Full Length Articles

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

E. Alberca-Reina, J.L. Cantero, M. Atienza *

*Laboratory of Functional Neuroscience, Spanish Network of Excellence for Research on Neurodegenerative Diseases (CIBERNED), Pablo de Olavide University, Seville, Spain*

## ARTICLE INFO

## 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.

© 2015 Elsevier Inc. All rights reserved.

## 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

* Corresponding author at: Laboratory of Functional Neuroscience, Pablo de Olavide University, Carretera de Utrera, Km 1, 41013 - Seville Spain.
 E-mail address: matirui@upo.es (M. Atienza).

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; Heikkilä et al., 2015; Maril 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 synchronization (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.

## Materials and methods

### 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.

### 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 (semantically incongruent faces, SIF), the same profession. 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).