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Sleep stage II contributes to the consolidation of declarative memories

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ABSTRACT

Various studies suggest that non-rapid eye movement (NREM) sleep, especially slow-wave sleep (SWS), is vital to the consolidation of declarative memories. However, sleep stage 2 (S2), which is the other NREM sleep stage besides SWS, has gained only little attention. The current study investigated whether S2 during an afternoon nap contributes to the consolidation of declarative memories. Participants learned associations between faces and cities prior to a brief nap. A cued recall test was administered before and following the nap. Spindle, delta and slow oscillation activity was recorded during S2 in the nap following learning and in a control nap. Increases in spindle activity, delta activity, and slow oscillation activity in S2 in the nap following learning compared to the control nap were associated with enhanced retention of face-city associations. Furthermore, spindles tended to occur more frequently during up-states than down-states within slow oscillations during S2 following learning versus S2 of the control nap. These findings suggest that spindles, delta waves, and slow oscillations might promote memory consolidation not only during SWS, as shown earlier, but also during S2.

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1. Introduction

Research of the last decade has produced a large corpus of evidence indicating that sleep plays a key function in the consolidation of newly acquired memories. Consolidation refers to the process by which newly acquired and therefore labile memories are strengthened, stabilized and integrated into long-term memory (Squire, Cohen, & Nadel, 1984). Consolidation in different memory systems is not equally influenced by the various sleep stages (e.g., Plihal & Born, 1997). Central to the present study is the finding that declarative memories – i.e., memories for facts and events that one can consciously recollect (Squire, 1987) – profit from the deep sleep stage slow-wave sleep (SWS). Plihal and Born (1997, 1999) showed that new declarative memories are better remembered if recall follows a period of sleep that is rich in SWS compared to a period of sleep rich in rapid eye-movement (REM) sleep. While there is growing evidence for the relevance of SWS in declarative memory consolidation (for reviews see Diekelmann & Born, 2010; Marshall & Born, 2007), little is known about the specific role of sleep stage 2 (S2), which is the

other sleep stage besides SWS that constitutes human non-rapid eye-movement (NREM) sleep. Our study aims at investigating whether and how S2 is involved in declarative memory consolidation. We asked whether sleep spindle activity, delta wave activity, and slow oscillation activity as measured during S2 in daytime naps, are related to the consolidation of newly acquired declarative memories. Spindles are transient electroencephalographic oscillations of at least 0.5 s duration with a frequency between 11–15 Hz. They are a defining feature of S2 but do occur during SWS as well. Slow oscillations and delta waves are large amplitude electroencephalographic waves of 0.5–1 Hz and 1–4 Hz, respectively. They are defining features of SWS but are also present during S2.

Here, we focus on spindles and slow oscillations because they are thought to contribute to memory consolidation by coordinating the reactivation of memories during sleep and by enhancing the effect of memory reactivation on the neuronal substrate (Diekelmann & Born, 2010; Marshall & Born, 2007). Standard models of memory consolidation (Diekelmann & Born, 2010; Marshall & Born, 2007) posit that new declarative memories (Rasch, Büchel, Gais, & Born, 2007; Rudoy, Voss, Westerberg, & Paller, 2009) are reactivated during sleep. The reactivation of memories presumably leads to long lasting plastic synaptic changes within the neuronal networks that represent these memories. The consolidating effect of sleep is believed to be

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accomplished by these synaptic changes. The beneficial effect of spindles and slow oscillations is assumed to be strongest if spindles occur during the neuronally active up-states of slow oscillations.

We also focus on the activity in the delta frequency range (1–4 Hz) because delta waves might contribute to memory consolidation in similar ways as slow oscillations. Although delta waves differ from slow oscillations with regard to how they are generated (thalamo-cortical versus cortical-cortical interactions; see Steriade, Nunez, & Amzica, 1993a), delta waves may still be functionally similar to slow oscillations (e.g., Sirota, Csicsvari, Buhl, & Buzsáki, 2003; Steriade, 2006). Some authors suggested that delta waves might be faster and less potent exemplars of slow oscillations (Buzsáki, 2006; Marshall & Born, 2007).

Growing evidence suggests that high spindle activity (Clemens, Fabó, & Halász, 2005, 2006) and high slow oscillation activity (Marshall, Helgadóttir, Mölle, & Born, 2006) and delta activity (Marshall, Mölle, Hallschmid, & Born, 2004) recorded during NREM sleep or SWS contribute to declarative memory consolidation. In addition, learning prior to sleep has been shown to redistribute spindles to the neuronally active up-states within slow oscillations during NREM sleep (Möller, Eschenko, Gais, Sara, & Born, 2009). Whether spindles, slow oscillations and delta waves occurring during S2 would also contribute to declarative memory consolidation has rarely been investigated. Some studies suggest that spindles (Gais, Mölle, Helms, & Born, 2002; Genzel, Dresler, Wehrle, Grözinger, & Steiger, 2009; Meier-Koll, Bussmann, Schmidt, & Neuschwander, 1999; Schabus et al., 2004; van der Helm, Gujar, Nishida, & Walker, 2011) and delta waves (Wamsley, Tucker, Payne, & Stickgold, 2010) during S2 might be relevant to the consolidation of declarative memories. However, most investigations on the memory functions of S2 point to a role of S2 in the consolidation of procedural motor memories – i.e., nondeclarative memories (Backhaus & Junghans, 2006; Genzel et al., 2009; Smith & Macneill, 1994). Performing new procedural motor tasks before going to sleep increases not only the amount of time spent in S2 (Fogel & Smith, 2006; Fogel, Smith, & Cote, 2007) but also the spindle density in S2 (Fogel & Smith, 2006; Fogel et al., 2007; Peters, Ray, Smith, & Smith, 2008). Both, the increased amount of S2 (Nishida & Walker, 2007; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002) and the increased spindle density (Fogel & Smith, 2006; Nishida & Walker, 2007; Peters, Smith & Smith, 2007) were correlated with the gain in the performance of the motor task from pre- to post-sleep.

Here, we investigated whether and how S2 during a brief afternoon nap contributes to the consolidation of declarative memories. We administered an associative learning task prior to an afternoon nap and measured retrieval performance with a cued recall task given both before and following the nap. We computed performance changes in the cued recall task from pre- to post-sleep and correlated these changes with the occurrence of sleep spindles, delta waves and slow oscillations during S2. We also correlated the performance change across sleep with the difference in participants' spindle, delta and slow oscillation activity between their experimental nap (that followed the declarative memory task) and their control nap (that did not follow a declarative memory task). We expected an association between memory retention and a heightened spindle, delta and slow oscillation activity in S2 during the experimental but not the control nap.

2. Method

2.1. Participants

Participants were 24 men between 19 and 30 years of age ($M=23.5$, $SD=3.2$). They reported no current or past neurological or psychiatric symptoms and denied to take prescription or illegal drugs. Sleep diaries and actigraphy confirmed that all

participants had normal sleep routines. We excluded habitual nappers from participation because habitual napping has been associated with sleep pathologies (Masa et al., 2006) and irregular sleep-wakefulness patterns (Vela-Bueno et al., 2008). The local ethics committee approved the study.

2.2. Design and procedure

Participants were tested in two sessions that each comprised an afternoon nap. The first session included a declarative associative learning task and constituted the experimental condition. One or two weeks later, we scheduled the second session with the same participants (within subjects design). The second session constituted the control condition, which included the same associative learning task that was now given subliminally for unconscious associative encoding. Because retrieval testing revealed no effects of subliminal encoding (see results), this condition may be regarded a non-learning control condition. The sequence of the two conditions was not counterbalanced because we had hoped that subliminal learning would profit from the experience gathered in a first session with similar procedures (Eckstein & Perrig, 2007; Kiefer & Martens, 2010; Reber & Henke, 2011).

Preparation for both test sessions was identical: participants were asked to sleep only 5 h (from 2 a.m. to 7 a.m.) in the night preceding each session. Sleep restriction was used to increase the amount of sleep in the laboratory. On both test sessions, participants arrived at 10 a.m. in the laboratory and were prepared for standard polysomnography (PSG). At 12 p.m. they were served lunch in the laboratory.

2.2.1. Experimental condition

In the experimental condition, participants took a declarative learning task following lunch. They learned new associations between 24 faces and a European or a North American city. To this end, we presented images of faces with a written city underneath (e.g., Berlin or New York). The presentation duration of each face-city combination was 5 s. The encoding task was to judge whether it was easy or hard to imagine the depicted person acting in a scene within the particular city. This is an incidental encoding procedure, i.e., participants were not aware of being in a learning situation that would be followed by a memory test. The naivety regarding memory testing was important because it precluded an active rehearsal between study and test, which might bias the data. We assumed that the generation of idiosyncratic mental images of a person acting in a specific scene within the indicated city would yield strong declarative memories for the face-city associations. To enhance associative encoding, all face-city combinations were presented 3 times with the instruction to imagine the same scene for a given person and city in all three learning trials. To conceal the memory purpose of the task, participants were told that the task measured imagination and creativity alone. Memory for the learned face-city associations was assessed with a cued recall test. Half of the learned faces were given as cues for the recall of associated cities (verbal response) 5 min following learning, i.e., before going to sleep (presleep recall), and the other half following the 90-minute-nap (postsleep recall).

2.2.2. Control condition

In the control condition, participants were presented with 24 masked face-city combinations (new stimulus set) for unconscious associative encoding. Procedures for subliminal encoding and retrieval were the same as in Henke et al. (2003) and Duss, Oggier, Reber, and Henke (2011). For subliminal encoding, we presented faces combined with written names of cities short enough to escape conscious perception. During the subliminal presentation of face-city combinations, of which participants were oblivious, they performed an attention task that directed their gaze to a periodically flashed fixation cross that appeared in the center of the projection screen. Participants' tasks were to indicate by button press when a horizontal or vertical line segment was being presented instead of a fixation cross. Participants needed to pay close attention to the center of the screen in order to detect those trials. The stimuli that were critical for the attention task (A) consisted of a black background with either a white central fixation cross (A_{FIX}) or a white central line segment with vertical (A_V) or horizontal (A_H) orientation. These attention task stimuli were presented for 233 ms with a SOA of 1 s. The subliminal face-city combinations (s) were presented twelvefold for 17 ms within a 6 s encoding trial, interleaved with the attention task stimuli and forward and backward masks. Masks were presented for 183 ms and consisted of black-and-white visual noise images. Here is an example stream of images that would form one encoding trial: $A_{FIX}-m-s-m-m-s-m-A_{FIX}-m-s-m-m-s-m-A_{FIX}-m-s-m-m-s-m-A_H-m-s-m-m-s-m-A_{FIX}-m-s-m-m-s-m-A_{FIX}-m-s-m-m-s-m$. The position within the 6 s time window and the orientation of the line segment, to which participants were supposed to react, was varied between encoding trials.

As in the experimental condition, memory for the subliminal face-city combinations was assessed with a cued retrieval test, which in the control condition was administered with indirect retrieval instructions. Faces from subliminal encoding were now re-presented suprathreshold, for 5 s each, as cues to reactivate memories of associated cities. Half of faces were used for the presleep

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