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Nap sleep preserves associative but not item memory performance

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ABSTRACT

Many studies have shown that sleep improves memory performance, and that even short naps during the day are beneficial. Certain physiological components of sleep such as spindles and slow-wave-sleep are thought to be particularly important for memory consolidation. The aim of this experiment was to reveal the role of naps for hippocampus-dependent associative memory (AM) and hippocampus-independent item memory (IM) alongside their corresponding ERP old/new effects. Participants learnt single words and word-pairs before performing an IM- and an AM-test (baseline). One group was subsequently allowed to nap (~90 min) while the other watched DVDs (control group). Afterwards, both groups performed a final IM- and AM-test for the learned stimuli (posttest). IM performance decreased for both groups, while AM performance decreased for the control group but remained constant for the nap group, consistent with predictions concerning the selective impact of napping on hippocampus-dependent recognition. Putative ERP correlates of familiarity and recollection were observed in the IM posttest, whereas only the later recollection-related effect was present in the AM test. Notably, none of these effects varied with group. Positive correlations were observed between spindle density during slow-wave-sleep and AM posttest performance as well as between spindle density during non-REM sleep and AM baseline performance, showing that successful learning and retrieval both before and after sleep relates to spindle density during nap sleep. Together, these results speak for a selective beneficial impact of naps on hippocampus-dependent memories.

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1. Introduction

Sleep is thought to play an important role in memory consolidation. An increasing number of studies have shown benefits in different memory tasks after sleep compared to a comparable time awake (Diekelmann & Born, 2010; Diekelmann, Wilhelm, & Born, 2009). In declarative memory tasks, sleep benefits have been demonstrated, amongst others, for associated items (Marshall, Molle, Hallschmid, & Born, 2004; Tucker & Fishbein, 2008; Tucker et al., 2006) and in spatial memory tasks (Peigneux et al., 2004; Plihal & Born, 1999). It is currently thought that hippocampusdependent memory consolidation benefits from non-REM (NREM) sleep, in particular from slow oscillations (<1 Hz) during slow-wave-sleep (SWS) and associated sleep spindles (oscillations between 12 and 15 Hz) (Born, Rasch, & Gais, 2006; Born & Wilhelm, 2012).

Although there is increasing evidence for the beneficial impact of sleep on declarative memory consolidation, less is known about

E-mail addresses: s.studte@mx.uni-saarland.de (S. Studte), e.bridger@mx. uni-saarland.de (E. Bridger), mecklinger@mx.uni-saarland.de (A. Mecklinger). the impact of nap sleep on recognition memory. The aim of the present study was to use behavioral and ERP measures of recognition memory together with polysomnographic data to investigate the benefits of nap sleep and the mechanisms by which nap sleep enhances declarative memory retention.

To date, a number of studies have shown that the density of sleep spindles is associated with enhanced declarative memory (Gais, Molle, Helms, & Born, 2002; Mednick et al., 2013; Saletin, Goldstein, & Walker, 2011; Schabus et al., 2004; Schmidt et al., 2006). Mednick et al. (2013) experimentally increased spindle density with a drug during a daytime nap, which led to better word-pair associate memory performance compared with a placebo. A recent study by Cox, Hofman, and Talamini (2012) indicated that the beneficial effect of sleep spindles on memory is specific to SWS by showing not only that spindle density in SWS is higher than in light sleep (S2) but that only spindle density in SWS and not in light sleep was positively correlated with memory performance. This pattern suggests that the beneficial effect of sleep spindles on memory consolidation is dependent on the co-occurrence of slow oscillations (Cox et al., 2012).

According to the active system consolidation hypothesis, benefits come about because new declarative information is initially encoded in both the hippocampus and neocortex from where, in a





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second step, it is gradually transformed so that neocortical memories become independent of the hippocampus (O'Reilly, Bhattacharyya, Howard, & Ketz, 2011; Rasch & Born, 2013). It is assumed that much of this transfer takes place during sleep by covert neuronal reactivations (Born & Wilhelm, 2012; Diekelmann & Born, 2010). Consistent with this view, neuronal reactivation has been reported during sleep, particularly in regions that were active during encoding (Ji & Wilson, 2007; Peigneux et al., 2004; Rasch, Buechel, Gais, & Born, 2007; Sirota, Csicsvari, Buhl, & Buzsaki, 2003).

Although some of the neurophysiological mechanisms by which sleep can boost declarative memory have been identified, findings of sleep effects on recognition memory are less consistent and much less is known about how recognition memory can benefit from sleep or from nap sleep in particular (Daurat, Terrier, Foret, & Tiberge, 2007; Drosopoulos, Wagner, & Born, 2005; Hu, Stylos-Allan, & Walker, 2006; Mograss, Godbout, & Guillem, 2006: Mograss, Guillem, & Godbout, 2008: Wagner, Kashvap, Diekelmann, & Born, 2007), According to dual process models, recognition memory is composed of two processes (Yonelinas, Aly, Wang, & Koen, 2010). One is a fast and context-free process, called familiarity and the second, named recollection, is thought to be a slower and effortful process by which contextual details of a prior episode can be recovered (Yonelinas, 2002). These two processes are not mutually exclusive but there is nevertheless evidence that recollection- and familiarity-based recognition decisions are supported by distinct neuronal systems (Skinner, Manios, Fugelsang, & Fernandes, 2014; Yonelinas, Otten, Shaw, & Rugg, 2005). In agreement with the general assumption that hippocampus-dependent memory consolidation benefits from sleep, some studies investigating sleep effects on recognition memory demonstrate benefits only for recollection but not for familiarity (Daurat et al., 2007; Drosopoulos et al., 2005). Using a word list discrimination task together with a process dissociation procedure to estimate familiarity and recollection, Drosopoulos et al. (2005) found that especially early night sleep enhanced recollection, whereas familiarity was not affected by sleep. Daurat et al. (2007) used a remember/know paradigm to examine the effects of SWS and REM sleep on familiarity and recollection. The recollection estimate was enhanced after a 3-h retention interval filled with SWS as compared to retention intervals filled with REM sleep or no sleep at all. Once again, familiarity was not modulated by any of the retention interval manipulations.

It remains to be shown, however, whether recollection-specific increases in performance can be induced on the basis of SWS-rich nap sleep alone. This was addressed in the current study using two independent approaches to assess recollection and familiarity. Firstly, two separate recognition tasks – differing in the extent to which recollection is required for task performance – were employed. Secondly, indices of putative neural correlates of recollection and familiarity were recorded.

One kind of memory task which is thought to make familiaritybased decisions insufficient to support correct responding are associative tests (Yonelinas et al., 2010). Whereas in item memory (IM) tests stimuli can be either classified as old (learnt) or new (not learnt) on the basis of familiarity as well as recollection, in associative memory (AM) tests subjects are required to discriminate between old (learnt) pairs and recombined (learnt but new configurations of items) pairs. By this, associative memory tests provide a more sensitive measure for recollection than item memory tests, because old and recombined pairs cannot be discriminated on the basis of familiarity (Hockley & Consoli, 1999; Yonelinas, 1997)¹ and finding sleep related changes in an associative memory

task and no corresponding differences in an item memory task can be taken as evidence that recollection is principally affected by nap sleep. Notably, familiarity- and recollection-based processes have also been associated with distinct event-related potential (ERP) old/new effects (Friedman & Johnson, 2000; Mecklinger, 2000; Rugg & Curran, 2007). An early mid-frontal old/new effect has been shown to operate in a way which is consistent with an index of familiarity (Bridger, Bader, & Mecklinger, 2014) while the late parietal old/new effect has been shown to correlate with recollection-based memory judgments (Curran & Cleary, 2003) and the amplitude of this late parietal old/new effect varies with the amount recollected (Vilberg, Moosavi, & Rugg, 2006). To our knowledge, only Mograss et al. (2006, 2008) explored sleep effects on recognition memory using ERPs as a dependent measure so far. They report enhanced performance and larger ERP old/new effects at frontal and posterior recording sites for a sleep as compared to a wake control group. Unfortunately, however, these data were not used to explore the possibility that familiarity and recollection might be differentially impacted by sleep. Polysomnographic data was also not recorded during sleep periods in these studies, precluding the possibility to test for correspondences between enhanced memory performance and specific sleep parameters.

In the present study, the effects of nap sleep on associative and item recognition memory and their reflection in the ERP correlates of familiarity and recollection were examined using a dual process perspective. Based on the aforementioned data points indicating that hippocampus-dependent (declarative) memory seems to benefit from sleep, in particular SWS, we predicted a beneficial effect of sleep on memory performance only in the AM test. This should be reflected by less deterioration from pre- to post-sleep in AM as compared to IM performance for the nap compared to control group. Furthermore, AM posttest performance within the nap group should be associated with high spindle density (in particular spindle density during SWS (Cox et al., 2012)). Corresponding correlations between IM performance and sleep EEG parameters, as well as group differences in IM performance and the ERP correlate of familiarity at posttest were not expected. In line with the expectation that the benefit of hippocampusdependent memory from sleep reflects an enhancement of recollection, we anticipated that the late parietal old/new effect, the putative ERP correlate of recollection, would be larger after sleep compared to the control group.

2. Materials and methods

2.1. Participants

73 healthy young adults from Saarland University/HTW Saarland participated in this experiment. Data from 17 subjects were excluded due to being at chance level in their baseline memory performance (average performance across conditions at or below 50% in the IM baseline test and/or 33% in the AM baseline test). The remaining 56 participants were randomly divided into two groups, either a nap or a control group. Data from an additional 15 subjects were excluded due to performance below 2 SD of the mean of the group at IM posttest and/or AM posttest (n = 5), not sleeping (no occurrence of stage 2 sleep) in the nap group (n = 5), or sleeping (occurrence of stage 2 sleep) while being in the wake control group (n = 5). From the remaining 41 participants, the nap group (n = 22) consisted of 13 females and 9 males with a mean age of 22.1 (SD 2.4). The mean age of the control group (n = 19, 10 females) was 22.1 (SD 2.2) years. All participants stated that they did not have any sleep disorders, had no known neurological problems and that they were right-handed (Oldfield, 1971). All participants gave written informed consent and were paid at a rate of $8 \in /h$ or with course credit.

¹ Under some circumstances familiarity is thought to be useful in associative tests, i.e. with certain kinds of semantic associations (Kriukova, Bridger, & Mecklinger, 2013). The current study used unrelated word-pairs to minimize this.

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