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Semantic congruence reverses effects of sleep restriction on associative encoding

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ABSTRACT

Encoding and memory consolidation are influenced by factors such as sleep and congruency of newly learned information with prior knowledge (i.e., *schema*). However, only a few studies have examined the contribution of sleep to enhancement of schema-dependent memory. Based on previous studies showing that total sleep deprivation specifically impairs hippocampal encoding, and that coherent schemas reduce the hippocampal consolidation period after learning, we predict that sleep loss in the pre-training night will mainly affect schema-unrelated information whereas sleep restriction in the post-training night will have similar effects on schema-related and unrelated information. Here, we tested this hypothesis by presenting participants with face–face associations that could be semantically related or unrelated under different sleep conditions: normal sleep before and after training, and acute sleep restriction either before or after training. Memory was tested one day after training, just after introducing an interference task, and two days later, without any interference. Significant results were evident on the second retesting session. In particular, sleep restriction before training enhanced memory for semantically congruent events in detriment of memory for unrelated events, supporting the specific role of sleep in hippocampal memory encoding. Unexpectedly, sleep restriction after training enhanced memory for both related and unrelated events. Although this finding may suggest a poorer encoding during the interference task, this hypothesis should be specifically tested in future experiments. All together, the present results support a framework in which encoding processes seem to be more vulnerable to sleep loss than consolidation processes.

1. Introduction

Accumulated evidence suggests that natural sleep is critical for successful formation, storage and recovery of new memories (Cirelli & Tononi, 2008; Walker & Stickgold, 2006). Consequently, all these processes may be negatively affected by sleep loss, a common condition associated with modern lifestyle, aging, and prevalent neuropsychiatric disorders. Regarding the particular case of hippocampus-dependent episodic memories, results indicate that total sleep deprivation before training impairs encoding, retention and retrieval of new memories (Drummond et al., 2000; Harrison & Horne, 2000a; Yoo, Hu, Gujar, Jolesz, & Walker, 2007); whereas total sleep deprivation (or chronic sleep restriction) after training impairs consolidation of true memories (for a review see Marshall & Born, 2007; Prince & Abel, 2013), makes them more vulnerable to interference (Alger, Lau, & Fishbein, 2012), and hinders processes of monitoring and decision making (Durmer & Dinges, 2005; Harrison & Horne, 2000b) which may account for enhanced retrieval of false memories that are semantically associated with the encoded event (Diekelmann, Landolt, Lahl, Born, & Wagner, 2008).

However, evidence does not directly support that sleep plays a specific role in all memory stages. In fact, consolidation and neural activity underlying re-activation and strengthening of distributed cortico-cortical connections may also occur during wakefulness (Axmacher, Haupt, Fernández, Elger, & Fell, 2008; Jadhav, Kemere, German, & Frank, 2012). Alternatively, it has been proposed that the specific memory function of sleep could be more related to acquisition processes (Axmacher, Draguhn, Elger, & Fell, 2009). This assumption mainly relies on the synaptic homeostasis hypothesis of sleep (Tononi & Cirelli, 2006). This hypothesis suggests that sleep-dependent synaptic homeostasis may increase signal-to-noise ratios in relevant brain circuits and, hence, serve an important function in memory consolidation; but it further contemplates that the synaptic downscaling may be necessary to encode new information the next day. Accordingly, both total sleep

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deprivation and the selective disruption of slow-wave activity in the pre-training night reduced hippocampal activation during encoding and hindered memory retrieval tested a few days later (Van der Werf et al., 2009; Yoo et al., 2007). Given that a few hours of sleep loss can limit the ability of synapses to increase their strength as a result of experience-dependent plasticity (Cirelli, 2013), we hypothesize that memory formation should also be impaired following acute sleep restriction on a single night.

There is evidence indicating that the influence of sleep on memory encoding may depend on the extent to which the hippocampus is required (e.g., Van der Werf et al., 2009), whereas a vast amount of literature supports the role of sleep in the consolidation of both hippocampal-dependent and hippocampal-independent memories (for recent reviews see Diekelmann & Born, 2010; Rasch & Born, 2013; Stickgold & Walker, 2013). Collectively, prior studies suggest that the magnitude of memory impairment resulting from acute sleep restriction on a single night either before or after training may depend on the level of engagement of the hippocampus during encoding.

The present study is aimed at testing this assumption. For this purpose, one group of subjects was allowed to sleep normally in the night before and after training (control group), whereas two other groups underwent acute sleep restriction either in the pre-training or post-training night. All participants were required to encode and retain coupled faces of famous people. These faces could share, or not, the same profession, which allowed us to test retrieval for semantically congruent and incongruent faces. The reason behind this design is the suggestion that the presence of coherent preexisting knowledge (or *schemas*) facilitates memory encoding and rapid consolidation in the neocortex (Brod, Werkle-Bergner, & Shing, 2013; van Kesteren, Ruiter, Fernández, & Henson, 2012). In our particular case, the prediction is that semantic congruence will facilitate memory formation in the neocortex because only in this condition can the activated associative networks related to the two faces be interconnected through one common schema, the profession. Consequently, if the negative impact of acute sleep restriction on initial memory formation specifically affects the hippocampus (Drummond et al., 2000; Harrison & Horne, 2000a; van der Werf et al., 2009; Yoo et al., 2007), and the benefit of semantic congruence on encoding is mainly mediated by the neocortex (Atienza, Crespo-Garcia, & Cantero, 2011; Crespo-Garcia, Cantero, & Atienza, 2012), memories for semantically incongruent faces should be more negatively affected by sleep restriction in the night before training than memories for semantically congruent faces. However, the same sleep reduction applied in the night after training is expected to have a similar effect on both kinds of memories.

2. Materials and methods

2.1. Participants

Sixty young university students [age 22 ± 2.7 (mean ± SD), range 18–27 yr, 31 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 questionnaires, and regular sleeping habits confirmed by a structured interview and sleep-diaries over a period of one week prior to participation in the experiment (no group differences were found in the mean sleep-time reported in the sleep-diaries, $P > 0.7$). Participants were instructed to abstain from drugs, alcohol, and caffeine for the week before the first experimental session until the end of the experiment. This experiment received Institutional approval by the Ethical Committee for Human Research at the University Pablo de Olavide. Written informed consent was obtained from each participant after a detailed explanation of the experimental protocol.

2.2. Stimuli

Visual stimuli consisted of 96 oval faces in gray-scale, obtained from pictures of Spanish celebrities whose professions were actor, singer, or TV host/newsreader. An equal number of faces was selected for each one of these professional categories and counterbalanced as a function of their popularity and familiarity after performing two pilot studies (see SM1 in Supplementary material). Faces were presented in different experimental conditions, matched in gender, age and emotional expression (either neutral or positive). Face pairs were presented in the center of a 17-in., flat panel computer screen on black background.

2.3. Experimental paradigm

All participants underwent one initial training session and two additional sessions of memory testing one and two days after training respectively. Our main interest was evaluating the effect of sleep restriction on encoding and consolidation of memory for face–face associations under different conditions of semantic congruence. Representative trials of the encoding and retrieval tasks are illustrated in Fig. 1.

In the evening of day 1 (5:00 PM), prior to the study phase, subjects performed two tasks to familiarize themselves with the names and professions of the different faces (see SM2 in Supplementary material). The study phase started an hour and a half later (6:30 PM). During this phase, participants performed a semantic/perceptual-matching task, and were informed that memory for face–face associations would be tested in the two following days. This information is important because sleep selectively enhances consolidation of memories that are relevant for future behavior (Wilhelm et al., 2011). In this task, two faces corresponding to two celebrities of the same gender that could share (semantically congruent faces) or not the same profession (semantically incongruent faces) were presented for 2 s. After an interval of 5 s in which subjects were trained to retain faces and their professions, one face and one profession were presented in the center of the screen. The position of the face and profession, on the left or right side, corresponded to the study face in that particular position. Participants were instructed to give 4 possible responses depending on whether or not the face and profession matched one or both of the two studied faces. As each trial was repeated four times in different blocks, the response was different each time. Face pairs were presented in 8 blocks (48 face pairs per block) separated by short intervals of 2 min and by a longer break of 10 min in the middle of the task.

Previous evidence has shown that introducing a retroactive interference task just before memory testing was a successful strategy to reveal the positive effect of sleep on consolidation of associative memory (Ellenbogen, Hulbert, Stickgold, Dinges, & Thompson-Schill, 2006). In the morning of day 2 (9:00 AM), our subjects performed a retroactive interference task before testing associative memory. In this interference task, faces presented in the semantic/perceptual-matching task were coupled in different ways, maintaining the congruence condition associated to each face.

After an hour of resting (11:30 AM), associative memory for original face pairs was evaluated. This time, all face–face associations were presented as in the original training task but intermixed with the same number of face pairs coupled in a different way (controlling that rearranging maintained the congruence condition associated with each face but never matched face–face associations in the retroactive interference task). Participants were asked to say