HHS Public Access
Author manuscript
Trends Cogn Sci. Author manuscript; available in PMC 2020 March 01.

Published in final edited form as:
Trends Cogn Sci. 2019 March ; 23(3): 171–173. doi:10.1016/j.tics.2018.12.007.

Memory Consolidation during Waking Rest

Erin J. Wamsley[*,1]

[1]Department of Psychology and Program in Neuroscience, Furman University, Greenville, SC, USA

Abstract

Recent studies show that brief periods of rest after learning facilitate consolidation of new memories. This effect is associated with memory-related brain activity during quiet rest, and suggests that in our daily lives, moments of unoccupied rest may serve an essential cognitive function.

Keywords

memory consolidation; offline processing; resting state; mind wandering; declarative memory

---

In our everyday lives, we often consider “resting” to be a waste of time, when productivity ceases and we do nothing. Yet new evidence suggests this is far from the case – periods of unoccupied rest may actually be essential to the process of memory consolidation (Box 1). Recent studies demonstrate that experimentally introducing brief periods of quiet waking rest following learning benefits memory, in comparison to equivalent periods of time spent engaged in sensorimotor or cognitive tasks ([1–3], Fig1). This memory benefit is likely due to an active process of memory reactivation and consolidation, occurring selectively during periods of reduced attentional demand.

The acquisition of new memory and its subsequent consolidation are thought to be to some degree mutually exclusive, with consolidation requiring entry into offline brain states during which new encoding is reduced, while the neurobiological milieu favors consolidation. Consistent with this hypothesis, many dozens of studies have shown that sleep following learning leads to enhanced memory at later test, relative to an equivalent duration of wakefulness [4]. Yet the vast majority of these studies have compared sleep to an “active” wake condition, during which participants complete tasks, watch videos, or go about their normal daily routine (*Active Wake* conditions, Fig1). Thus, while convenient, these active wake conditions do not control for the potential impact of simply lying down and closing one’s eyes, as all participants do in sleep conditions. Might the simple act of “doing nothing” and resting with one’s eyes closed benefit memory?

In fact, a growing body of evidence suggests that short periods of unoccupied waking rest can facilitate consolidation in a manner similar to that proposed to occur during sleep (*Quiet Wake* conditions, Fig1; [1–3,5,6]). Our group and others have demonstrated that a 15min

---

*Correspondence: erin.wamsley@furman.edu (E.J. Wamsley).

period of eyes-closed rest following encoding enhances memory for both procedural [5] and declarative [1,2] memory tasks, compared to an equivalent period spent completing a distractor task. Other recent studies have demonstrated that post-learning rest enhances subsequent memory for spatial and temporal information [7], facilitates insight into a complex problem [3], and enhances auditory statistical learning [6]. These memory effects can be maintained for a week or more after the rest intervention [2,7]. Together, these observations suggest that even during wakefulness, memory is preferentially consolidated during offline states characterized by reduced attentional demands.

Of course, it has long been known that some aspects of memory consolidation must occur during daytime wakefulness. While systems-level reorganization of memory over long timescales might plausibly require sleep (see Box 1), local cellular-level consolidation beginning immediately after encoding is sufficient to stabilize memory against interference for at least the short term (minutes-to-hours), even in the absence of sleep. Even the early stages of systems-level consolidation are thought to begin within the first hours after encoding. If these earliest stages of consolidation require entry into an offline brain state, this must be occurring during daytime wakefulness. Thus, the fundamental insight yielded by these new studies of waking rest is not so much that consolidation can occur during wakefulness, but that consolidation is not uniformly distributed throughout all of wakefulness. Instead, memory is preferentially facilitated during periods of unoccupied time in which attentional and cognitive demands are reduced [1,2,5]. This insight helps us to understand the necessary and sufficient conditions for consolidation to occur. Increasingly, it appears that for many forms of consolidation, sleep-specific neural mechanisms may not be strictly required. Instead, both sleep and other offline states share common neurobiological features essential for consolidation to take place.

Indeed, many of the same neurobiological mechanisms thought to underlie sleep's effect on memory are shared in common by waking rest. First, cellular-level memory "reactivation" occurs during quiescent waking rest, in the hippocampus as well as in other brain regions (Box 1). During this process, sequences of neuronal firing representing recent experience are reiterated offline. Blocking these reactivations impairs learning and memory [8]. In humans, a growing number of neuroimaging studies demonstrate memory-related brain activity during periods of post-training rest that predicts subsequent memory. For example, fMRI has been used to demonstrate that patterns of hippocampal activity characterizing encoding persist into post-learning rest, and that this predicts subsequent memory [9]. Our own group has meanwhile reported that low frequency EEG oscillations thought to support consolidation during sleep similarly predict memory retention across quiet waking rest [1]. And the neuromodulatory environment during quiet rest is also well-suited to facilitate consolidation – in both sleep and quiet rest, acetylcholine levels are substantially reduced from active waking levels, thought to promote hippocampal-cortical communication dynamics that benefit consolidation, as opposed to new learning. Thus, converging lines of evidence suggest that like sleep, rest benefits memory by enabling an *active* process of consolidation, facilitated by the offline reactivation and synaptic plasticity.

Still, there are several potential alternative explanations for rest's mnemonic benefit. First, it could simply be that participants resting quietly have an increased opportunity to consciously and intentionally rehearse just-learned information. Arguing against this possibility, rest shows an equivalent benefit for difficult-to-rehearse materials [5,10] and spontaneously thinking about just-learned information during rest does not predict subsequent memory [1]. It could also be that rest's memory effect is explained by the reduction of interfering sensory input during this state, rather than an active process during which memories are reactivated and synaptic plasticity is induced. But this protection-from-interference hypothesis is inconsistent with several lines of evidence. First, as described above, there is clear evidence that the reactivation of memory is occurring during quiet rest, and predicts subsequent memory performance. Beyond this, while passive protection of memory from interference would certainly be predicted to prevent forgetting, it is not clear how this could lead to the more complex qualitative changes in memory underlying, for example, insight into the solutions to problems [3]. Also, if rest benefits memory due a reduction in sensory interference, one would predict that the amount of sensory stimulation during a post-learning state should be the primary predictor of its effect on memory. But to the contrary, even internally focused attention to mental tasks blocks the mnemonic benefit of rest [11]. Together, these observations suggest (but do not prove) that the effect of rest on memory is not due to a simple reduction in sensory interference, nor to effortful rehearsal of learned information, but instead to an active and automatic process in which consolidation is supported by an iterative reactivation of recently formed memory traces.

In summary, even while awake, forming enduring memories may require us to intermittently enter an "offline" state optimized for the consolidation of new information. Of course, in our hectic lives, extended periods of completely unoccupied rest are rare. Outside the laboratory, it could be that consolidation occurs during the many briefer moments of rest interspersed between and within the activities of our day. Indeed, even seconds-long rest breaks during a learning experience have been shown to trigger memory-related activity that predicts later test performance [12]. Thus, far from being a waste of time, "rest" during wakefulness may end up being a crucial and widely underappreciated contributor to long-term memory formation in everyday life.

Acknowledgements

Our laboratory's work in this area has been funded by the BIAL Foundation and the National Institute of Mental Health (R15MH107891, R21MH098171). Thank you to the many students and research assistants who have contributed to our work in this area, especially Graelyn Humiston and Ted Summer.

References

1. Brokaw K et al. (2016) Resting state EEG correlates of memory consolidation. Neurobiol. Learn. Mem 130, 17–25 [PubMed: 26802698]
2. Dewar M et al. (2012) Brief Wakeful Resting Boosts New Memories Over the Long Term. Psychol. Sci 23, 955–960 [PubMed: 22829465]
3. Craig M et al. (2018) Rest on it: Awake quiescence facilities insight. Cortex DOI: 10.1016/j.cortex.2018.09.009
4. Stickgold R (2005) Sleep-dependent memory consolidation. Nature 7063, 1272
5. Humiston GB and Wamsley EJ (2018) A Brief Period of Eyes-Closed Rest Enhances Motor Skill Consolidation. Neurobiol. Learn. Mem 155, 1–6 [PubMed: 29883710]
6. Gottselig JM et al. (2004) Sleep and rest facilitate auditory learning. Neuroscience 127, 557–561 [PubMed: 15283955]

7. Craig M et al. (2015) Rest Boosts the Long-term Retention of Spatial Associative and Temporal Order Information. Hippocampus DOI: 10.1002/hipo.22424

8. Jadhav SP et al. (2012) Awake Hippocampal Sharp-Wave Ripples Support Spatial Memory. Science 336, 1454–1458 [PubMed: 22555434]

9. Tambini A and Davachi L (2013) Persistence of hippocampal multivoxel patterns into postencoding rest is related to memory. Proc. Natl. Acad. Sci 110, 19591–19596 [PubMed: 24218550]

10. Dewar M et al. (2014) Boosting Long-Term Memory via Wakeful Rest: Intentional Rehearsal Is Not Necessary, Consolidation Is Sufficient. PLoS ONE 9, e109542 [PubMed: 25333957]

11. Craig M et al. (2014) Autobiographical thinking interferes with episodic memory consolidation. PloS One 9, e93915 [PubMed: 24736665]

12. Ben-Yakov A et al. (2013) Hippocampal immediate poststimulus activity in the encoding of consecutive naturalistic episodes. J. Exp. Psychol. Gen 142, 1255 [PubMed: 23815458]

Box 1.

Glossary

Offline States

As distinguished from “online” processing of stimuli, during “offline” states such as sleep and quiet rest attention to external sensory stimuli is reduced, while cognitive resources are devoted to spontaneous, internally focused processes including thought, dreaming, imagination, and the consolidation of memory.

Memory Consolidation

Following learning, memories undergo a process of “consolidation”, during which new memory traces become increasingly stabilized against interference, and in some cases, even reorganized in the brain. Neuroscientists distinguish between at least two general timescales for consolidation processes – one that operates to stabilize just-encoded memory traces within local circuits, on a timescale of seconds to hours (*cellular-level* consolidation), and a related process that reorganizes memory traces on a systems-level across a longer timescale of hours to weeks (*systems-level* consolidation).

Memory Reactivation

One proposed mechanism of consolidation is the iterative “reactivation” of memory traces in the brain. In the 1990s, it was first demonstrated that after rats navigated through an environment, neuronal firing patterns in the hippocampus describing this experience were “reactivated” during subsequent sleep. It is now known that this neural-level reactivation of memory occurs with equivalent frequency during waking rest, and in diverse other regions of the brain.

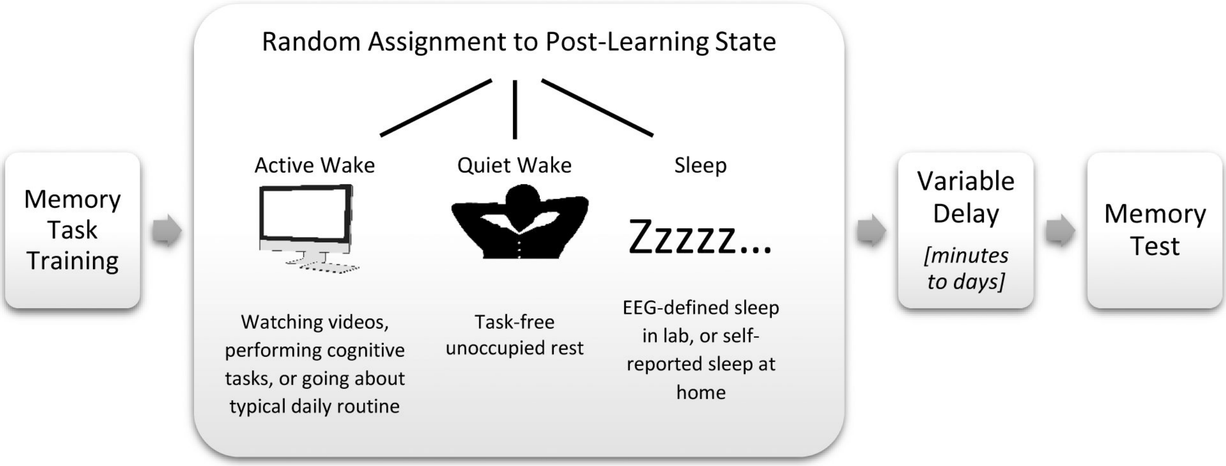

Figure 1. An Experimental Paradigm for Testing the Effect of Post-Learning State on Memory.
Studies demonstrating that rest and sleep benefit memory often follow the general experimental paradigm outlined here (e.g. [1–3,5]). After training on a memory task, participants are randomly assigned to engage in one of three general categories of post-learning condition: In *Active Wake* conditions, participants are engaged in sensorimotor activities that might include completing a distractor task, watching videos, listening to music, or leaving the laboratory to go about their daily activities; In *Quiet Wake* conditions, participants sit quietly and are not engaged in any overt sensory or motor activity; In *Sleep* conditions, participants either nap or sleep overnight, in the laboratory or home setting. Numerous experiments have established that post-training *Sleep* improves memory, relative to *Active Wake* control conditions. But here, we review new evidence that sleep *per se* is not required to achieve this memory benefit – states of *Quiet Wake* following learning similarly benefit memory, in comparison to *Active Wake*.