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Research report

Evidence for two distinct sleep-related long-term memory consolidation processes

Monika Schönauer [a,b,c,*], *Melanie Grätsch* [b] *and Steffen Gais* [b,c]

[a] *Bernstein Center for Computational Neuroscience, LMU BioCenter, Planegg-Martinsried, Germany*
[b] *General and Experimental Psychology, Department of Psychology, Ludwig-Maximilians-Universität München, Munich, Germany*
[c] *Medical Psychology and Behavioral Neurobiology, Eberhard Karls Universität Tübingen, Tübingen, Germany*[1]

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ABSTRACT

Numerous studies examine the effect of a night's sleep on memory consolidation, but few go beyond this short time-scale to test long-lasting effects of sleep on memory. We investigated long-term effects of sleep on typical memory tasks. During the hours following learning, participants slept or stayed awake. We compared recall performance between wake and sleep conditions after delays of up to 6 days. Performance develops in two distinct ways. Word pair, syllable, and motor sequence learning tasks benefit from sleep during the first day after encoding, when compared with daytime or nighttime wakefulness. However, performance in the wake conditions recovers after another night of sleep, so that we observe no lasting effect of sleep. Sleep deprivation before recall does not impair performance. Thus, fatigue cannot adequately explain the lack of long-term effects. We suggest that the hippocampus might serve as a buffer during the retention interval, and consolidation occurs during delayed sleep. In contrast, a non-hippocampal mirror-tracing task benefits significantly from sleep, even when tested after a 4-day delay including recovery sleep. This indicates a dissociation between two sleep-related consolidation mechanisms, which could rely on distinct neuronal processes.

1. Introduction

Sleep represents an important part of daily life. Whereas early theories of sleep function emphasized mainly recuperation and energy conservation, more recently, its role in cognitive performance has come into focus. Astonishingly, only few aspects of cognition have proven to be consistently affected by sleep, the most prominent of which are probably sustained attention and memory. Sustained attention is impaired by lack of sleep (Killgore, 2010); memory performance is enhanced by sleep (Diekelmann & Born, 2010). Systems memory consolidation is one mechanism by which sleep can support memory formation. By reactivation and consequent

* *Corresponding author*. Medical Psychology and Behavioral Neurobiology, Eberhard Karls Universität Tübingen, Silcherstr. 5, 72076 Tübingen, Germany.
E-mail addresses: monika.schoenauer@medizin.uni-tuebingen.de (M. Schönauer), steffen.gais@uni-tuebingen.de (S. Gais).
[1] Tel.: +49 7071 29 77321.

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strengthening, neuronal traces of newly learned memories are thought to be integrated into existing memory networks and made more durable (Rasch, Büchel, Gais, & Born, 2007; Stickgold & Walker, 2013). Reactivation is supposed to originate in the hippocampus. Hippocampal reactivation then leads reactivation in neocortical or striatal areas (Ji & Wilson, 2007; Lansink, Goltstein, Lankelma, McNaughton, & Pennartz, 2009). This mechanism can therefore be assumed to underlie mainly hippocampus-dependent memory (Inostroza & Born, 2013). However, it has been proposed to also mediate consolidation of some procedural tasks with hippocampal contributions, possibly linked to explicit aspects of these tasks (Cohen, Pascual-Leone, Press, & Robertson, 2005; Geyer, Mueller, Assumpcao, & Gais, 2013; Robertson, Pascual-Leone, & Press, 2004; Schönauer, Geisler, & Gais, 2014; Walker, Stickgold, Alsop, Gaab, & Schlaug, 2005). Reactivation of learning-related neural activity during sleep can be observed not only in the hippocampus, but in many of the regions involved in learning (Maquet et al., 2000). Whether consolidation in all memory systems relies on the same neuronal processes is still unclear.

When considering typical experimental designs used to study the effects of sleep on declarative memory, large gaps in our knowledge become apparent. Mostly, participants have to learn some kind of material before a period of sleep or wakefulness, and they are asked to retrieve this material afterward. The duration of the retention interval usually lies between 1 and 24 h. Often, retention periods filled with sleep are directly compared with periods filled with wakefulness. While appropriate for many research questions, some central positions cannot be analyzed using this experimental design. First, it is difficult to distinguish between effects of sleep on consolidation of previously learned memory and effects of sleep on following memory retrieval: memory retrieval may be impaired because of fatigue after a night of sleep deprivation. Confounds include effects of prior sleep on following memory encoding and circadian factors when comparing morning–evening versus evening-morning settings. Finally, because many studies use short retention intervals, only little is known about long-term effects of sleep on memory. Examining long-term effects of sleep on memory can give a more comprehensive view of the extended consolidation process and its neuronal dynamics. It can thus shed further light on the specific mechanisms that mediate consolidation in different memory systems.

As mentioned above, most studies on declarative memory test performance within the first 24 h after learning. Only occasionally, experimental designs include recovery sleep, mainly with the intention to avoid effects of acute fatigue in designs using sleep deprivation. Just a few studies systematically explore longer retention intervals after sleep deprivation, and most of these are quite old (Rasch & Born, 2013). The longest interval tested for non-emotional declarative memory – six days between learning and recall – was investigated by Graves (1937). She tested whether learning in the evening (sleeping after learning) or learning in the morning (staying awake after learning) influenced retention after 24, 48, 72, 96 or 144 h. She used nonsense syllables as learning material and the savings method as performance measure, i.e., the reduction in the number of relearning repetitions required for perfect list reproduction. Graves found a long-range effect of sleep on syllable recall developing after 72 h, but none before that. Apart from being only a single-participant study – testing the author herself – and not using a standardized method of presentation, this study confounds circadian effects with effects of sleep. The finding was replicated by another study, which used a very similar study design and the same task, but employed a larger group of participants and better-controlled experimental conditions (Richardson & Gough, 1963). These authors also find a similar delay in the onset of effects. They find no difference between the sleep and wake conditions after 24 and 48 h, but only after 144 h. These results stand in contrast to a large body of recent literature which stresses immediate effects of sleep on memory performance (Diekelmann & Born, 2010).

Apart from these older findings, some more recent studies examined memory performance following consolidation in sleep or wakefulness after 2- or 3-day intervals. Gais et al. (2007) saw a significant sleep effect on word-pair learning after a 44-h retention interval comprising two nights of sleep or one night of sleep deprivation and one night of recovery sleep. In a comparable study design, Gais, Lucas, and Born (2006) found a positive effect of sleep on foreign language vocabulary after a 48-h interval containing two undisturbed nights of sleep or one night of sleep deprivation and one night of recovery sleep. However, no significant effect of sleep versus sleep deprivation on behavioral performance was found after 3 days for spatial memory in a virtual maze task (Orban et al., 2006). Sterpenich et al. (2007) tested recognition in a remember/know paradigm and found a significant positive effect of sleep on recollection of neutral and emotionally positive images when comparing three nights of sleep with one night of sleep deprivation and two recovery nights. In the same study, emotionally negative material did not show long-term benefits of sleep. Smith (1995) briefly reports of a study that did not find effects of sleep deprivation after learning on word recognition and figure reproduction one week later.

Regarding retention intervals longer than a few days, evidence is exceptionally scarce. There are several fMRI studies that assessed performance after 6-months delays, demonstrating clear differences in recall-related brain activity, but finding no significant differences in performance between participants who slept or were sleep-deprived after learning (Gais et al., 2007; Rauchs et al., 2008; Sterpenich et al., 2009). Only one study reports that three hours of sleep after learning dramatically increase recognition memory for emotional texts in an unannounced test four years after the original experiments (Wagner, Hallschmid, Rasch, & Born, 2006). In the same experiment, non-emotional texts did not benefit from sleep.

In the domain of non-declarative memory, effects induced by one night of sleep deprivation can be long lasting: participants will not benefit from practicing a visual discrimination task if they are sleep deprived for one single night after learning the task, even if performance is measured after several recovery nights. The benefit of sleep, on the other hand, persists even after a week (Stickgold, James, & Hobson, 2000). Similarly, a motor adaptation task shows sleep-induced improvements three days after a night of sleep or sleep