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Resting state EEG correlates of memory consolidation

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A B S T R A C T

Numerous studies demonstrate that post-training sleep benefits human memory. At the same time, emerging data suggest that other resting states may similarly facilitate consolidation. In order to identify the conditions under which non-sleep resting states benefit memory, we conducted an EEG (electroencephalographic) study of verbal memory retention across 15 min of eyes-closed rest. Participants ($n = 26$) listened to a short story and then either rested with their eyes closed, or else completed a distractor task for 15 min. A delayed recall test was administered immediately following the rest period. We found, first, that quiet rest enhanced memory for the short story. Improved memory was associated with a particular EEG signature of increased slow oscillatory activity (<1 Hz), in concert with reduced alpha (8–12 Hz) activity. Mindwandering during the retention interval was also associated with improved memory. These observations suggest that a short period of quiet rest can facilitate memory, and that this may occur via an active process of consolidation supported by slow oscillatory EEG activity and characterized by decreased attention to the external environment. Slow oscillatory EEG rhythms are proposed to facilitate memory consolidation during sleep by promoting hippocampal–cortical communication. Our findings suggest that EEG slow oscillations could play a significant role in memory consolidation during other resting states as well.

1. Introduction

A growing literature confirms that memory is better retained when participants sleep after learning, as opposed to staying awake. It is widely proposed that this effect is due to an active process of memory consolidation during sleep (Diekelmann & Born, 2010; Stickgold, 2005). This hypothesis is supported by studies demonstrating that improved memory is associated with specific features of the sleep EEG linked to consolidation, including slow waves (Alger, Lau, & Fishbein, 2012; Diekelmann, Biggel, Rasch, & Born, 2012), slow oscillations (Huber, Ghilardi, Massimini, & Tononi, 2004; Marshall, Helgadóttir, Mölle, & Born, 2006), and sleep spindles (Cox, Hofman, & Talamini, 2012; Mednick et al., 2013; Schabus et al., 2004).

Yet it is increasingly clear that a full night of sleep is not required to boost memory. Even a partial night of sleep or a short nap can facilitate memory, with effect sizes comparable to those following a full night (Mednick, Nakayama, & Stickgold, 2003; Plihal & Born, 1997; Tucker & Fishbein, 2009; Tucker et al., 2006). Furthermore, the duration of nap sleep is often unrelated to its memory effect, with even very short naps providing the same memory benefit as longer sleep periods (Payne et al., 2015; Tucker et al., 2006; Wamsley, Tucker, Payne, & Stickgold, 2010), although see (Alger et al., 2012; Mednick et al., 2003). Even a nap as short as 6 min has been reported to lead to a memory-enhancing effect (Lahl et al., 2008). What enables such short periods of sleep to enhance memory performance? One possibility is the presence of fast-acting offline consolidation mechanisms that do not require the completion of a full sleep cycle. Moreover, some propose that consolidation can occur during any state of sleep or alertness, when the encoding of new information is sufficiently reduced during the consolidation period (Mednick, Cai, Shuman, Anagnostaras, & Wixted, 2011).

Might short periods of quiet wakefulness impact memory, even in the absence of sleep? Most studies investigating the effect of sleep on memory have done so in comparison to waking control conditions in which participants watch videos (Lau, Tucker, & Fishbein, 2010; Tucker et al., 2006), listen to music (Elizabeth & McDevitt, 2014; Mednick, Makovski, Cai, & Jiang, 2009), or leave the laboratory to go about their daily activities (Ellenbogen, Hulbert, Stickgold, Dinges, & Thompson-Schill, 2006; Payne et al., 2012). These studies have clearly established that sleep benefits

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memory relative to an equivalent duration of *active wakefulness*, during which participants encode new sensory information. In contrast, the effect of *quiet resting* wake on memory – in the absence of cognitive tasks, activities, and sensory stimulation – has not been sufficiently characterized.

The notion that periods of unoccupied rest can retroactively facilitate memory actually dates back to the earliest days of experimental psychology, when Müller and Pilzecker first suggested that retroactive interference occurs even when the interpolated activity is highly dissimilar to the learned material (Müller & Pilzecker, 1900). But in more recent years, this question of whether a general reduction of mental effort during wakefulness (rest) facilitates consolidation has received little attention. Just in the last several years, emerging new evidence has begun to suggest that quiet wake does in fact facilitate memory, at least under some conditions (Craig, Dewar, Della Sala, & Wolbers, 2015; Dewar, Alber, Butler, Cowan, & Della Sala, 2012; Dewar, Alber, Cowan, & Della Sala, 2014). Several recent experiments report that a brief period of resting wake following learning can improve later memory in both elderly (Dewar et al., 2012, 2014) and young participants (Craig et al., 2015; Mercer, 2015). But because these studies have not employed EEG-monitoring, it is uncertain whether participants might have obtained brief periods of sleep during the retention interval. Beyond this, we have little understanding of the mechanisms by which resting wakefulness might enhance memory, nor the conditions under which this benefit emerges. Neurophysiological correlates of memory changes across sleep have now been extensively documented (Clemens, Fabó, & Halász, 2005, 2006; Holz et al., 2012; Nishida & Walker, 2007; Schabus et al., 2004; van Dongen, Takashima, Barth, & Fernández, 2011), but corresponding studies of resting wakefulness are lacking.

Quiet rest might facilitate memory via active consolidation mechanisms similar to those operating during sleep. Much of the neurophysiology purported to support consolidation during sleep is also present during resting wake. Like sleep, quiet rest is characterized by a dramatic reduction in sensory processing. Freed from the demands of stimulus processing, mental experience is focused inward, as participants engage in "mindwandering" – thinking about the past, imagining the future, and creating fictitious scenarios (Andrews-Hanna, 2011; Andrews-Hanna, Reidler, Huang, & Buckner, 2010; Antrobus, Singer, Goldstein, & Fortgang, 1970; Baird et al., 2012). Meanwhile, the "reactivation" of recent memory in the hippocampus and cortex that was first observed during slow wave sleep is also expressed during resting wake in rodents (Carr, Jadhav, & Frank, 2011; Davidson, Kloosterman, & Wilson, 2009; Foster & Wilson, 2006; Gupta, van der Meer, Touretzky, & Redish, 2010; Karlsson & Frank, 2009). Although this form of memory reactivation has not been directly observed in humans, the hippocampal "sharp-wave ripples" associated with reactivation are prevalent during quiet rest in humans (Axmacher, Elger, & Fell, 2008; Clemens et al., 2011). Consolidation-promoting neurochemical features of sleep are also partially replicated during rest, including decreased acetylcholine levels during quiet resting wakefulness (Marrosu et al., 1995).

Finally, several EEG oscillations proposed to support consolidation during sleep also have analogs during quiet rest. Although the predominant frequencies are different, in comparison to more active states of wakefulness EEG slowing characterizes both sleep and eyes-closed quiet rest. In wakefulness, candidate oscillations that we hypothesized might relate to memory processing are the EEG alpha oscillation (8–12 Hz) and the slower theta (4–7 Hz) and slow/delta oscillations (0.5–2 Hz). Alpha is the primary EEG signature of eyes-closed waking rest that distinguishes this state from active wakefulness, and is one of the main EEG correlates of the fMRI-defined "default-mode" resting state network, which includes a number of memory-related brain regions including the hippocampus, parahippocamal cortex, and medial frontal cortex (Jann et al., 2009; Knyazev, Slobodskoj-Plusnin, Bocharov, & Pylkova, 2011). On the phenomenological level, alpha rhythms are associated with a decreased focus on external stimuli and increased attention to internal states, including memories of the past (Foulkes & Fleisher, 1975). Alpha has recently been studied as a mediator of effective memory encoding and retrieval (Klimesch, 1997; Klimesch, Schimke, & Schwaiger, 1994; Vogt, Klimesch, & Doppelmayr, 1998; Williams, Ramaswamy, & Oulhaj, 2006). But slower EEG frequencies are also present during quiet rest. In sleep, slow oscillations ($\approx$1 Hz) and slow waves (up to 2 Hz) are thought to be major contributors to systems-level memory consolidation, synchronizing hippocampal sharp-wave ripples with cortical activity (Clemens et al., 2007, 2011; Mölle, Eschenko, Gais, Sara, & Born, 2009) and thus promoting hippocampal–cortical communication and synaptic plasticity (Rosanova & Ulrich, 2005). $\approx$1 Hz rhythms are present during quiet rest as well, and these may be relatively attenuated during the execution of directed cognitive tasks (Alper et al., 2006; Demanuele, Sonuga-Barke, & James, 2010). Thus, a number of mechanisms proposed to account for the effects of sleep on memory are also present during quiet wake, which suggests the hypothesis that the memory benefits of rest and sleep could arise from overlapping active consolidation mechanisms.

The aims of the current study were to (1) confirm that a period of EEG-verified quiet rest benefits memory, in the absence of any sleep, (2) isolate EEG correlates of this memory effect, and (3) describe the mental activity associated with this memory effect. We examined memory retention for a short story across a 15-min interval with continuous EEG monitoring. We hypothesized that 15 min of quiet rest would lead to improved memory at a subsequent test, and expected to find that this effect was related to both EEG slowing and increased "mindwandering" (Andrews-Hanna et al., 2010; Baird et al., 2012; Mason et al., 2007) during the rest period, both potential signatures of a sleep-like offline state conducive to memory consolidation.

2. Methods

2.1. Participants

29 college students (19 female) age 19–22 (M = 20 yrs ($\pm$0.8 SD)) were recruited by email, advertisement, or word-of-mouth, and paid $10/h for their participation. By self-report using a 3-day sleep log, participants stated that they slept an average of 7.4 h ($\pm$1.1 SD) per night on the 3 nights prior to the study.

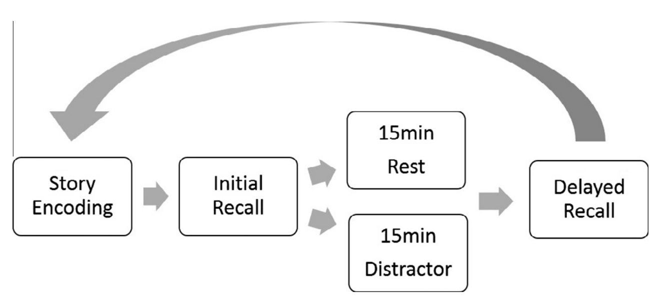

Fig. 1. Experimental timeline. Participants learned a short story just prior to a 15 min retention interval during which they either rested quietly with eyes closed or completed a distractor task. A recall test was administered both immediately and following the retention interval.

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