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Impact of sleep loss before learning on cortical dynamics during memory retrieval

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ABSTRACT

Evidence shows that sleep loss before learning decreases activation of the hippocampus during encoding and promotes forgetting. But it remains to be determined which neural systems are functionally affected during memory retrieval after one night of recovery sleep. To investigate this issue, we evaluated memory for pairs of famous people’s faces with the same or different profession (i.e., semantically congruent or incongruent faces) after one night of undisturbed sleep in subjects who either underwent 4 hours of acute sleep restriction (ASR, N = 20) or who slept 8 hours the pre-training night (controls, N = 20). EEG recordings were collected during the recognition memory task in both groups, and the cortical sources generating this activity localized by applying a spatial beamforming filter in the frequency domain. Even though sleep restriction did not affect accuracy of memory performance, controls showed a much larger decrease of alpha power relative to a baseline period when compared to sleep-deprived subjects. These group differences affected a widespread frontotemporoparietal network involved in retrieval of episodic/semantic memories. Regression analyses further revealed that associative memory in the ASR group was negatively correlated with alpha power in the occipital regions, whereas the benefit of congruency in the same group was positively correlated with delta power in the left lateral prefrontal cortex. Retrieval-related decreases of alpha power have been associated with the reactivation of material-specific memory representations, whereas increases of delta power have been related to inhibition of interferences that may affect the performance of the task. We can therefore draw the conclusion that a few hours of sleep loss in the pre-training night, though insufficient to change the memory performance, is sufficient to alter the processes involved in retrieving and manipulating episodic and semantic information.

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1. Introduction

The previous studies evaluating the neural correlates of memory encoding, either after one night of total sleep deprivation (Drummond et al., 2000; Yoo et al., 2007) or superficial sleep (Van Der Werf et al., 2009, 2011), have consistently shown a decrease in the activity of the medial temporal lobe during encoding, followed by poorer memory performance during retrieval. The hippocampus is the structure of the medial temporal lobe most affected by manipulations of sleep in the night preceding learning (Yoo et al., 2007; Van Der Werf et al., 2009, 2011). This cerebral structure, critical to episodic memory, is thought to support both binding representations of stimuli with a specific spatiotemporal context during encoding (Diana et al., 2007; Ekstrom et al., 2011; Mitchell and Johnson, 2009; Staresina and Davachi, 2009), and the subsequent reactivation of memory traces during retrieval (Marr, 1971; Tulving and Thomson, 1973). As a matter of fact, there is evidence that content-specific reactivation occurs not only at different levels of the sensory hierarchy (e.g., Bosch et al., 2014) but also in hippocampal neurons (Cameron et al., 2001; Gelbard-Sagiv et al., 2008), supporting the view that the same cognitive processes engaged during encoding are re-engaged during retrieval (e.g., Johnson and Rugg, 2007). Based on this reinstatement of encoding-related processing during retrieval, we postulated that cortical vulnerability to sleep loss should also be evident during memory retrieval after one night of undisturbed sleep.

To our knowledge, previous studies that have evaluated the relationship between sleep disruption and the neural mechanisms of memory retrieval have applied total sleep deprivation before the fMRI scanning (Bell-McGinty et al., 2004; Chee and Choo, 2004; Habeck et al., 2004). Under these circumstances, it is difficult to disentangle the effects on attention from the effects on memory. On the other hand, although many studies have evaluated the impact of acute total sleep deprivation and chronic partial sleep restriction on different aspects of memory (for a review, see Alhola and Polo-Kantola, 2007), only one study to date has assessed the impact of acute sleep restriction during the night before memory acquisition on subsequent retrieval measured after one night of normal sleep (Alberca-Reina et al., 2014). This study reported enhanced memory recognition for famous people’s faces with the same
profession compared to celebrities of different profession, regardless of whether subjects had slept normally or only a few hours in the pre-training night, adding further support to the notion that semantic congruency during encoding enhances memory performance (e.g., Atienza et al., 2011; Craik and Tulving, 1975; Crespo-Garcia et al., 2012; Heikkinä et al., 2015; Marić et al., 2011; Schulman, 1974; Staresina et al., 2009; van Kesteren et al., 2010). Here, by using the same experimental paradigm, we assessed whether acute sleep restriction before encoding induced changes in EEG oscillations during the recognition memory task that could help to interpret the behavioral results obtained in the previous study.

Aside from the effects that acute sleep restriction during encoding may have on different levels of the sensory hierarchy during memory retrieval, we expected to find regional differences related to the hierarchical cognitive control in the prefrontal cortex. This hypothesis was based on evidence showing that improved memory was associated with encoding-related enhancement of dorsolateral activation in subjects who slept normally before learning, and with increasing ventrolateral activation in those who were deprived of sleep (Yoo et al., 2007). Although differential patterns of activity within the prefrontal cortex may compensate for reduced hippocampal activation (Yoo et al., 2007) and for sleep deprivation itself (Drummond et al., 2000, 2005; Habeck et al., 2004), they could alternatively reveal the emergence of different strategies of cognitive control for accomplishing successful encoding (e.g., Blumenfeld et al., 2011; Blumenfeld and Ranganath, 2006; Murray and Ranganath, 2007). Regardless of the interpretation and based on the idea that neural activity associated with the processing of an episode during encoding should be reinstated, at least partially, upon later recollection via activation of a hippocampally stored representation of that pattern of activity (Johnson and Rugg, 2007), we expected that a similar regional dissociation in the prefrontal cortex would arise during memory recognition after one night of sleep restriction in the pre-training night.

To test these hypotheses, we assessed changes in the power of EEG oscillations and estimated localization of the generating sources while subjects performed an associative recognition memory task. A large body of evidence suggests that oscillatory EEG dynamics in all frequency bands are linked to different memory processes (Buzsáki and Draguhn, 2004; Fell and Axmacher, 2011; Hanslmayr and Staudigl, 2014; Klimesch, 2012). These studies typically compare the power of EEG oscillatory activity in a post-stimulus period with the EEG power in a pre-stimulus baseline period. This comparison results in relative increases and decreases of power that are known as event-related desynchronization (ERS) and desynchronization (ERD) of the EEG (Pfurtscheller and Lopes da Silva, 1999). Evidence has shown that ERS in the delta (0.5–3.5 Hz), theta (4–7.5 Hz), and gamma (>30 Hz) frequency ranges as well as ERD in the alpha (8–12.5 Hz) and beta (13–30 Hz) band correlate with different stages of memory formation (Düzel et al., 2010; Hanslmayr et al., 2012; Harmony, 2013; Nyhus and Curran, 2010). The frequency of EEG oscillations reflects the engagement of specific functional networks likely involved in distinct memory processes. The frequency further determines the temporal processing window and indirectly the size of neuronal populations and the types of connections involved. In general, fast and slow EEG oscillations favor local and global integration, respectively. In line with this view, EEG studies conducted during retrieval revealed that changes in delta/theta ERS reflected higher order memory control processes, whereas changes in alpha/beta ERD indexed reactivation of the sensory features of the memory trace (Hanslmayr et al., 2012). Consequently, we expected that a single night of sleep restriction to 4 h impacted these two kinds of processes differently. In particular, and given that no memory impairment was seen in a previous study applying the same experimental design (Alberca-Reina et al., 2014), a deficit in one of these processes was predicted to produce a compensatory change in the other.

2. Materials and methods

2.1. Subjects

Forty young university students (age 21.8 ± 2.7 [mean ± SD], range 18–27 years, 21 females) participated in the study. They were native Spanish speakers and had normal or corrected-to-normal vision, apparent good health as revealed by personal interview and health questionnaires, and regular sleeping habits confirmed by a structured interview and sleep-diaries over a period of 1 week prior to the experiment. Participants were instructed to abstain from drugs, alcohol, and caffeine, as well as from taking naps for the week before the first experimental session until the end of the experiment. All subjects gave informed consent to the experimental protocol approved by the Ethical Committee for Human Research at the University Pablo de Olavide according to the principles outlined in the Declaration of Helsinki.

2.2. Experimental paradigm and study protocol

The experimental paradigm used in the present study has been described elsewhere in detail (Alberca-Reina et al., 2014). Fig. 1 includes a schematic representation of the training and memory tasks. Briefly, during the training session, participants were instructed to perform a semantic/perceptual-matching task, for which they were presented with 48 pairs of famous people’s faces that could share (semantically congruent faces, SCF), or not, the same profession (semantically incongruent faces, SIF). Faces were counterbalanced, all of them appearing under congruent and incongruent conditions. Face pairs were presented in 8 blocks, and each pair was repeated four times in alternating blocks in order to increase the probability of having the sufficient number of correct recognitions required to achieve the signal-to-noise ratio needed during memory retrieval. Each block included 12 congruent and 12 incongruent face pairs appearing in random order. Following face pair presentation for 2 s, subjects were trained to maintain faces and their professions for 5 s while looking at a cross in the center of the screen. In this way, we forced subjects to direct endogenous attention to perceptual and semantic aspects of the episodic event, while, at the same time, we were testing whether or not they knew that information. In order to assess this knowledge, one face and one profession (probe stimuli) were presented in the center of the screen for 3 s, and subjects were then asked to respond whether the face and profession, on the left or right side, corresponded to the study face in that particular position. Participants were given a maximum of 4.5 s to respond from stimulus probe presentation, and were instructed to give 4 possible responses depending on whether the face and profession matched one or both of the two studied faces. Participants were asked to press the central button in the response box (Cedrus® model RB-530, Cedrus Corporation, San Pedro, CA, USA) with the right hand if both the face and the profession matched the studied faces presented at the start of the trial, whereas in the opposite case no response was required. If information in the probe stimulus only matched the face presented either on the left or right side, participants were asked to press the left or right button with the left or right hand, respectively. Fig. 1 (left panel) includes an example of target stimuli for congruent and incongruent trials, as well as an example of each kind of response for the congruent condition. By forcing participants to give a different response in each repeated trial, we further guaranteed that they maintained attention focused on the relevant information during the retention period. Importantly, participants were informed that memory for face–face associations would be tested the following morning, since there is evidence that sleep facilitates retention of associative memories based on relevance for future utilization (Van Dongen et al., 2012).

Recognition memory for face–face associations was tested the next morning 1 hour after subjects had performed a retroactive interference task, which revealed itself as a successful strategy to unmask the role of sleep in memory consolidation (Ellenbogen et al., 2006).
The interference task was similar to the semantic/perceptual-matching task but faces were coupled in different ways and presented in only one trial. During the old/new recognition task, all faces were presented four times coupled with the same face as in the training phase and another four times coupled with a different face in different blocks, controlling that they maintained the congruence condition associated with each face but never matched face–face associations in the retroactive interference task. Every trial in the old/new recognition task begins with a fixation cross which is followed by the probe stimulus. Two possible examples for congruent and incongruent faces are shown, as well as the correct response in each case. Every trial in the recognition task was repeated four times in alternating blocks. SCF = semantically congruent faces; SIF = semantically incongruent faces.

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Fig. 1. Temporal sequence of one trial for the perceptual/semantic-matching task and for the recognition memory task performed on day 1 and day 2, respectively. The temporal sequence in one trial of the semantic/perceptual-matching task includes the initial fixation cross, target stimulus (for semantically congruent or incongruent faces), retention period with fixation cross, and the four possible probe stimuli (for semantically congruent faces) that could appear in four alternating blocks. The correct response for each probe stimulus is also indicated. Every trial in the old/new recognition task begins with a fixation cross which is followed by the probe stimulus. Two possible examples for congruent and incongruent faces are shown, as well as the correct response in each case. Every trial in the recognition task was repeated four times in alternating blocks. SCF = semantically congruent faces; SIF = semantically incongruent faces.

Fig. 2. Temporal sequence of one trial for the perceptual/semantic-matching task and for the recognition memory task performed on day 1 and day 2, respectively. The temporal sequence in one trial of the semantic/perceptual-matching task includes the initial fixation cross, target stimulus (for semantically congruent or incongruent faces), retention period with fixation cross, and the four possible probe stimuli (for semantically congruent faces) that could appear in four alternating blocks. The correct response for each probe stimulus is also indicated. Every trial in the old/new recognition task begins with a fixation cross which is followed by the probe stimulus. Two possible examples for congruent and incongruent faces are shown, as well as the correct response in each case. Every trial in the recognition task was repeated four times in alternating blocks. SCF = semantically congruent faces; SIF = semantically incongruent faces.

Fig. 2. Schematic representation of the study protocol. The gray and white bars refer to the sleep and waking periods, respectively, in two consecutive days. Both the control and ASR groups were trained in the semantic/perceptual-matching task in the evening of day 1 and were tested the next day in the morning, after performing the interference task. EEG was recorded while subjects were performing the recognition memory task.
(ASR group: 04:00–08:00 am). All participants slept in the laboratory the night before and after training. During the sleep deprivation session, subjects were allowed to read and watch videos while a technician observed them to prevent them from sleeping.

Subjects followed regular sleep schedules during the week before training, as revealed by results averaged across the 1-week sleep diaries. Most of them slept 7–8 h approximately, (control = 7.9 ± 0.7; ASR = 7.8 ± 0.4), went to sleep between 11:30 pm and 00:30 am (control = 00:03 ± 0.3; ASR = 00:29 ± 0.4), got up between 7:20 am and 8:30 am (control = 7.7 ± 0.8; ASR = 7.4 ± 0.6), and reported sleep latencies shorter than 5–10 minutes. Indeed, group differences did not achieve statistical significance for any of these variables (0.1 < P < 0.5).

2.3. Behavioral analysis

RT and the hit and false alarm rate were analyzed for SCF and SIF during the semantic/perceptual-matching task employed during training and interference. Behavioral indices of sustained attention were further derived from these tasks by analyzing false alarms in two or more consecutive trials, anticipations (RT shorter than 300 ms), long delays (RT longer than 4000 ms), and intra-subject variability of RT to correctly recognized face pairs calculated with the intra-individual coefficient of variation (iCV; ratio between the intra-individual standard deviation and the individual mean). Additionally, subjective sleepiness levels were assessed before performing the training and interference task through the Epworth Sleepiness Scale (Johns, 1991).

Measurements of accuracy for recognition (d′) were derived from the signal detection theory (Yonelinas et al., 1998). This index was computed for the SCF and SIF separately, and also for the combination of the two conditions to obtain a measurement of global episodic memory (associative d′). We further calculated the benefit of congruency as revealed by differences in d′ between SCF and SIF (semantic d′). In all cases, d′ resulted from subtracting the z-score for the false alarm rate from the z-score for the hit rate.

The influence of sleep restriction and semantic congruency on the different behavioral indices was evaluated by two-way mixed analyses of variance (ANOVA) with semantic congruence (SCF vs. SIF) as the within-subject factor, and group (control vs. ASR) as the between-subject factor. Homogeneity of variance was assessed with the Levene test. Pairwise comparisons (t-tests) were only applied if the interaction effect reached statistical significance.

We further assessed whether the hit and false alarm rate obtained during the training and/or interference task were related to indices of accuracy derived from the recognition task by performing Pearson correlation analyses across subjects and within groups. The same analyses were performed with RT. For those correlations that achieved statistical significance in at least one of the two groups, we further evaluated group differences between regression slopes. In order to deal with the problem of multiple comparisons, the familywise error rate (FWE) was controlled by applying Bonferroni’s correction.

2.4. EEG recordings and signal preprocessing

EEG recordings were collected during the recognition memory task from 59 scalp electrodes referenced to linked-mastoids and positioned according to the extended International 10–20 system (Fp1, AF7, AF3, AFz, F7, F5, F3, F1, Fz, FT7, FC5, FC3, FC1, FC2, T7, C5, C3, C1, Cz, TP7, CP5, CP3, CP1, CP2, P7, P5, P3, P1, Pz, PO7, PO3, POz, and O1, together with their right-sided counterparts). Additional electrodes were employed for monitoring horizontal and vertical eye movements as well as the submental muscle tone. Skin-electrode impedances were maintained below 5 kΩ in all EEG sensors. The electrophysiological variables were amplified (BrainAmp MR, Brain VisionVA), filtered (0.1–100 Hz bandpass), digitized (250 Hz, 16-bit resolution), and stored in digital format for subsequent analysis. Extracerebral artifacts were partially removed by applying independent component analysis (Infomax algorithm) as implemented in the BrainVision Analyzer software v. 1.05 (Brain Products® GmbH). The remaining noisy epochs were manually selected and excluded from further analyses. Artifact-free epochs were transformed into the common average reference to partially avoid noisier effects of the reference (Schiff, 2005). In this study, we analyzed only studied face–face associations that were correctly recognized (hits) in the recognition memory task. To balance differences in the signal-to-noise ratio, the same number of face–face associations per congruence condition was selected, provided that they were correctly recognized in at least three trials.

2.5. Time–frequency EEG analysis

In order to identify the time at which changes in the power of oscillatory activity in different frequencies were present, we calculated baseline-corrected time–frequency representations (TFR) of spectral power across trials for each group and semantic condition in the recognition memory task with the Fieldtrip toolbox (http://fieldtrip. fcgonders.n). Spectro-temporal information of frequencies ranged from 2 to 25 Hz was obtained by using a Morlet wavelet of 6 cycles. To obtain task-related TFR of power decreases/increases relative to baseline, power values (P) for each individual frequency (f) were normalized for every time point (t) as follows:

\[ P(t, f) = \frac{P(t, f)_{baseline}}{P(f)_{baseline}} \]

where \( P(t, f)_{baseline} \) represents the mean EEG power for a particular frequency bin within the baseline period, defined from −1000 to −500 ms before presentation of the face pair, and \( P(f)_{baseline} \) refers to the EEG power for a particular frequency bin and time point within the 4000 ms period following the face pair onset. When transformed to percentage, these normalized power values were equivalent to the ERD/ERS measurements mentioned earlier in the introduction (Pfurtscheller and Lopes da Silva, 1999).

We computed the partial least square (PLS) to identify at the sensor level the strongest statistical effects in frequency, time, and space domains simultaneously, by using the PLSmd Matlab toolbox (http://www.rotman-baycrest.on.ca/pls/source). PLS decomposes time–frequency data into components (latent variables) that show correlations with behavior or differences between experimental conditions. In our particular case, this multivariate statistical technique attempted to explain the covariance between two blocks of explanatory (contrasts or memory indices like associative d′ and semantic d′) and dependent variables (normalized EEG activity) by a small number of uncorrelated variables known as latent vectors. By applying this approach, we evaluated differences with respect to the baseline period, the effects of sleep restriction, and semantic congruence on the power of EEG oscillations, as well as the relationship between behavioral data and EEG oscillations. PLS analysis was later combined with permutation tests to determine whether the effect of each latent variable reached statistical significance. Thus, to evaluate the effect of sleep restriction on EEG oscillations, subjects were randomly reassigned 10,000 times without replacement to different experimental conditions (normal sleep or sleep restriction), whereas for the effect of semantic congruence, we permuted 10,000 times the congruent and incongruent conditions within each subject. The latter permutation was also applied to comparisons with the baseline period. For testing correlations, the behavioral indices were permuted across subjects. Finally, we computed 2000 bootstrap estimations of the standard errors of the weights of the original variables to determine the significance of nonzero weights for the variables of the corresponding latent vector.

Within each spectro-temporal window where the PLS yielded significant results, we performed t-tests for related samples in the case of semantic congruence, t-tests for independent samples in the case of group differences, and/or Spearman correlations to evaluate the relationship between behavior and the EEG power averaged over significant sensors. To correct the FWE rate for all time point comparisons, the maximum statistic approach was employed (Maris, 2004). For every time sample after the onset of the face pair, we computed the corresponding statistic.
This was repeated for each data randomization (N = 1000), selecting the maximum (or minimum) statistic across all samples. The 95th quantile of the distribution derived from the selected maximum (or minimum) statistics was used as a critical threshold to retain or reject the null hypothesis of either no differences between experimental conditions or no correlation between normalized power and behavior.

2.6. Source modeling of EEG oscillations

The next step was to identify the cortical sources responsible for generating EEG activity measured on the scalp. As EEG oscillations during cognitive tasks showed considerable phase variability from trial to trial, we first extracted the field distribution of coherent EEG oscillations from single trials by calculating phase differences between sensor pairs at each time point of each single trial (Guderian and Düzel, 2005). This field information, including both absolute amplitude and phase information, was later used to localize the brain sources that produce this oscillatory activity. To this aim, we applied a spatially adaptive beamforming filter in the frequency domain (Gross et al., 2001). This filter estimated the amount of activity at any given location in the brain after having minimized the contribution (variance) of remaining locations. As conventional beamforming techniques fail to reconstruct multiple highly correlated sources, we applied a beamformer technique able to identify multiple, simultaneously active, correlated networks (Diwakar et al., 2011).

In the present study, cortical EEG sources were estimated in those spectro-temporal windows showing a significant increase/decrease of normalized power with respect to the baseline period for at least 500 ms. These differences could be further accompanied by a significant main effect of either group or semantic congruence. As briefly stated earlier, we first obtained from single trials the constant field distributions of non-phase locked oscillatory activity for the frequency bins of interest (Guderian and Düzel, 2005). To this aim, we calculated phase differences between sensor pairs at each time point of each single trial for the frequency bin showing the maximum statistic after averaging those sensors where the PLS yielded significant differences. This procedure calculates, for each subject, the phase lag index of all sensors with respect to the sensor with the maximum power. Next, we applied the inverse wavelet transformation to bring oscillatory amplitude information back to the time domain. Consequently, the field distribution included both absolute amplitude and phase information (for more details on the phase alignment procedure, see Guderian and Düzel, 2005).

To estimate the cortical sources of EEG oscillations within the interval of interest, we used the dual-core beamformer approach (Diwakar et al., 2011), which allowed us to identify the main pairs of correlated sources that co-existed in each individual dataset. We performed 1000 searches for each dataset and selected all source pairs separated by more than 5 cm that were found in more than 1.5% of the searches. Afterwards, a multiple-constrained beamformer with correlated source suppression was applied to obtain the ultimate spatial filters from the time-of-interest and baseline mean covariate matrices, respectively. This procedure generates pseudo-z maps for each trial, which are computed as time-of-interest/baseline power map ratios (Van Veen et al., 1997). This normalization step was required to reduce the undesired contribution of noise power, which increased with depth and distance from sensors (Vrba and Robinson, 2001).

The cortical space was divided into a regular 5-mm voxel grid, and sensor outputs from unit dipoles in the three Cartesian directions were computed at each grid location. We used a realistic boundary-element model (Oostenveld et al., 2001) based on a standard template (Collin27 T1-weighted averaged MRI). This volume conduction model consisted of 3 closed compartments with conductivities of 0.33, 0.0042, and 0.33 S/m corresponding to skin, skull, and brain, respectively. The regularization parameter was set at 0.001% of the largest eigenvalue of the covariance matrices.

2.7. Statistical analysis of cortical source imaging

We used a hierarchical statistical model to reduce the influence of inter-subject variability in oscillatory responses derived from across-subjects analyses (Holmes and Friston, 1998). First, voxel-wise statistical analyses were computed for each participant on the original source activation maps obtained from all trials (or from congruent and incongruent trials, separately). Next, the corresponding contrast was applied at the group level. The individual analyses included comparisons with the baseline (one-sample t-tests), and comparisons between congruent and incongruent trials (two-sample t-tests). At the group level, we evaluated the main effects of group and congruence, the interaction effect, and Spearman correlations (across-subjects and within each group, separately) with different memory indices on the t-maps or R-maps derived from the previous step. Unlike Pearson correlations, Spearman correlations are quite robust to outliers and do not require that the joining distribution be multivariate normal. If these correlations reached statistical significance in at least one of the two groups, between-group analyses were performed using the Fisher method for independent samples applied to correlations. To this aim, R-maps were first transformed to z-score maps for each group and then the corresponding Fisher test was applied to obtain Z-statistic values.

FWE rates were controlled by applying non-parametric permutation tests combined with suprathreshold cluster analyses (Nichols and Holmes, 2002). Before cluster analysis, all t-maps and mean activation maps were smoothed with an isotropic Gaussian kernel of 10 mm. The cluster was defined as the sum of the R-, t- or Z-values obtained from contiguous voxels (cluster mass). After applying a primary threshold to voxels, P-values (α = 0.05) were assessed using the Monte Carlo method implemented in the Fieldtrip toolbox (N = 1000 permutations).

Coordinates of peak voxels and local maxima statistic values within each significant cluster were transformed into the Talairach space (Talairach and Tournoux, 1988) by using a nonlinear transformation. Cluster voxels were labeled according to the Brodmann area (BA) atlas included in the WFU Pick Atlas toolbox (Maldjian et al., 2003), using the same brain template employed for EEG source analyses.

2.8. Time course reconstruction of EEG sources

In order to reconstruct the entire EEG source time-courses, peak voxels and local maxima were selected for each significant contrast. We applied the same hierarchical model described above for statistical analysis. Briefly, we first obtained the optimal dipole orientation (Equation 8, Gross et al., 2001), then computed the power estimates using the voxel spatial filters and the mean covariate matrix of the time-of-interest described previously (Equations 4 and 5 in Gross et al., 2001). Next, the optimal spatial filter was obtained by multiplying every optimal orientation value by its corresponding voxel spatial filters. The output of this computation was then multiplied by the filtered signal in the corresponding frequency bin of interest. Power decreases/increases relative to the baseline were computed in single-trial EEG source signals, as performed at the sensor level. Time series of normalized power values were averaged across the frequency bins of interest before performing statistical analyses in the time domain. Finally, the maximum statistic approach (Maris, 2004; Nichols and Holmes, 2002) was used to control the FWE rate.

3. Results

3.1. Demographics and levels of daytime sleepiness

Both controls and sleep-deprived subjects were statistically homogeneous in age and gender and showed comparable levels of subjective daytime sleepiness. Consequently, these variables were not introduced
as covariates in subsequent analyses. Table 1 shows descriptive statistics of these variables for each group.

### 3.2. Behavioral results

#### 3.2.1. Behavioral indices obtained in the training and interference tasks

Behavioral indices of sustained attention were not affected by sleep restriction. In fact, no subject showed false alarms in 2 or more consecutive trials and/or anticipations, neither in the training nor in the interference task. The number of lapses (RT > 4000 ms) in the training task was also extremely low (controls: 0.08 ± 0.24; ASR = 0.08 ± 0.33), whereas no lapses were evident in the interference task. The iCV was statistically similar (0.2 < P < 0.8) in the control (Training: 0.27 ± 0.04; Interference: 0.24 ± 0.07) as compared with the ASR group (Training: 0.27 ± 0.04; Interference: 0.22 ± 0.04), and was not correlated with any memory index (0.1 < P < 0.6). Therefore, it was unlikely that impaired attention due to sleep loss had influenced memory performance after one night of recovery sleep.

Fig. 3 shows the mean hit rate, false alarm rate, and RT obtained by each group under congruent and incongruent conditions during the training task performed in the evening of day 1 and during the interference task applied on the morning of day 2, just before evaluating the recognition memory for associations studied in the training task.

The mixed ANOVA showed a significant main effect of congruence for the hit rate in the training (F(1,38) = 5.2; P < 0.03) and in the interference task (F(1,38) = 16.62; P < 0.001), revealing a higher percentage of hits under congruent rather than incongruent conditions. The false alarm rate was significantly higher for SIF than for SCF in the training task (F(1,38) = 5.2; P < 0.03), but these differences were not extended to the interference task (P > 0.2). The congruency effect was equally evident for RT, at least in the interference task (F(1,38) = 25.8; P < 10^-5).

But in the training task, the ANOVA yielded a significant group by congruence effect (F(1,38) = 6.2; P < 0.02), because the congruency benefit was more than twofold (P < 0.05) in the control (mean difference = 123 ms) than in the ASR group (mean difference = 52 ms). No main effect of group and no other group by congruence interaction were found for any of the behavioral indices evaluated in these two encoding tasks.

#### 3.2.2. Behavioral indices of memory recognition

Fig. 4 shows the mean accuracy and RT obtained by each group during retrieval of semantically congruent and incongruent faces. In agreement with previous studies (e.g., Atienza et al., 2011; Craik and Tulving, 1975; Crespo-Garcia et al., 2012; Heikkinä et al., 2015; Maril et al., 2011; Schuman, 1974; Staresina et al., 2009; van Kesteren et al., 2010), memory recognition was better for SCF than for SIF as revealed by the significant main effect of congruency yielded by the mixed ANOVA applied on both accuracy (F(1,38) = 15.6; P < 0.001) and RT (F(1,38) = 23.9; P < 10^-5). However, the magnitude of the congruency benefit did not change after sleep restriction as inferred from lack of a main effect of the group (P > 0.8). Neither was the group by congruence interaction significant (P > 0.6). The mean accuracy difference between SCF and SIF (semantic d’) was 0.31 (±0.36) in the control group and 0.24 (±0.50) in the ASR group. The global measure of associative memory (i.e., mean d’ for SCF and SIF) was also highly similar (P > 0.8) in the two groups (control = 0.55 ± 0.39; ASR = 0.57 ± 0.38). Although control subjects were around 100 ms faster than the ASR group, mainly due to differences in the SCF responses, neither the main effect of the group (P > 0.3) nor the group by congruence interaction were significant, although in the latter case there was a trend for statistical significance (F(1,38) = 3.1; P < 0.09).

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**Table 1**

Demographic profile of the control (N = 20) and ASR (N = 20) group.

<table>
<thead>
<tr>
<th>Group</th>
<th>Age (years)</th>
<th>Gender (men/women)</th>
<th>Mean TST</th>
<th>ESS training task</th>
<th>ESS interference task</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>21.6 ± 2.1</td>
<td>10</td>
<td>7.92 ± 0.73</td>
<td>2.16 ± 0.83</td>
<td>1.79 ± 0.53</td>
</tr>
<tr>
<td>ASR</td>
<td>22.3 ± 2.7</td>
<td>11</td>
<td>7.77 ± 0.44</td>
<td>2.75 ± 1.02</td>
<td>1.55 ± 0.51</td>
</tr>
</tbody>
</table>

ASR = acute sleep restriction in the pre-training night; ESS = Epworth Sleepiness Scale; TST = total sleep time averaged across one week as revealed by the sleep diary.

---

**Fig. 3**

Mean of the hit rate, false alarm rate, and RT to hits obtained during encoding of semantically congruent (SCF) and incongruent faces (SIF) during the training phase performed on day 1, and during the interference task performed on day 2 by the control and ASR groups. Vertical lines refer to the standard error of the mean. Long horizontal lines with an asterisk refer to the significant main effect of congruence, whereas the short horizontal line with an asterisk refers to the significant post hoc derived from a significant group by congruence interaction effect.
3.2.3. Relationship between memory indices and behavioral indices derived from the training and interference task

Accuracy and RT obtained during the recognition task were correlated with the behavioral indices derived from training and interference tasks, separately. Results revealed significant correlations across subjects between memory and performance in the training task. In particular, the \( d' \) index for SCF was positively correlated with the hit rate for both SCF \((r = 0.41; P < 0.004)\) and SIF \((r = 0.49; P < 0.001)\). The \( d' \) index for SIF only correlated with the hit rate for SIF in the training task \((r = 0.43; P < 0.003)\). All these correlations were statistically significant after Bonferroni's correction within the ASR group \((0.54 < R < 0.58; 0.004 < P < 0.006)\), and the correlation between the hit rates for SIF during training and retrieval also reached statistical significance in the control group \((R = 0.68; P < 0.0005)\). But there were no group differences in the regression slopes for any of the significant correlations \((0.3 < P < 0.9)\). Correlation analyses for RT also provided highly significant results. Thus, RT in response to SCF during training was positively correlated with RT obtained during successful retrieval of SCF \((R = 0.68; P < 10^{-6})\) and of SIF \((R = 0.66; P < 10^{-5})\). The same result applied to RT in response to SIF \((R = 0.72; P < 10^{-6})\). Even though none of these correlations were statistically significant after Bonferroni’s correction within any of the groups \((P > 0.03)\), we compared the regression slopes of the two groups, but again, there were no group differences \((0.1 < P < 0.8)\).

3.3. Effects of sleep restriction at the sensor level

Fig. 5A shows the TFR averaged across sensors, semantic conditions, and subjects for the control and ASR group. The two groups exhibited a significant decrease of alpha power \((8–12\) Hz) between 500 and 2000 ms after presentation of faces, but this decrease was more pronounced in the control than in the ASR group (Fig. 5A). The PLS analysis confirmed this result (Fig. 5B, left panel), revealing group differences in the alpha ERD between 500 and 1000 ms \((P_{\text{cluster-corrected}} < 0.03)\), mainly over centro-parietal sensors (Fig. 5B, right panel). The frequency bin showing the maximum statistic after correcting for multiple comparisons across time was 10 Hz, which was later used to estimate the EEG sources of this activity. These differences were equally evident for SCF and SIF as inferred from the lack of interaction effect \((P > 0.5)\).

The TFR also showed an increase of delta \((0.1–3.5\) Hz) and theta \((4–7.5\) Hz) power with respect to the baseline. This result was not affected either by the semantic congruence or by the sleep condition and was confirmed by the PLS for the entire post-baseline analysis period. Nevertheless, after averaging the EEG power over the sensors showing a significant increase in the PLS, the maximum t-statistic was located in the delta band \((3\) Hz) over posterior sensors within the first 500 ms after presentation of faces (Fig. 5C). This spectro-temporal window was later used to estimate the EEG sources of this activity.

3.4. Effects of sleep restriction at the source level

As for the sensor level, group differences reached statistical significance for 10 Hz oscillations at the source level. Relative to controls, the ASR group showed a significant decrease of the alpha ERD over frontotemporoparietal regions, as illustrated in Fig. 6. Table 2 includes different parameters of peak voxels within each significant cluster for the main effect of group. Group differences were evident around 250 ms in the left superior temporal gyrus, and extended up to 1000 ms. Around 150 ms later, the higher alpha ERD shown by the control group emerged in the middle temporal and fusiform gyrus, and in different regions of the frontal lobe including the left insula, right anterior cingulate gyrus, and right superior and middle frontal gyri. Finally, around 550–600 ms, significant group differences were observed in other regions of the frontal lobe as well as in the left inferior parietal lobe. These differences between controls and sleep-deprived subjects were about the same size for SCF and SIF as evidenced by the lack of interaction between the two factors.
3.5. Effects of semantic congruence at the source level

The main effect of semantic congruence was only significant for brain sources of 3 Hz oscillatory activity, the delta power being higher during retrieval of SCF than during retrieval of SIF (Fig. 7 and Table 3). The earliest main effect occurred at approximately 50 ms from the onset of the face–face association in a cortical network comprising the middle frontal, precentral, and posterior cingulate gyrus of the right hemisphere as well as the left angular gyrus. Around 150 ms, differences between the two conditions of semantic congruence became evident in the right precentral, right postcentral gyrus, and left inferior frontal gyrus. Differences also reached statistical significance in the right anterior cingulate gyrus around 300 ms.

3.6. Relationship between EEG power and behavior at the source level

To investigate EEG oscillatory correlates of successful recognition memory, we performed correlation analyses on the source-activation maps using the associative and semantic d’ indices as regressors. As shown in Table 4 and illustrated in Fig. 8 (left panel), analyses on the source activation maps and on the reconstructed time signals showed that associative d’ was positively correlated with the power of delta oscillations in medial and lateral areas of the right temporal lobe around 100–400 ms from stimulus onset. The two groups did not differ in the strength of this relationship. When the same analysis was restricted to 10 Hz in the ASR group, the higher the associative memory, the lower the alpha power in medial and lateral parieto-occipital areas of the right hemisphere, around 600–900 ms from stimulus onset. In this case, significant differences between the regression slopes of the two groups were restricted to the right angular gyrus (BA 39).

Regression analyses with semantic d’ did not yield significant results across subjects. But we found significant correlations in different frequencies when analyses were conducted in each group separately. In controls, the higher the alpha ERD was in the left temporal pole and inferior parietal lobe (BA 40), the higher the benefit of congruence. Whereas in the ASR group, the higher the delta power in the left middle frontal gyrus (BA 10), the higher the congruency effect on memory recognition (Fig. 8, right panel). While the latter effect was significant within the first 500 ms from stimulus onset, the former was significant from 700 to 900 ms from stimulus onset.

Table 2

<table>
<thead>
<tr>
<th>Contrast Cortical region</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Tsource</th>
<th>Time (ms)</th>
<th>Ttime</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control – ASR (P cluster &lt; 0.003)</td>
<td>R Superior frontal gyrus</td>
<td>6</td>
<td>8</td>
<td>20</td>
<td>57</td>
<td>53</td>
<td>3.1</td>
<td>464–1088</td>
</tr>
<tr>
<td></td>
<td>R Middle frontal gyrus</td>
<td>10</td>
<td>45</td>
<td>57</td>
<td>13</td>
<td>3</td>
<td>2.1</td>
<td>412–520</td>
</tr>
<tr>
<td></td>
<td>R Inferior frontal gyrus</td>
<td>46/45</td>
<td>60</td>
<td>32</td>
<td>3</td>
<td>2.4</td>
<td>464–1036</td>
<td>3.0–2.6</td>
</tr>
<tr>
<td></td>
<td>R Anterior cingulate</td>
<td>24/32</td>
<td>5</td>
<td>17</td>
<td>33</td>
<td>3.4</td>
<td>464–1140</td>
<td>3.0–2.6</td>
</tr>
<tr>
<td></td>
<td>R Insula</td>
<td>13</td>
<td>40</td>
<td>22</td>
<td>33</td>
<td>2.6</td>
<td>568–1088</td>
<td>2.9–2.6</td>
</tr>
<tr>
<td></td>
<td>L Superior frontal gyrus</td>
<td>8</td>
<td>–20</td>
<td>32</td>
<td>53</td>
<td>2.9</td>
<td>672–1140</td>
<td>3.0–2.6</td>
</tr>
<tr>
<td></td>
<td>L Insula</td>
<td>13</td>
<td>–45</td>
<td>–13</td>
<td>18</td>
<td>2.6</td>
<td>412–776</td>
<td>3.0–2.6</td>
</tr>
<tr>
<td></td>
<td>L Precentral gyrus</td>
<td>6/4</td>
<td>–45</td>
<td>–8</td>
<td>63</td>
<td>2.5</td>
<td>412–1140</td>
<td>2.8–2.6</td>
</tr>
<tr>
<td></td>
<td>L Postcentral gyrus</td>
<td>3</td>
<td>–55</td>
<td>–13</td>
<td>43</td>
<td>2.1</td>
<td>568–724</td>
<td>2.8–2.5</td>
</tr>
<tr>
<td></td>
<td>L Inferior parietal lobe</td>
<td>45</td>
<td>–45</td>
<td>–43</td>
<td>48</td>
<td>2.5</td>
<td>620–880</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>L Superior temporal gyrus</td>
<td>22</td>
<td>–65</td>
<td>–38</td>
<td>23</td>
<td>2.9</td>
<td>256–1036</td>
<td>3.1–2.4</td>
</tr>
<tr>
<td></td>
<td>L Middle temporal gyrus</td>
<td>38</td>
<td>–40</td>
<td>–3</td>
<td>–22</td>
<td>2.7</td>
<td>308–1088</td>
<td>3.5–2.5</td>
</tr>
<tr>
<td></td>
<td>L Fusiform gyrus</td>
<td>21</td>
<td>–65</td>
<td>–3</td>
<td>7</td>
<td>2.7</td>
<td>412–1088</td>
<td>3.5–2.4</td>
</tr>
<tr>
<td></td>
<td>L Occipital gyrus</td>
<td>37</td>
<td>–45</td>
<td>–43</td>
<td>2</td>
<td>2.8</td>
<td>464–1088</td>
<td>2.7–2.4</td>
</tr>
</tbody>
</table>

Note: representative voxels correspond to clusters including a minimum of 20 voxels showing significant differences in the time domain after correcting for multiple comparisons across time. ASR = acute sleep restriction; BA = Brodmann area; x, y, z correspond to MNI (Colin27) coordinates of representative voxels; Tsource = range of t-values derived from analyses in the time domain; L = left hemisphere; R = right hemisphere; P = range of P-values derived from analyses in the time domain.
500 to 1000 ms. It is important to note that there were no differences between groups in the strength of these relationships.

4. Discussion

In this study, we investigated whether a few hours of sleep loss the night before learning are sufficient to produce changes in functional cortical networks during memory retrieval, even if such changes are not accompanied by behavioral memory impairment. Accordingly, the group that suffered the sleep restriction during memory encoding showed, compared to controls, (i) a smaller decrease of alpha power in cortical networks involved in episodic and semantic successful retrieval, (ii) a stronger relationship between the decrease of alpha power in visual associative regions and the associative memory performance, and (iii) a positive correlation between the power of delta oscillations in prefrontal regions involved in executive functions and the memory benefit of congruence.

Several studies have examined cerebral hemodynamic changes during memory retrieval following total sleep deprivation (Bell-McGinty et al., 2004; Chee and Choo, 2004; Habeck et al., 2004). But, to the best of our knowledge, this is the first study evaluating the effects of acute sleep restriction during the night before learning on EEG oscillatory patterns associated with memory retrieval after one night of recovery sleep. Despite there being no differences in memory recognition, a few hours of sleep restriction during the night before memory acquisition produced less pronounced retrieval-induced decreases of alpha power over a widespread functional network comprising lateral and medial prefrontal cortices bilaterally, and lateral regions of the temporal and

Table 3
Cortical regions showing the highest effect of semantic congruence (SCF > SIF) on delta ERS during successful recognition memory.

<table>
<thead>
<tr>
<th>Group</th>
<th>Cortical region</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>T_source</th>
<th>Time (ms)</th>
<th>T_time</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>SCF &gt; SIF (P_cluster &lt; 10⁻¹⁰)</td>
<td>R Posterior cingulate gyrus</td>
<td>31</td>
<td>4</td>
<td>−32</td>
<td>44</td>
<td>4.0</td>
<td>48–516</td>
<td>2.7/4.2</td>
<td>0.0001–0.01</td>
</tr>
<tr>
<td></td>
<td>R Precuneus</td>
<td>7</td>
<td>15</td>
<td>−43</td>
<td>58</td>
<td>3.2</td>
<td>152–412</td>
<td>2.7/3.1</td>
<td>0.003–0.009</td>
</tr>
<tr>
<td></td>
<td>R Postcentral gyrus</td>
<td>3</td>
<td>35</td>
<td>−18</td>
<td>43</td>
<td>3.0</td>
<td>152–360</td>
<td>2.7/3.1</td>
<td>0.004–0.008</td>
</tr>
<tr>
<td></td>
<td>R Middle frontal gyrus</td>
<td>9</td>
<td>40</td>
<td>−12</td>
<td>38</td>
<td>3.1</td>
<td>48–360</td>
<td>2.7/3.3</td>
<td>0.002–0.009</td>
</tr>
<tr>
<td></td>
<td>R Anterior cingulate</td>
<td>31/24</td>
<td>30</td>
<td>−33</td>
<td>38</td>
<td>2.4</td>
<td>308–360</td>
<td>2.8/2.9</td>
<td>0.006–0.008</td>
</tr>
<tr>
<td></td>
<td>R Precentral gyrus</td>
<td>4/6</td>
<td>40</td>
<td>−13</td>
<td>48</td>
<td>2.8</td>
<td>48–412</td>
<td>2.8/3.1</td>
<td>0.003–0.008</td>
</tr>
<tr>
<td>P_cluster &lt; 0.005</td>
<td>L Angular gyrus/middle occipital gyrus</td>
<td>19/39</td>
<td>−35</td>
<td>−78</td>
<td>28</td>
<td>3.9</td>
<td>48–1036</td>
<td>2.8/4.2</td>
<td>0.0002–0.008</td>
</tr>
<tr>
<td>P_cluster &lt; 0.05</td>
<td>L Inferior frontal gyrus</td>
<td>10/47</td>
<td>−50</td>
<td>47</td>
<td>−12</td>
<td>3.6</td>
<td>152–1452</td>
<td>2.8/3.5</td>
<td>0.001–0.009</td>
</tr>
</tbody>
</table>

Note: representative voxels correspond to clusters including a minimum of 20 voxels showing significant differences in the time domain after correcting for multiple comparisons across time. BA = Brodmann areas; x, y, z correspond to MNI (Colin27) coordinates of representative voxels; T_time = range of t-values derived from analyses in the time domain; L = left hemisphere; R = right hemisphere; P = range of P-values derived from analyses in the time domain.

Table 4
Cortical regions showing significant correlations between EEG power and behavior; and significant group differences after comparing the regression slopes during successful retrieval.

<table>
<thead>
<tr>
<th>Correlation (Cortical region (group))</th>
<th>BA</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>R/</th>
<th>Z(source)</th>
<th>Time (ms)</th>
<th>R/</th>
<th>Z(time)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delta EEG vs. associative d&lt;sup&gt;+&lt;/sup&gt; (all subjects)</td>
<td>Parahippocampal gyrus</td>
<td>30/29/26</td>
<td>10</td>
<td>−38</td>
<td>3</td>
<td>0.4</td>
<td>100–308</td>
<td>0.4</td>
<td>0.006–0.02</td>
<td></td>
</tr>
<tr>
<td>P_cluster &lt; 0.003</td>
<td>R Inferior parietal lobe</td>
<td>40</td>
<td>65</td>
<td>−18</td>
<td>28</td>
<td>0.5</td>
<td>48–568</td>
<td>0.4/0.5</td>
<td>0.0004–0.03</td>
<td></td>
</tr>
<tr>
<td>P_cluster &lt; 0.004</td>
<td>R Postcentral gyrus</td>
<td>43</td>
<td>60</td>
<td>−23</td>
<td>18</td>
<td>0.4</td>
<td>152–412</td>
<td>0.4/0.6</td>
<td>0.0001–0.02</td>
<td></td>
</tr>
<tr>
<td>P_cluster &lt; 0.004</td>
<td>R Superior temporal gyrus</td>
<td>22</td>
<td>50</td>
<td>−18</td>
<td>−2</td>
<td>0.4</td>
<td>204–360</td>
<td>0.4</td>
<td>0.01–0.02</td>
<td></td>
</tr>
<tr>
<td>P_cluster &lt; 0.004</td>
<td>R Fusiform gyrus</td>
<td>20</td>
<td>40</td>
<td>−43</td>
<td>−17</td>
<td>0.3</td>
<td>256–308</td>
<td>0.4</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Alpha EEG vs. associative d&lt;sup&gt;+&lt;/sup&gt; (ASR)</td>
<td>39/19</td>
<td>40</td>
<td>−73</td>
<td>18</td>
<td>−0.6</td>
<td>620–932</td>
<td>−0.5/−0.4</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P_cluster &lt; 0.003</td>
<td>R Angular gyrus</td>
<td>39</td>
<td>55</td>
<td>−73</td>
<td>13</td>
<td>1.8</td>
<td>516–568</td>
<td>2.2</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Alpha EEG vs. semantic d&lt;sup&gt;+&lt;/sup&gt; (control)</td>
<td>Parahippocampal gyrus</td>
<td>30/29/26</td>
<td>10</td>
<td>−38</td>
<td>3</td>
<td>0.4</td>
<td>100–308</td>
<td>0.4</td>
<td>0.006–0.02</td>
<td></td>
</tr>
<tr>
<td>P_cluster &lt; 0.003</td>
<td>L Inferior parietal lobe</td>
<td>40</td>
<td>−50</td>
<td>−33</td>
<td>63</td>
<td>−0.7</td>
<td>516–984</td>
<td>−0.6/−0.5</td>
<td>0.002–0.02</td>
<td></td>
</tr>
<tr>
<td>P_cluster &lt; 0.004</td>
<td>L Temporal pole</td>
<td>38</td>
<td>−40</td>
<td>7</td>
<td>−22</td>
<td>−0.5</td>
<td>828–880</td>
<td>−0.5</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>P_cluster &lt; 0.004</td>
<td>L Postcentral gyrus</td>
<td>2</td>
<td>−35</td>
<td>−28</td>
<td>28</td>
<td>−0.5</td>
<td>568–776</td>
<td>−0.5</td>
<td>0.02–0.03</td>
<td></td>
</tr>
<tr>
<td>Delta EEG vs. semantic d&lt;sup&gt;+&lt;/sup&gt; (ASR)</td>
<td>10/10</td>
<td>−35</td>
<td>47</td>
<td>8</td>
<td>0.7</td>
<td>48–464</td>
<td>0.5/0.7</td>
<td>0.0006–0.02</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: representative voxels correspond to clusters including a minimum of 20 voxels showing significant correlations in the time domain after correcting for multiple comparisons across time. ASR = acute sleep restriction in the pre-training night; BA = Brodmann areas; x, y, z correspond to MNI (Colin27) coordinates of the representative voxel; R-values correspond to Spearman correlations within a particular group; Z-values result from comparing the regression slopes of the two groups; R/| | Z(source) = range of R- and Z-values derived from analyses in the time domain. L = left hemisphere; R = right hemisphere; P = range of P-values derived from analyses in the time domain.
posterior parietal lobe of the left hemisphere. Previous studies investigating EEG oscillations during retrieval have shown that alpha power decreases were related to reactivation of sensory features of a memory trace (Khader and Rösler, 2011; Waldhauser et al., 2012) and that the topography of alpha ERD reflected the kind of material that was being reactivated (Khader and Rösler, 2011). In the present study, we found that group differences in the sources of alpha oscillations were highly distributed over the cortex, likely indicating a deficit of the ASR group to reactivate different information contents of the episodic event. Accordingly, the cortical regions showing group differences in alpha power decrease are part of a well-known cerebral network that is distinctly activated during episodic and semantic retrieval (Burianova et al., 2010; Lee et al., 2002; Mummery et al., 1999).

In line with this interpretation, the ASR group showed difficulties in recruiting brain regions related to semantic processing such as the middle and inferior frontal gyri, and the anterior temporal lobe (Leveroni et al., 2000; Thompson-Schill et al., 1997; Wagner et al., 1998). As stated by recent studies, the anterior temporal lobe comprises not only the temporal pole but also the middle and superior temporal gyrus (Bonner and Price, 2013; Visser et al., 2010), the same regions showing significant group differences in the current study. Interestingly, results from studies conducted in patients with right and left anterior temporal lobe lesions suggest that different components of the semantic system are processed and stored in the same regions of the two hemispheres. In particular, information stored in the right temporal lobe appears to be mainly based on perceptual knowledge, whereas information stored in the left side relies more on integration between sensorimotor and linguistic information, mainly involved in naming mechanisms (Gainotti, 2007). In our study, the ASR group showed less alpha power decrease than controls in the left anterior temporal lobe, whereas no changes occurred in homologous areas of the right hemisphere. This result might be indicating deficits in accessing semantic knowledge derived from names of famous faces. It is well known that people have more difficulty and are slower retrieving a name that is associated with a specific face than more abstract information such as occupation (Johnston and Bruce, 1990; Young et al., 1988), despite the name being an essential part of a person's identity (e.g., Hanley and Cowell, 1988). Evidence further indicates that personal names are more vulnerable to forgetting under different conditions susceptible to producing cognitive impairment, such as disease (for a review, see Yasuda et al., 2000) and conditions of extremely high altitude (Pelamatti et al., 2003). Therefore, it is likely that sleep restriction hampers name retrieval during encoding, thus hindering recognition based on the kind of semantic information that is accessed through the name.

Despite the differences mentioned above, successful retrieval benefited from similar functional networks synchronized through delta oscillations in the two groups. Accordingly, all subjects showed a positive correlation between associative memory and delta power in the parahippocampal cortex and occipitotemporal regions responsible for face recognition (Haxby et al., 2000; Gobbini and Haxby, 2007; Zhen et al., 2013), as well as higher delta ERS during retrieval of semantically congruent than of incongruent faces over a functional semantic network including nodes in the inferior frontal gyrus, posterior cingulate, and angular gyrus (Binder et al., 2009). The main conclusion drawn from this meta-analysis regarding the function of these regions is that they might play a role in complex information integration and retrieval of conceptual information. However, and unlike controls, memory performance in the ASR group was related to changes in additional sources of delta and alpha band oscillations. Thus, the higher the memory recognition, the higher the power of alpha oscillations in the temporoparietal regions; whereas the higher the memory benefit of congruence, the higher the power of delta oscillatory activity in the left ventrolateral prefrontal cortex. Previous studies have reported increases of delta oscillations in the frontal lobe while subjects performed
different tasks [for a review, see Harmony, 2013]. Although the role of these oscillations in cognitive function is not clear, they have been associated with motivation (Knyazev, 2012) and inhibition of the sensory afferences that may interfere with the performance of the task (Fernández et al., 2012; Harmony et al., 2009). This interpretation is consistent with the results of the present study. The ASR group showed a deficit in recruiting cortical regions involved in episodic/semantic retrieval that, however, was not accompanied by memory impairment. In this group, memory retrieval might be facilitated by the reactivation of information in highly integrative nodes like the angular gyrus, and by the role of the prefrontal cortex in inhibiting information that may interfere with task demands.

Changes seen in the functional networks involved in memory retrieval as a result of reducing the amount of sleep during the night before training might be attributed to the homeostatic sleep response during the subsequent night. However, this hypothesis is unlikely considering results from previous studies assessing the influence of chronic sleep restriction on sleep homeostatic responses (e.g., Goel et al., 2014; Van Dongen et al., 2003). These studies demonstrated that contrary to total sleep deprivation, chronic restrictions of sleep periods to 4 h per night did not produce significant changes neither in the duration of slow-wave sleep nor in the delta power, two putative markers of sleep homeostasis. In the light of the findings, the functional changes observed in large-scale oscillatory networks in the ASR group most likely resulted from changes in encoding processes as a consequence of sleep restriction during the night before. Accordingly, and while we found no main effect of group on the performance of the different tasks, we observed a tight relationship between the different behavioral indices obtained during the training and recognition memory task. We also found that the only evidence of cognitive impairment shown by the ASR group during encoding, longer responses to SCF than controls, was also evident during retrieval, although in the latter case the group by congruence interaction did not reach statistical significance. All these results lead us to believe that memory retrieval in the ASR group, revealed by both behavioral and EEG measurements, are a reflection of encoding processes rather than of homeostatic changes during recovery sleep.

5. Conclusions

A single night of restricted sleep before training had no apparent negative consequences on behavioral memory recognition assessed after one night of recovery sleep. However, it produced remarkable changes in brain activation patterns during retrieval, as reflected by changes in the power of EEG alpha/delta oscillations in cortical regions involved in the reactivation of semantic/episodic information, as well as by differences in the relationship between the power of this oscillatory activity and behavior. All together, these findings suggest that the two groups are equally successful at remembering face–face associations, most likely because of using different strategies of memory retrieval. Thus, in the control group, memory recognition appears to rely on reinstatement of episodic and semantic aspects of the event, while in the ASR group, it seems to depend on reactivation of different aspects of face perception as revealed by the recruitment of additional perceptual mechanisms in visual association regions through alpha oscillations. Furthermore, the relationship shown by the ASR group between semantic congruency and delta ERS in the ventrolateral prefrontal cortex might also be reflecting activation of additional control strategies that could further serve to either inhibit potential interferences or to compensate for any deficit when accessing semantic and/or episodic information. It remains to be investigated, however, whether differences induced by sleep restriction in different functional cortical networks through alpha and delta oscillations during retrieval translate into memory impairment with the passage of time.

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