



The role of sleep in false memory formation

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ABSTRACT

Memories are not stored as exact copies of our experiences. As a result, remembering is subject not only to memory failure, but to inaccuracies and distortions as well. Although such distortions are often retained or even enhanced over time, sleep's contribution to the development of false memories is unknown. Here, we report that a night of sleep increases both veridical and false recall in the Deese–Roediger–McDermott (DRM) paradigm, compared to an equivalent period of daytime wakefulness. But while veridical memory deteriorates across both wake and sleep, false memories are preferentially preserved by sleep, actually showing a non-significant improvement. The same selectivity of false over veridical memories was observed in a follow-up nap study. Unlike previous studies implicating deep, slow-wave sleep (SWS) in declarative memory consolidation, here veridical recall correlated with *decreased* SWS, a finding that was observed in both the overnight and nap studies. These findings lead to two counterintuitive conclusions – that under certain circumstances sleep can promote false memories over veridical ones, and SWS can be associated with impairment rather than facilitation of declarative memory consolidation. While these effects produce memories that are less accurate after sleep, these memories may, in the end, be more useful.

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0. Introduction

Growing evidence suggests that sleep plays an important role in memory consolidation (Payne, Ellenbogen, Walker, & Stickgold, 2008b; Rasch & Born, 2007; Smith, 1995; Stickgold, 2005; Walker & Stickgold, 2006). While sleep's benefit was once thought to apply mainly to procedural forms of memory, it has recently been shown to benefit declarative memory as well (see Marshall & Born, 2007; Payne et al., 2008b for review). Memory consolidation is often conceptualized as a time-dependent, off-line process that stabilizes memories against interference and decay, allowing them to persist over time (McGaugh, 2000). This notion of memory stabilization implies that memories are solidified in high fidelity, true to their original form. Yet substantial evidence shows that memories can become increasingly distorted with time (Bartlett, 1932; McDermott, 1996; Payne, Elie, Blackwell, & Neuschatz, 1996; Seamon

et al., 2002), suggesting that the process of consolidation does not always yield veridical representations of our experiences.

A large body of research has focused on the formation of false memories, in which people recollect events that never occurred (Brainerd & Reyna, 2005; Gallo, 2006; Roediger & McDermott, 2000; Schacter & Slotnick, 2004). Yet, while a growing number of studies support a role for sleep in the consolidation of veridical information, it is unknown whether sleep also influences the development of false memories. Understanding whether sleep affects the formation of false memories is important because it is directly related to questions about how memories are consolidated and stored, how memory representations change over time, and whether these changes can be useful and adaptive.

Here, we tested whether sleep influences false recall, using a list learning task known as the Deese–Roediger–McDermott (DRM) paradigm (e.g. Roediger & McDermott, 1995). This declarative memory task reliably produces high rates of confident false memories for unstudied “critical” words (e.g. *window*) that are semantically associated to studied wordlists (e.g. *door, glass, pane, shade, ledge, sill, house, open, curtain*, etc.). Previous research has demonstrated that long-term memory for critical words actually exceeds veridical memory for studied words (McDermott, 1996; Payne et al., 1996; Seamon et al., 2002; Toglia, Neuschatz, & Goodwin,

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1999). For example, McDermott (1996) demonstrated that a 2-day delay between study and test produced levels of false recall that exceeded levels of veridical recall, noting that, unlike many DRM studies of immediate memory where veridical and false recall tend to increase together, over longer delays false memories persist over veridical ones. Thus, in addition to the encoding and retrieval factors known to influence false memory (Brainerd & Reyna, 2005; Gallo, 2006), these studies raise the possibility that slow, offline memory consolidation processes influence false memory development as well. This prediction seems particularly plausible given growing evidence that sleep-based consolidation does more than just stabilize memories in veridical form, but also transforms them in ways that render memories less accurate in some respects, but perhaps more useful in the long run (Ellenbogen, Hu, Payne, Titone, & Walker, 2007; Payne, Stickgold, Swanberg, & Kensinger, 2008a; Wagner, Gais, Haider, Verleger, & Born, 2004).

There is a growing consensus in the literature that the consolidation of hippocampus-dependent memories is modulated by deep, slow-wave sleep (SWS) (Marshall & Born, 2007). SWS is characterized by slow (1–4 Hz), high amplitude brain waves in the EEG and is associated with hippocampal sharp wave-ripples (SPW-Rs), events that may provide a means of communication between hippocampal and neocortical memory stores as memories undergo the process of consolidation (Buzsaki, 1996, 1998). Spatial navigation studies in rodents and humans have shown that hippocampal networks involved in spatial memory acquisition can be reactivated during sleep – particularly SWS (Peigneux et al., 2004; Wilson & McNaughton, 1994), and that this reactivation is linked to improved performance the following day in humans (Peigneux et al., 2004). SWS appears to play a similar role in the veridical consolidation of hippocampus-dependent declarative memories (Marshall & Born, 2007 for review; Rasch, Buchel, Gais, & Born, 2007). For example, Rasch et al. (2007) exposed human subjects to an odor cue (a rose scent) while they learned object-location pairings in the memory game ‘concentration’ during the evening. fMRI revealed increased hippocampal activation in response to the odor when presented during SWS the following night, and this led to improved declarative memory retention the following morning. Accurate performance on this task, which requires good memory for objects, as well as the ability to correctly bind objects to their specific locations, requires the highly specific relational contextual processing known to depend on the hippocampus (Cohen & Eichenbaum, 1995; Davachi & Wagner, 2002; Giovanello, Schnyer, & Verfaellie, 2004; O’Keefe and Nadel, 1978). These studies and others (e.g. Takashima et al., 2006) strongly suggest that SWS plays a role in the consolidation of hippocampus-dependent forms of memory.

The DRM task differs from these tasks, however, in that it draws on both of the major components of declarative memory – episodic (context-specific event memory), and semantic (context-independent conceptual knowledge).¹ Remembering detailed information about the experimental context, such as the sound of the words as they were presented and characteristics of the speaker’s voice, are episodic memory components (i.e. specific to the experimental context or episode), whereas knowing that all of the words in a list are related in meaning is a semantic memory component (i.e. based on pre-existing knowledge of the shared meaning among the words).

While false memory of critical words is thought to rely solely on semantic processing (because there is no contextual information available for non-presented words), correct memory for studied words relies on both context-specific episodic processing and, perhaps to a greater degree, on context-independent semantic pro-

cessing (simply knowing the theme of a word list allows some accurate retrieval). Consistent with this notion, recent neuroimaging studies have demonstrated that both false and veridical memory formation in the DRM task rely heavily on regions associated with semantic processing, such as the left ventrolateral prefrontal cortex and left lateral temporal cortex, while veridical memory formation also relies on medial temporal regions, including the hippocampus (Dennis, Kim, & Cabeza, 2007; Kim & Cabeza, 2007a; Kubota et al., 2006). Thus, although performance on spatial and episodic memory tasks benefit from SWS, accurate performance on the DRM task, with its strong semantic component, may draw on a different complex of neural resources and thus different sleep-stages than the strictly hippocampus-dependent tasks described in the sleep and memory literature to date.

1. Experiment 1

1.1. Methods

1.1.1. Participants

Healthy, medication-free college students (mean age = 20.5) from two Boston area colleges participated for payment or course credit. We initially conducted this experiment at Merrimack College in N. Andover, MA ($n = 101$ total), and subsequently repeated it at Harvard University ($n = 84$ total). The Harvard study served to replicate the sleep/wake differences observed in the Merrimack subjects (see *Results*), and to provide a matched baseline for subsequent sleep polysomnographic (PSG) experiments using the Harvard population (see Experiments 2 and 3). Because performance patterns in the two colleges were virtually identical, all analyses in the main text reflect their combined performance. Individual college statistics can be found in the [Supplementary Information](#) online. Given that Merrimack and Harvard colleges represent different populations, the similarities across schools increase our confidence in the robustness and reliability of the results.

All subjects provided informed consent, which was approved by local IRBs, and were screened for self-reported sleep and mental health disorders, irregular sleep habits, and medication use. Subjects maintained their normal sleep schedule for two days prior to the experiment, and were required to sleep for at least 6 h each night. Subjects reported mean bedtimes of 12:28AM, rise times of 8:12AM, and sleep times of 7.4 h. In addition, participants abstained from caffeine and alcohol for two days before and throughout the experiment.

1.1.2. Procedures

All subjects listened to a recording of eight DRM wordlists (Roediger & McDermott, 1995), and later attempted to recall them. Subjects were randomly assigned either to study the lists at 9AM, returning for testing at 9PM that evening (“Wake” group, $n = 29$ at Merrimack; $n = 43$ at Harvard), or to study the lists at 9PM, returning for testing at 9AM the next morning (“Sleep” group, $n = 27$ at Merrimack; $n = 41$ at Harvard). Two additional Merrimack College groups studied the wordlists at either 9AM ($n = 24$) or 9PM ($n = 21$) and were tested for recall just 20 min later (“AM” and “PM Control” groups, respectively), in order to obtain baseline measures of memory recall after a short delay, and also to rule out potential circadian influences on encoding and retrieval. Note that because the AM and PM control groups were run at Merrimack College only, all analyses comparing Sleep and Wake performance to these 20 min delay baselines (e.g. Fig. 2) were performed using Merrimack subjects.

Subjects were tested in small groups. They were told that they were participating in a memory test, and that they should listen carefully to the words they were about to hear because they would be tested on them later. They were then presented with eight DRM

¹ It should be noted that while many theorists agree that episodic and semantic memories represent separate memory systems, with episodic memories relying more on hippocampal processing than semantic memories (Moscovitch et al., 2005), not all researchers agree with this idea (Manns, Hopkins, & Squire, 2003).

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