed a pattern of enhanced connectivity in HR within the DMN and between the DMN and the right

PFC and AG. Remarkably, all these regions have been associated with memory processes. Indeed, a meta-analysis of the brain areas associated with episodic encoding and retrieval [46] found that the precuneus, PFC, SFG, and AG were among the largest clusters associated with retrieval success. These are almost the same regions found to be more functionally connected in HR than in LR during the first minutes following awakening. In sum, our findings confirm that the cerebral functioning of HR and LR is different, as previously demonstrated with EEG and PET [9, 10, 13], and show that specific group differences in memory-related brain regions are present during the sleep-wake transition.

It is generally admitted that sleep inertia interferes more with memory retrieval on awakening than with memory consolidation [14, 32, 47, 48]. This fits well with our results showing a dream recall difference between groups at awakening but no difference in the memory recall of the comic strip that was read by the participants before the nap. These findings suggest that the pattern of enhanced functional connectivity within the DMN in HR at awakening facilitates the maintenance of short term memory content during the transition between sleep and wake rather than long-term memory recall.

Building on this interpretation, one may expect to find a clear between-group difference in DST performance immediately after awakening, given that this task is considered to recruit both short-term and working memories. This counterintuitive result may be partly explained by the long delay between awakening and the first post-nap DST (the total delay is the duration of the scan plus the average delay between awakening and the onset of the scan, i.e. about 10 min), which is a consequence of our decision to prioritize the measure of brain functioning over the measure of performance upon awakening. One may hypothesize that the between-group difference at the DST would have been larger if this latter was performed immediately after awakening, as is the case in most studies using this specific task [14, 15, 47]. However, future studies are needed to confirm or refute this speculation.

Altogether, our findings suggest that an increased DMN connectivity upon awakening in HR facilitates the maintenance of dreams in short-term memory during the sleep-wake transition. This hypothesis is coherent with the known cerebral correlates of short-term memory, which consistently involve the PFC and AG [49, 50]. In addition, the MPFC and precuneus

Table 3. Seed-based functional connectivity results for the HR > LR contrast

Seed	Scan	Brain region	MNI coordinates			Peak T-value	Cluster size
			X	Y	Z		
MPFC	Pre-nap	N.S.					
	5 min	Precuneus (L)	-4	-76	52	4.75	487
PCC	25 min	Putamen (R)	14	14	-8	5.15	361
	Pre-nap	N.S.					
	5 min	PFC (R)	36	56	14	4.22	505
		SFG (R)	20	28	46	3.90	378
LP	25 min	N.S.					
	Pre-nap	N.S.					
	5 min	SFG (R)	22	26	48	4.26	372
		AG (R)	36	-54	42	4.05	309
	25 min	N.S.					

The seed regions are the MPFC (center of mass in MNI coordinates = 1, 55, -3), the PCC (1, -61, 38), and the lateral parietal cortices (LP, right = 47, -67, 29, left = -39, -77, 33; the functional connectivity contrast was done using the main effect of both hemispheres). These three seeds are part of the DMN, a network that has been suggested to be involved in dream recall and/or production. The functional connectivity between the seed and the regions reported was higher in HR than LR (see also Figure 3). Statistical analyses were performed using a cluster-defining voxel-wise height threshold of $p < 0.01$ (uncorrected, two-sided) and a whole-brain FWE corrected extent threshold of $p < 0.05$. PFC, prefrontal cortex; SFG, superior frontal gyrus; AG, angular gyrus; (L), left hemisphere; (R), right hemisphere; N.S., not significant.

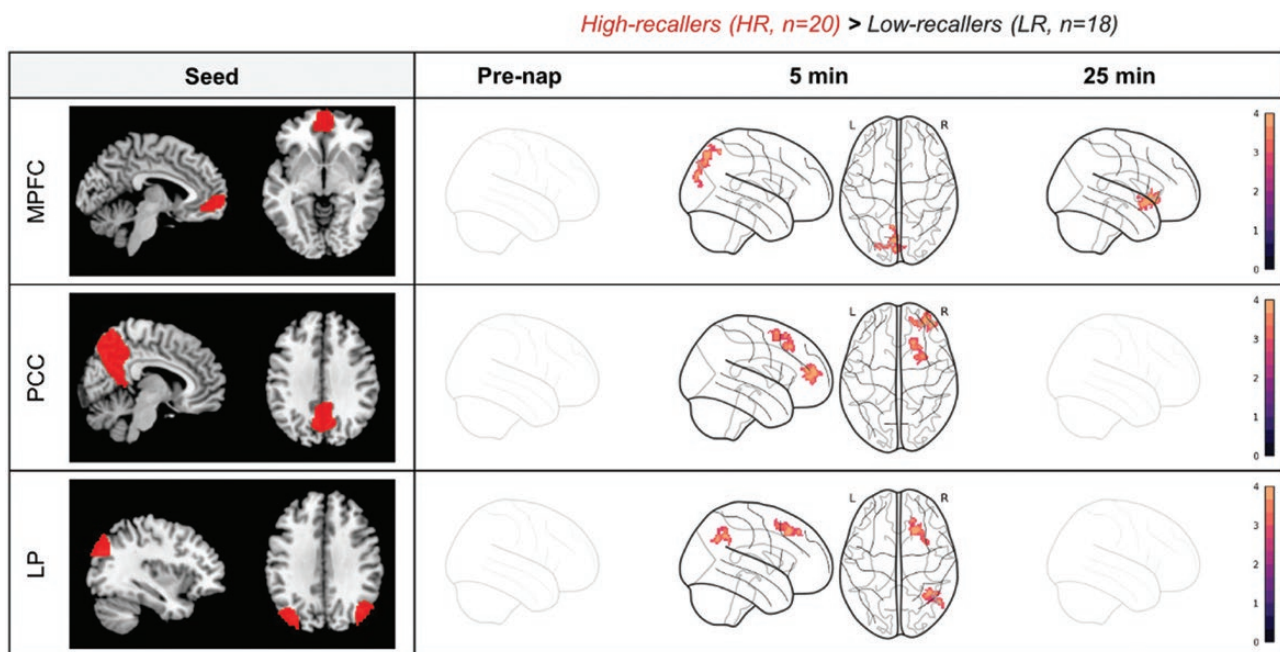


Figure 3. Functional connectivity differences between HR and LR during pre-sleep scan, 5 min post-awakening scan and 25 min post-awakening scan. The seed regions are the MPFC (center of mass in MNI coordinates = 1, 55, -3), the PCC (1, -61, 38), and the lateral parietal cortices (LP, right = 47, -67, 29, left = -39, -77, 33; the functional connectivity contrast was done using the main effect of both hemispheres combined). These three seeds are part of the DMN, a network that has been suggested to be involved in dream recall and/or production. Statistical parametric maps are superimposed on a glass brain using an uncorrected two-sided cluster-defining voxel-wise height threshold of $p < 0.01$ and a whole-brain FWE-corrected extent threshold of $p < 0.05$. Faded brain denotes an absence of significant differences between the two groups for this specific seed and time point (see also Table 3).

are known to be involved in a state of mind attribution such as envisioning the future (prospection), and remembering the past (episodic memory) [25, 46, 51, 52]. A proper functional coupling between these brain areas seems thus appropriate to maintain in working memory a mental representation involving fragment of episodic memory [53, 54] and an imaginary/prospective experience with interacting characters (more than 95% of dream reports involve characters [55]).

In conclusion, our results suggest that the increased functional connectivity in HR after awakening would promote

successful dream recall at awakening by facilitating the maintenance of short-term memory. More broadly, we argue that brain activity at awakening is a critical parameter to explain the difference in DRF between HR and LR.

Limitations and future directions

Participants underwent a partial sleep deprivation on the night before the scanning session, which may have impacted

functional connectivity at awakening of the early afternoon nap [56]. The rationale for doing a partial sleep deprivation was twofold. First, by increasing sleep pressure, we hoped that the subjects would have less trouble falling asleep in the uncomfortable MR environment [57]. Second, because sleep inertia is known to be higher following sleep deprivation, we hoped to maximize sleep inertia upon awakening. We believe that the partial sleep deprivation does not undermine the relevance of our findings since naps are usually taken as a strategy to compensate for sleep loss [58]. Furthermore, it is likely that the impact of the partial sleep deprivation on the functional connectivity, if any, was similar in HR and LR (though this remains to be tested). Future studies are needed to determine whether our results replicate for morning awakenings without prior sleep deprivation.

Second, building on previous experimental findings from our team, we decided to focus solely on the relationship between sleep inertia and trait dream recall, that is, interindividual differences in DRF. Future studies should investigate whether state dream recall factors (such as the different sleep stages) involve the recruitment of the same functional networks that were identified in the current study. For intra-individual variability, based on our current findings, one may expect that enhanced connectivity between the DMN and memory-related brain areas would be also associated with higher dream recall, that is, that within an individual there would be a positive correlation between higher DMN connectivity at awakening and successful dream recall. It could notably explain the nonrapid eye movement (NREM) versus REM sleep difference in dream recall since the DMN is known to be more functionally connected during REM sleep than during NREM sleep [31, 59].

It is also important to stress that dream recall and content (complexity, vividness, and bizarreness) of dream reports are not only modulated by the sleep stage prior to awakening but also by a circadian-driven cortical arousability, which results in a strong decrease in the recall frequency and content differences between N2 and REM dreams at the end of the night. That is, at the end of the night, reports may be as frequent in N2 and REM sleep and some N2 dream reports are indistinguishable from REM sleep dream reports [4, 60–62]. Anecdotally, in the current study, some participants reported vivid and bizarre dreams resembling REM morning dreams, even though they were awakened from N2 or N3 sleep (e.g. one participant awakened in N3 sleep had a very vivid dream that a deer was having lunch with him in the lab and then taking him to the MRI facility). Further research is needed to understand how seemingly different brain states (NREM and REM) can lead to a similar subjective experience.

A promising avenue of research to understand the relationship between the awakening brain and dream recall is the emerging concept of local sleep [63]. For instance, it would be interesting to explore more locally how memory-related brain regions show an intrusion of sleep-like features during the process of awakening, as has been done in rodents [64]. Increased (inhibitory) slow-wave activity in memory-related regions upon awakening, in particular, could explain low dream recall. Intracranial EEG would be the ideal technique to address this issue in humans (see e.g. [65] even if it presents several important limitations [66], that is, investigation of an epileptic brain, with the hippocampus being often part of the epileptic zone). The identification of local sleep inertia in humans should help to reconcile seemingly contradicting results from previous research.

Lastly, while our results provide evidence that a specific pattern of functional connectivity upon awakening, involving the DMN and memory-related brain areas, is related to interindividual differences in dream recall, it is still unknown whether that same brain pattern is similarly involved in dream production while asleep, as hypothesized by some [27, 67]. A major obstacle to test this hypothesis is that there is currently no objective neurophysiological marker of dreaming during sleep [3], which means that researchers cannot study the dreaming brain while the dreamer is asleep, and must rely instead on dream reports collected after induced or spontaneous awakening from sleep (noteworthy, some correlates of dream recall based on the pre-awakening EEG power have been reported, though results are somewhat inconsistent across studies [68–72]). Still, there are reasons to believe that the DMN might be indeed involved in dream production. First, memory structures are certainly involved in the production of dreams since dream content is typically composed of episodic and autobiographical memory fragments [54, 55, 73–76]. Coherently, neuroimaging studies have shown that DMN and memory-related brain regions are active during sleep (especially REM sleep [77–79], and even more so in HR [13]). Second, lesions in core regions of the DMN lead to a complete cessation of dream reporting [21]. Third, daydreaming, which shares several phenomenological properties with night dreaming, is characterized by a recruitment of DMN regions [80]. Finally, the DMN is known to be more functionally connected during the REM sleep stage (as compared to NREM sleep) which is the stage associated with the highest DRF [31, 59].

Related to this issue of differentiating dream production and dream recall, another question pertains to the availability of dream content upon awakening from sleep. Can only the dream content that is present in short-term memory at the time of awakening be remembered? Or rather, is there some form of online consolidation of dream content while dreaming which would allow the dreamer to remember dream content beyond the limited capacity of short-term memory? If so, an ideal candidate would be the intermediate-term memory system, in which memories can be recovered after several hours even after dropping out of the attentional focus [81]. Here again, the absence of a physiological marker of dreaming during sleep makes it difficult to answer these questions. However, future studies could use lucid dreaming with eye movements signaling [82] as a proxy to assess the dream-related memorization mechanisms during sleep (see for example [83]; though we recently advised caution in translating findings from lucid dreaming to non-lucid dreaming [84]).

Conclusion

The present study showed that interindividual trait differences in DRF are associated with differences in brain functional connectivity in the first minutes following awakening. Specifically, HR showed a higher functional connectivity upon awakening between regions involved in short term and episodic memory, which could facilitate the maintenance in short term memory of the pre-awakening experience (i.e. the dream) and thus promote dream recall. More broadly, these results contribute to the growing body of evidence that trait differences in dream recall are supported by trait neurophysiological differences between HR and LR. Further work is needed to better delineate the links

between neurophysiological factors, psychological factors, and interindividual differences in dream recall.

Supplementary material

Supplementary material is available at SLEEP online.

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Author contribution

R.V, A.N, and P.R designed the study. R.V and P.R acquired the data and wrote the first draft of the paper. A.N provided access to his sleep unit to conduct the overnight partial sleep deprivation. All authors read the final version of the manuscript.

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