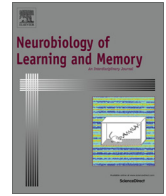




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Sleep's role in the reconsolidation of declarative memories



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ABSTRACT

Sleep is known to support the consolidation of newly encoded and initially labile memories. Once consolidated, remote memories can return to a labile state upon reactivation and need to become reconsolidated in order to persist. Here we asked whether sleep also benefits the reconsolidation of remote memories after their reactivation and how reconsolidation during sleep compares to sleep-dependent consolidation processes. In three groups, participants were trained on a visuo-spatial learning task in the presence of a contextual odor. Participants in the 'reconsolidation' group learned the task on day 1. On day 2, they were subjected to a reactivation procedure by presenting the odor cue and a mock recall test in the learning context before a 40-min sleep or wake period. Participants in the 'remote consolidation' group followed the same procedure but did not receive reactivation on day 2. Participants in the 'recent consolidation' group skipped the procedure on day 1 and learned the task immediately before the sleep or wake period. After the sleep or wake interval, memory stability was tested in all subjects. The results show that this short 40-min sleep period significantly facilitated the reconsolidation of reactivated memories, whereas the consolidation of non-reactivated remote memories was less affected and recently encoded memories did not benefit at all. These findings tentatively suggest that sleep has a beneficial effect on the reconsolidation of remote memories, acting at a faster rate than sleep-associated consolidation.

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1. Introduction

Recently acquired memories are initially labile and susceptible to interference and forgetting. They require consolidation, a process in which they are qualitatively transformed and stabilized into long-term memory (Dudai, Karni, & Born, 2015; Kandel, Dudai, & Mayford, 2014). Once consolidated, memories are relatively resistant to alteration or disruption by amnesic treatments (Nader & Hardt, 2009). When such remote memories are reactivated by active recall or reminders they can again become labile and require reconsolidation to persist, which has been demonstrated in different organisms (from sea slugs to humans) and different memory types (from fear conditioning to spatial memory) (Nader & Einarsson, 2010; Nader & Hardt, 2009). In humans, consolidated

memories have been shown to have returned to a labile state by reactivation in procedural learning (Walker, Brakefield, Hobson, & Stickgold, 2003), declarative syllable-pair associations (Forcato et al., 2007), episodic memories of real-world items (Hupbach, Gomez, Hardt, & Nadel, 2007; Hupbach, Gomez, & Nadel, 2011; Hupbach, Hardt, Gomez, & Nadel, 2008), and even fear responses (Schiller et al., 2010). While the precise timescale on which reconsolidation operates is still unknown, there is evidence suggesting that reconsolidation processes act faster than original consolidation processes (Debiec, LeDoux, & Nader, 2002; Gordon, 1977).

Sleep is known to facilitate the consolidation and stabilization of new memories. A sleep period following new learning improves subsequent memory retrieval as well as memory stability when compared to a wake retention interval of equal length (Diekelmann & Born, 2010; Rasch & Born, 2013). Specifically slow wave sleep (SWS) has been linked to the consolidation of declarative memories (Alger, Lau, & Fishbein, 2012; Plihal & Born, 1997; Yaroush, Sullivan, & Ekstrand, 1971) with some evidence pointing to a particularly important role of sleep stage 4, i.e. deepest SWS (Barrett & Ekstrand, 1972; Fowler, Sullivan, & Ekstrand, 1973;

Abbreviations: SWS, slow wave sleep; NonREM, non-rapid eye movement; REM, rapid eye movement; TST, total sleep time; S1–4, sleep stages 1–4.

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Wilhelm et al., 2011). For sleep to benefit the consolidation of new declarative memories, a certain minimal amount of sleep seems to be necessary. A previous study found that a sleep period of 90 min successfully stabilized memories against interference, with this effect being associated with the amount of SWS obtained, whereas a 40 min sleep period was not sufficient for memory consolidation (Diekelmann, Biggel, Rasch, & Born, 2012).

Despite our increasing knowledge about consolidation processes during sleep, the role of sleep in the reconsolidation of declarative memories is unclear. Here we asked whether sleep facilitates the reconsolidation of declarative memories and how the effect of sleep on reconsolidation compares to the effect on consolidation. To study reconsolidation, we applied a reminder approach that combined learning-associated odor cues, the same learning environment (i.e. same room and experimenter), and a staged recall procedure to reactivate visuo-spatial memories that had been learned 24 h before. Following the reactivation session, subjects either were allowed to sleep for 40 min or stayed awake for an equivalent time interval before retrieval was tested. The 40 min sleep duration was chosen based on the idea that (i) reconsolidation processes act at a faster rate than consolidation processes (Debiec et al., 2002; Gordon, 1977) and (ii) that 40 min of sleep are not sufficient to consolidate new memories (Diekelmann et al., 2012). Accordingly, we hypothesized that 40 min of sleep following reminder presentation rapidly restabilize (reconsolidate) the labilized memory traces and thereby improve resistance to subsequent interference learning. In contrast to reconsolidation, we expected no effect of the 40-min sleep period on the consolidation of either remote memories that are not reactivated before sleep (remote consolidation) or recent memories that are encoded immediately before sleep (recent consolidation).

2. Methods

2.1. Participants

A total of 104 subjects (53 females) between 18 and 30 years (mean age \pm SD: 22.92 \pm 2.62 years) were allocated to one of three groups: the 'reconsolidation' group ($n = 34$), the 'remote consolidation' group ($n = 40$) or the 'recent consolidation' group ($n = 30$). In each of these groups, subjects were equally distributed into sleep and wake conditions. None of the participants reported ongoing medication, health problems, medical interventions, or a history of psychiatric, neurological, or sleep disorders. Further exclusion criteria were night or shift work as well as exam periods and other learning- or stress-intense occupations for at least three weeks prior to the experiment. On experimental days, daytime naps, extensive physical exercise as well as the intake of alcohol or caffeine were prohibited. Subjects in the sleep conditions spent an adaptation night in the sleep laboratory to habituate to sleeping under the experimental conditions. The study was approved by the local ethics committee of the medical faculty of the University Tübingen and all subjects gave written informed consent.

2.2. Experimental procedure

The experimental procedures are outlined in Fig. 1. In the reconsolidation and remote consolidation groups subjects learned an object-location task in the evening of day 1 between 20:30 and 21:30. The task was performed in the presence of an odor, linking this odor to the content and context of the learning task. An odor detection test (10 trials) that was performed before and after learning was designed to further strengthen the association between task and learning context. Following learning, participants left the laboratory for a full night of sleep at home.

On day 2 (around 24 h after learning), subjects in the reconsolidation group returned to the lab at around 21:00 for the reminder session. Participants in the sleep condition had EEG electrodes attached for later polysomnographic recordings before the start of the reminder session. The reminder session took place in the same learning context, i.e. the same building and same room, and included a staged testing procedure that was set up to act as a strong reminder of the initial learning situation. Subjects were told that they would be tested for their memory of the object-location task that they had learned the day before. However, during the first trial of the recall test, right before an answer could be given for the first cue, the program appeared to crash. Subjects were told that it had been a mistake to start the testing procedure at this point of the experiment and that the actual testing would take place later on. An extended odor detection test (with 30 instead of 10 trials) was performed before and after the staged recall, utilizing the property of odors to act as contextual reminders. After the reminder session, participants either went to bed at 23:00 ('sleep condition', $n = 16$) or stayed awake and watched a movie ('wake condition', $n = 18$). After about 40 min of sleep or wakefulness and another 30 min break, participants in both conditions learned an interference task. About 30 min after the end of interference learning, memory for the original object-location task was tested.

In the remote consolidation group ('sleep condition' $n = 18$, 'wake condition' $n = 22$), subjects followed the same procedure as in the reconsolidation group, with the important difference that on day 2 (a) the experiment was conducted at a different site (i.e. a different building and room) to reduce potential context reminders of the learning environment, and (b) they did not receive the reminder procedure (i.e. the staged recall and odor cues). Subjects arrived at the lab between 21:45 and 22:15 and in the sleep condition went to bed at around 23:00 after attachment of the EEG electrodes.

In the recent consolidation group, subjects arrived at the laboratory at 21:00 and learned the object-location task at 22:00, after attachment of the EEG electrodes for subjects in the sleep condition. Following the learning procedure, participants either slept ($n = 16$) or stayed awake ($n = 14$) like in the other groups. The remaining procedure was identical to the reconsolidation and remote consolidation groups.

2.3. Object-location task

Subjects performed a two-dimensional object-location memory task, in which locations of card pairs were learned, resembling the game 'concentration' (Diekelmann, Büchel, Born, & Rasch, 2011; Diekelmann et al., 2012; Rasch, Büchel, Gais, & Born, 2007). The task involves associative visuo-spatial memory and relies on structures in the medial temporal lobe (Sommer, Rose, & Gläscher, 2005). 15 card pairs, which depicted animals and everyday objects in full color, were shown on a computer screen in a 5×6 matrix. During learning, the locations of all 15 card pairs were presented twice. For each card pair, the first card was presented for one second, followed by the presentation of both cards for three seconds, with an inter-trial interval of three seconds until the next card pair appeared. The experimental odor was administered during the four seconds of stimulus presentation. After completing the two learning runs, immediate recall was tested. For this, the first card of each pair was presented and subjects were asked to indicate the location of the second card with the computer mouse. Visual feedback was given for each decision (either a green checkmark for 'correct' or a red cross for 'incorrect') and the cards were shown in their correct positions for two seconds. After recall of all card pairs was finished, visual feedback on the percentage of correct responses was given to the participant. The test was repeated until a criterion of

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