'Sleep-dependent' memory consolidation? Brief periods of post-training rest and sleep provide an equivalent benefit for both declarative and procedural memory

Serene Y. Wang,[1] Kirsten C. Baker, Jessica L. Culbreth, Olivia Tracy, Madison Arora, Tingtong Liu, Sydney Morris, Megan B. Collins, and Erin J. Wamsley

Department of Psychology, Furman University, Greenville, South Carolina 29609, USA

Sleep following learning facilitates the consolidation of memories. This effect has often been attributed to sleep-specific factors, such as the presence of sleep spindles or slow waves in the electroencephalogram (EEG). However, recent studies suggest that simply resting quietly while awake could confer a similar memory benefit. In the current study, we examined the effects of sleep, quiet rest, and active wakefulness on the consolidation of declarative and procedural memory. We hypothesized that sleep and eyes-closed quiet rest would both benefit memory compared with a period of active wakefulness. After completing a declarative and a procedural memory task, participants began a 30-min retention period with PSG (polysomnographic) monitoring, in which they either slept ($n = 24$), quietly rested with their eyes closed ($n = 22$), or completed a distractor task ($n = 29$). Following the retention period, participants were again tested on their memory for the two learning tasks. As hypothesized, sleep and quiet rest both led to better performance on the declarative and procedural memory tasks than did the distractor task. Moreover, the performance advantages conferred by rest were indistinguishable from those of sleep. These data suggest that neurobiology specific to sleep might not be necessary to induce the consolidation of memory, at least across very short retention intervals. Instead, offline memory consolidation may function opportunistically, occurring during either sleep or stimulus-free rest, provided a favorable neurobiological milieu and sufficient reduction of new encoding.

[Supplemental material is available for this article.]

Of the myriad new experiences we encode each day, only a fraction are remembered over the long-term. The formation of long-term memory is crucial for optimal functioning in our everyday lives and for building knowledge across days, weeks, and years. Such enduring memories require not only the effective encoding of new information, but also a set of postencoding processes, termed "consolidation," that function to stabilize and transform new memory traces over time (McGaugh 2000; Frankland and Bontempi 2005; Genzel and Wixted 2017).

Consolidation of memory is better supported by some states of consciousness than others. For example, sleep has long been known to optimize memory consolidation, purportedly due to specific neurobiology that actively promotes the consolidation process (Diekelmann and Born 2010). Numerous studies have demonstrated that sleep facilitates the consolidation of both declarative and procedural memories. Slow oscillations (Huber et al. 2004; Marshall et al. 2006) and slow wave sleep (SWS) (Alger et al. 2012; Diekelmann et al. 2012) are thought to especially benefit hippocampus-dependent, declarative memory. Meanwhile, various forms of implicit and procedural memory have been linked to rapid eye movement (REM) sleep (Plihal and Born 1997; Mednick et al. 2009) or non-REM stage 2 (N2) sleep (Walker et al. 2002; Tucker and Fishbein 2009).

A potential mechanism of offline memory consolidation during sleep is memory "reactivation," in which patterns of neural activity in the hippocampus and cortex associated with awake experience are reiterated after learning. For example, when rats sleep after being trained on a spatial learning task, hippocampal "place cells" fire again in the same order as when the animals were being trained on the task during wake (Lee and Wilson 2002; Ji and Wilson 2007). Such neural reactivation not only occurs in the hippocampus, but also concurrently in a variety of cortical areas (Ji and Wilson 2007; Peyrache et al. 2009; Kaefer et al. 2020). The recent advent of optogenetics has allowed experimental investigation of memory reactivation in animal models. Experimentally disrupting the hippocampal ripple oscillations during which reactivation occurs impairs memory (Girardeau et al. 2009; Ego-Stengel and Wilson 2010). Conversely, selectively reactivating neural ensembles related to a particular memory appears to induce consolidation, particularly when this manipulation is applied during sleep or light amnesia (de Sousa et al. 2019).

But is sleep the only brain state that facilitates memory consolidation in this way? It has been argued that sleep-specific neurobiology, including sleep slow waves (Alger et al. 2012), sleep spindles (Wamsley et al. 2012; Mednick et al. 2013; Laventure et al. 2016), and/or REM sleep (Karni et al. 1994; Stickgold et al. 2000; McDevitt et al. 2015; Boyce et al. 2016), is required for offline memory reactivation and consolidation to occur, or at least to

[1]**Present address Department of Psychology, Cornell University, Ithaca, NY 14853, USA**
Corresponding author: erin.wamsley@furman.edu
Article is online at http://www.learnmem.org/cgi/doi/10.1101/lm.053330.120.

occur optimally. However, a growing body of literature indicates that stimulus-free waking rest can similarly facilitate consolidation (Wamsley 2019). In two influential experiments, Dewar et al. (2012) demonstrated that compared with participants who completed a nonverbal distractor task, those who rested quietly with their eyes closed in a darkened room for 10 min after learning showed better memory for short stories encoded prior to the retention period. The rest group significantly outperformed the wake group after 15 min, 30 min, and 7 d (experiment 1), even in the absence of retrieval practice during the 7-d period (experiment 2).

This effect of post-training rest on memory retention has been reported in an increasing number of papers across the last decade (Gottselig et al. 2004; Mercer 2015; Martini et al. 2018; Wamsley 2019; Martini and Sachse 2020). Brokaw et al. (2016) replicated the behavioral observations of Dewar et al. (2012) and showed that this memory benefit was associated with EEG slow oscillation activity, which is thought to facilitate hippocampal–cortical communication and concomitant memory consolidation during sleep (Marshall et al. 2006; Mölle and Born 2011). A recent study by Sattari et al. (2019) also linked improved memory performance to waking EEG slow oscillations, suggesting that the memory-enhancing effects of rest and sleep may share a common mechanism.

Of course, it has been known for decades that at least some consolidation must occur during wakefulness. Local, cellular level consolidation begins to stabilize memory immediately following encoding (Bailey and Kandel 2008; Redondo and Morris 2011), enabling us to recall the events of the previous hours in the absence of intervening sleep. The novel suggestion of these more recent studies is that consolidation does not occur equivalently during all types of wakefulness (Dewar et al. 2012; Brokaw et al. 2016). Instead, stimulus-free rest periods appear to have features that are especially suited to facilitate memory.

Reduced sensory processing during eyes-closed rest may be one factor accounting for the memory facilitation effect. However, even internally generated stimuli can also function to block consolidation, as demonstrated by the fact that mental tasks such as retrieval of autobiographical memory and focused meditation are also associated with a reduction in rest's memory benefit (Craig et al. 2014; Collins and Wamsley 2020). Similarly, we reported in two previous studies that individuals with a high propensity for daydreaming show less memory benefit following a period of rest, presumably because intense internally generated mental activity inhibits consolidation (Humiston et al. 2019; Wamsley and Summer 2020).

Together, these observations suggest that consolidation occurs during wakefulness when sensory processing is reduced, when low-frequency EEG oscillations are increased, and when internally generated cognition is at a minimum. Therefore, consolidation may not depend on neural mechanisms specific to sleep, instead opportunistically occurring across multiple states of consciousness whenever the correct conditions are met (Mednick et al. 2011). According to the opportunistic theory of memory consolidation, the processes of encoding and consolidation are mutually exclusive: During any brain state in which we are not currently encoding new information, existing memories consolidate as the neural milieu becomes favorable (Mednick et al. 2011; Wamsley 2019). Unoccupied quiet rest, like sleep, is a state in which the encoding of new stimuli is reduced. In addition, quiet rest and sleep also share a number of neurobiological features that are thought to actively promote memory consolidation, including overall slower EEG in comparison with active wakefulness, increased activation of default-mode network brain structures (Buckner and Vincent 2007), and decreased levels of acetylcholine in the brain (Hasselmo and McGaughy 2004). Additionally, the cellular-level offline reactivation of memory occurs not only during sleep, but also during quiet rest (Foster and Wilson 2006; Karlsson and

Frank 2009; Carr et al. 2011; Staresina et al. 2013). At the same time, it must be noted that eyes-closed rest does not replicate all aspects of sleep neurobiology proposed to facilitate memory. For example, sleep spindle oscillations and sleep-specific neurohormonal changes are not present during eyes-closed rest.

While sleep and rest both benefit memory in comparison with active wakefulness, it is not known whether they do so equivalently. With few studies directly comparing the size of rest's memory benefit with that of sleep, it remains possible that sleep provides some benefit above and beyond that conferred by waking rest. The limited number of prior studies in this area have shown mixed results. As opposed to the type of truly task-free condition used in the waking rest studies reviewed above, most experiments comparing active wakefulness, rest, and sleep have used a "rest" condition in which participants are asked to complete an undemanding activity such as listening to music or books on tape. This approach sacrifices complete sensory restriction in return for allowing rest condition participants to maintain wakefulness for longer periods of time. For example, Mednick and colleagues have used quiet rest conditions in which participants listen to music or audiobooks, finding that this form of quiet rest facilitates memory equivalently to sleep for some forms of learning (Mednick et al. 2009; Sattari et al. 2019), but not for others (Mednick et al. 2002; McDevitt et al. 2014). Keeping rest participants awake via verbal instructions to alternately open and close their eyes, Simor et al. (2018) found no effect of post-training rest or sleep on performance of a serial reaction time task, relative to an active wake control. While these observations might indicate that only selected forms of memory can be consolidated during resting wakefulness, it is possible that the encoding of meaningful auditory stimuli during these rest conditions prevents optimal consolidation.

Only a few prior studies have compared the memory effects of sleep with those of an equivalent duration of eyes-closed, entirely task-free rest. For example, Gottselig et al. (2004) successfully compared the effects of sleep, quiet rest, and active wakefulness on memory consolidation using a carefully controlled rest condition without any stimuli presented to the participants. Using a statistical auditory sequence learning task, they reported that both sleep and rest equivalently facilitated retention. In contrast, using a declarative memory task, Piosczyk et al. (2013) found that neither quiet rest nor sleep improved memory more than active wakefulness. A recent study from our own laboratory directly compared sleep, rest, and active wakefulness using declarative and procedural tasks commonly used in studies of sleep and memory (Tucker et al. 2020). However, high rates of attrition (due to rest participants inadvertently falling asleep and sleep participants failing to obtain sleep) prevented a robust test of our hypothesis that sleep and quiet rest would equivalently benefit memory, relative to active wakefulness.

The goal of the current study was to directly compare the memory benefit of a brief nap (<30 min) with that of an equivalent duration of task-free quiet rest. We hypothesized that a brief period of sleep and quiet rest would have an equivalent effect on the consolidation of both declarative and procedural memories, significantly boosting memory retention compared with an equivalent duration of active wakefulness. Following our previous work, we expected that memory retention across sleep and quiet rest would be associated with slow oscillation EEG power in the <1-Hz range, but that participants with high trait daydreaming propensity would show less improvement across quiet rest.

Results

After training on two learning tasks (an Icelandic word pair associates task and the motor sequence task), participants were randomly

assigned to spend the next 30 min either resting with their eyes closed, lying down for a nap opportunity, or completing a distractor task. Afterwards, memory retention for both learning tasks was assessed. For the Icelandic word pairs task, performance improvement was assessed as the change in number of words recalled. For the motor sequence task, performance was assessed both as initial percent improvement from baseline to the first three of 12 test trials after the retention interval, and also as final percent improvement from baseline to the last three of 12 test trials after the retention interval (for more details, see the Materials and Methods).

Sample characteristics by group

Prior to the manipulation, the experimental groups were equivalent on relevant characteristics including age, sex, state and trait sleepiness, prestudy sleep schedule, preretention and postretention PVT scores, baseline MST and Icelandic word pair scores, and musical instrument experience (Table 1).

Quiet rest and sleep equivalently enhance memory retention

Icelandic word pair task

Across the 30-min retention interval, both the sleep and the quiet rest groups forgot significantly fewer Icelandic words than the active wake group (sleep: $M = -0.17$, SEM = 0.17; quiet rest: $M = -0.09$, SEM = 0.22; active wake: $M = -0.96$, SEM = 0.23), $F_{(2,71)} = 5.68$, $P = 0.005$ (Fig. 1). Change in recall score did not differ significantly between the sleep and the quiet rest groups ($P = 0.81$), but both showed less forgetting relative to the active wake group (sleep vs. active wake: $P = 0.007$; quiet rest vs. active wake: $P = 0.004$).

Motor sequence task

Overall, there was no significant difference between groups in the initial percent improvement in correct sequences during the first three test trials, $F_{(2,71)} = 1.93$, $P = 0.15$. However, the sleep and quiet rest groups showed similar initial percent improvement, and both improved marginally more than the active wake group (sleep: $M = 25.0\%$ [raw improvement of 5.3 sequences], $SEM = 3.1\%$ [0.55 sequences]; quiet rest: $M = 23.1\%$ [4.5 sequences], SEM = 3.2% [0.60 sequences]; active wake: $M = 17.8\%$ [4.2 sequences], SEM = 2.2%

[0.51 sequences]; sleep vs. quiet rest: $P = 0.65$; sleep vs. active wake: $P = 0.06$; quiet rest vs. active wake: $P = 0.18$) (Fig. 2).

By the end of the 12 test trials, however, final percent improvement varied significantly by group, $F_{(2,71)} = 4.21$, $P = 0.02$. Again, improvement was almost identical for the sleep and quiet rest groups ($P = 0.95$), both of which improved significantly more than the active wake group (sleep: $M = 16.0\%$ [raw improvement of 3.2 sequences], SEM = 2.4% [0.36 sequences]; quiet rest: $M = 15.8\%$ [2.8 sequences], SEM = 2.9% [0.51 sequences]; active wake: $M = 7.3\%$ [1.6 sequences], SEM = 2.3% [0.46 sequences]; sleep vs. active wake: $P = 0.01$; quiet rest vs. active wake: $P = 0.02$) (Fig. 2).

Sleep architecture

During the nap, the $n = 24$ sleep participants included in analysis obtained an average of 17.48 ± 6.44 SD min of sleep, including 5.60 ± 3.48 SD min of N1, 10.85 ± 6.47 SD min of N2, and 1.02 ± 2.86 SD min of N3. No participants entered REM sleep. Within the sleep group, improvement across the retention interval was not significantly related to total sleep time or to the amount of sleep in any stage (Supplemental Table S1).

Association between performance and SWS

Because only $n = 4$ participants entered SWS (N3), we additionally examined the presence of SWS as a dichotomous variable. The four participants who entered SWS obtained an average of 6.13 ± 0.29 SD min of N3 sleep and exhibited marginally more improvement in Icelandic word pairs recall than those who did not enter SWS, $t_{(22)} = 1.89$, $P = 0.073$, improving by 0.50 ± 0.29 SEM words compared with a decrease of 0.30 ± 0.18 SEM words for those without SWS. In contrast, entry into SWS was not associated with improved performance on the MST (initial percent improvement: $P = 0.60$; final percent improvement: $P = 0.66$).

Association between performance and N1 sleep in the quiet rest group

$N = 8$ quiet rest participants obtained an average of 1.19 ± 0.65 SD min of N1 sleep (range: 30 sec—2 min) (see the Materials and Methods). None entered N2 or N3 sleep. However, even this very small amount of N1 was associated with task performance, with participants who entered N1 showing significantly more initial percent improvement on the MST, $t_{(20)} = 2.27$, $P = 0.035$, as well as marginally more forgetting of the Icelandic word pairs,

Table 1. Participant characteristics by condition

	Sleep ($n = 24$)		Quiet Rest ($n = 22$)		Active wake ($n = 29$)		F/χ^2	P
	Mean	±SD	Mean	±SD	Mean	±SD		
Age (years)	19.88	1.15	19.95	1.36	19.97	1.18	0.04	0.960
ESS	15.79	4.15	16.41	4.73	16.48	3.55	0.21	0.810
SSS at training	2.58	0.65	2.86	0.83	2.90	1.18	0.84	0.436
SSS at test	2.54	0.98	3.41	1.26	3.28	1.49	3.21	0.046*
PVT at training (milliseconds)	354.75	38.37	351.83	35.96	351.97	34.33	0.05	0.951
PVT at test (milliseconds)	366.81	51.15	340.02	38.64	366.79	60.87	2.05	0.136
Baseline Icelandic[a]	8.29	4.35	8.36	4.75	9.18	4.52	0.31	0.735
Baseline MST[a]	23.18	7.76	20.34	5.41	23.40	4.95	1.82	0.169
Sex (percent male)	38%		23%		35%		1.29	0.526
Plays instrument	46%		18%		21%		5.61	0.061

Comparison of participant characteristics in the sleep, quiet rest, and active wake groups. Comparisons were conducted using one-way ANOVAs, except in the case of the dichotomous sex and instrument experience variables, which were compared across groups using χ^2 tests of independence. (SSS) Stanford Sleepiness Scale, (ESS) Epworth Sleepiness Scale total score, (baseline Icelandic) mean words correctly recalled on Icelandic word pair task at training, (baseline MST [motor sequence task]) mean correct sequences typed during the last three training trials, (PVT [psychomotor vigilance task]) average median reaction times (RT), in milliseconds.
[a]($N = 1$) Extreme outlier was excluded from analyses of the Icelandic word pair task, ($n = 1$) extreme outlier was excluded from analyses of the MST.
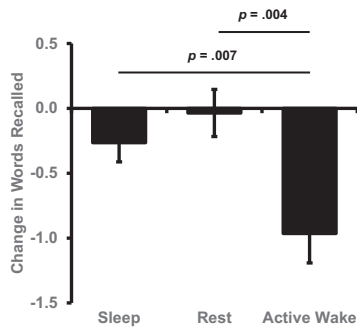(*) $P < 0.05$.

Figure 1. Mean change in the number of English translations recalled for the Icelandic word pair task by participants in the sleep, quiet rest, and active wake conditions. Error bars indicate ±SEM.

$t_{(20)} = 1.98$, $P = 0.061$ (Supplemental Table S4). N1 sleep was unrelated to MST final percent improvement ($P = 0.40$). Quiet rest participants with at least one epoch of N1 had marginally higher scores on the Stanford Sleepiness Scale at training, $t_{(20)} = 1.60$, $P = 0.12$, and significantly higher scores on the Stanford Sleepiness Scale at test, $t_{(20)} = 2.70$, $P = 0.014$, relative to participants without N1.

To assess whether the presence of N1 sleep in quiet wakefulness impacted the outcome of our main analyses, we reran the above ANOVAs to test the effect of group on performance, while excluding quiet rest participants who entered N1 sleep. For the Icelandic word pairs task, performance improvement continued to vary significantly by group ($F_{(2,63)} = 7.31$, $P = 0.001$), with both the quiet rest and the sleep groups showing less forgetting than the active wake group (quiet rest vs. active wake: $P = 0.001$; sleep vs. active wake: $P = 0.007$). Similarly, for MST final percent improvement, performance improvement also varied significantly by group ($F_{(2,63)} = 3.77$, $P = 0.028$), with both the quiet rest and the sleep groups showing less forgetting than the active wake group (quiet rest vs. active wake: $P = 0.09$; sleep vs. active wake: $P = 0.01$). As in our primary analyses, the effect of group on performance did not reach statistical significance for MST initial percent improvement ($P = 0.11$).

EEG spectral analysis and sleep spindles

The correlation between slow oscillation EEG power and memory retention did not reach statistical significance for either learning task. However, the association between quiet resting slow oscillation power and Icelandic word pair memory was in the hypothesized direction, $r_{(19)} = 0.33$, 95% CI = [−0.12, 0.67], $P = 0.14$, (Supplemental Table S2). Additionally, β power during sleep predicted subsequent word pair retention in the sleep group, $r_{(20)} = 0.50$, $P = 0.017$ (however, note that this association would not survive Bonferroni correction for multiple comparisons). Memory retention across sleep and quiet rest was unrelated to EEG spectral power in any other frequency band

(Supplemental Table S2). In the sleep condition, neither the total number of sleep spindles nor spindle density per min predicted change in memory for either learning task (Supplemental Table S2).

Experience with musical instruments

Twenty-one participants reported recent experience with musical instruments that require fine finger movements. Because such musical instrument experience has previously been reported to be associated with MST performance (Tucker et al. 2016), we ran additional ANOVAs including instrument experience as a factor. The main effect of instrument experience was not significant for either percent initial ($F_{(1,68)} = 0.64$, $P = 0.43$) or percent final MST improvement ($F_{(1,68)} = 3.60$, $P = 0.06$), nor was there any interaction between instrument experience and experimental group for either percent initial or percent final improvement ($P = 0.62$ and $P = 0.86$, respectively) (see Supplemental Table S5).

Association between performance and subjective experience

The experimental groups were equivalent in the extent to which they reported thinking about and imagining the memory tasks during the retention period (thinking about: $F_{(2,71)} = 0.61$, $P = 0.55$; imagining: $F_{(2,71)} = 0.94$, $P = 0.40$) (see Supplemental Table S3). However, the frequency that participants reported "trying to remember" the memory tasks differed across conditions, $F_{(2,71)} = 6.46$, $P = 0.003$. Specifically, participants in both the sleep ($P = 0.001$) and the quiet rest conditions ($P = 0.026$) reported trying to remember the memory tasks significantly more often than
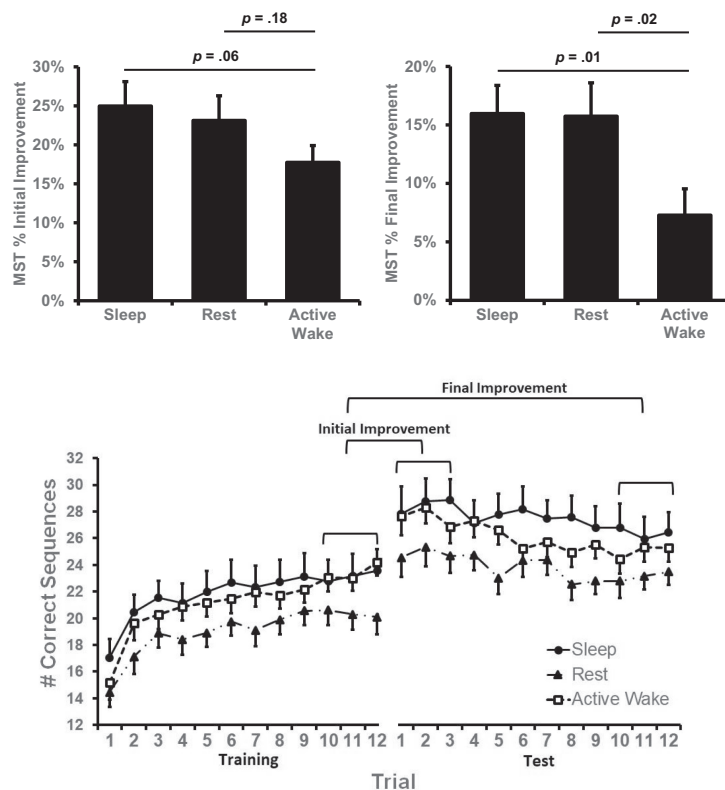

Figure 2. (*Top*) Mean initial percent improvement (*left*) and final percent improvement (*right*) on the MST in the sleep, quiet rest, and active wake conditions. (*Bottom*) Correct sequences by trial at training (before the retention interval) and test (after the retention interval). Error bars indicate ±SEM.

participants in the active wake condition. The effect of experimental group on memory remained statistically significant when controlling for this measure of rehearsal in an ANCOVA, for both the Icelandic word pairs task ($F_{(2,70)} = 4.01$, $P = 0.02$) and percent final improvement on the MST ($F_{(2,70)} = 4.82$, $P = 0.01$). Furthermore, reports of "trying to remember" the task did not significantly predict memory retention in either learning task ($P = 0.89$ for the word pairs task; $P = 0.67$ for the MST).

On the exit questionnaire (Supplemental Table S3), participants in the quiet rest group reported spending more time thinking about the future, relative to participants in the sleep group ($P = 0.01$); participants in the sleep group reported spending more time thinking about the learning tasks compared with participants in the active wake group ($P = 0.03$). There were no other significant effects of post-learning state on thought content. Meanwhile, only in the active wake condition, percent final improvement on the MST was positively associated with the amount of time that participants reported spending thinking about the past (Supplemental Table S3). In contrast, no thought category predicted memory for the Icelandic word pairs in any of the three experimental conditions.

Contrary to our hypotheses, trait daydream frequency was not related to performance improvement across the retention interval, either for all participants combined, or within any individual group (Icelandic word pairs: all P-values >0.13; MST: all P-values >0.30)

No effect of task order on performance improvement

The order in which participants completed the two memory tasks did not affect performance improvement on either task. Neither MST percent initial improvement ($t_{(72)} = 0.36$, $P = 0.72$) nor percent final improvement ($t_{(72)} = 0.89$, $P = 0.93$) differed across the two task orders. Change in recall on the Icelandic word pairs task was also not affected by task order, $t_{(72)} = 0.27$, $P = 0.79$.

Group differences in sleepiness

The experimental groups were initially equivalent in sleepiness, as measured by scores on the Stanford Sleepiness Scale, $F_{(2,72)} = 0.84$, $P = 0.44$ (Table 1). However, following the retention interval, the sleep group became significantly less sleepy than either wake group, $F_{(2,72)} = 3.21$, $P = 0.046$ (sleep vs. quiet rest: $P = 0.02$, sleep vs. active wake: $P = 0.04$.). Sleepiness at the time of test was not related to memory retention for either task (sleep group all P-values >0.4; quiet rest group all P-values >0.1; active wake group all P-values >0.1).

Discussion

This study demonstrates that quiet rest can facilitate declarative and procedural memory consolidation to the same degree as sleep, at least across brief retention intervals. This indicates that the initial stages of memory consolidation may not require sleep-specific neural mechanisms. Instead, our findings are consistent with the hypothesis that the absence of new encoding allows offline consolidation to occur during either sleep or stimulus-free wakefulness.

This study has both methodological and theoretical implications for sleep and memory research. First, our results provide further support for the opportunistic theory of memory consolidation (Mednick et al. 2011). By holding the presence of external stimulation constant across sleep and quiet rest, we confirmed that when active exposure to new stimuli is absent, memory performance is enhanced, regardless of whether the participants slept. Mednick et al. (2011) suggest that such opportunistic consolidation during a postencoding, offline period occurs on both the cellular and the systems levels. Whenever the brain is not currently encoding new information, synaptic connections associated with previously encoded memory are strengthened, and hippocampal networks are reactivated, facilitating the gradual integration of newly acquired memory traces into long-term memory stores in the cortex.

The timeframe of the current study is too short to assume that systems-level consolidation has been completed. However, our 30-min manipulation may have affected faster-timescale processes of cellular-level memory stabilization, and perhaps even the earliest stages of systems-level memory reorganization. It is well-established that molecular cascades supporting cellular-level consolidation begin in the first few minutes following encoding (Bailey and Kandel 2008; Redondo and Morris 2011), and that waking intervals can sometimes be sufficient to stabilize memory across the short term, even in the absence of sleep (Cohen et al. 2005). The brief rest and sleep intervals in the current study may thus have facilitated these early-timeframe consolidation processes to a greater degree than active wakefulness.

Second, we confirmed that a stimulus-free rest control is feasible to maintain long enough to allow a duration-matched nap condition to enhance memory. Prior studies using a stimulus-free rest condition have sometimes failed to detect the well-established effect of napping on memory, thus calling into question whether the retention interval allowed a sufficient duration of sleep (Piosczyk et al. 2013; Tucker et al. 2020). To our knowledge, this is only the second study to successfully use a task-free rest condition of this kind, alongside a duration-matched sleep condition that was demonstrably effective in enhancing memory (Gottselig et al. 2004). The majority of similar studies have instead relied on tasks such as listening to music to keep participants awake for the longer duration of a typical nap. While such tasks are minimally demanding, they arguably still drive substantial new hippocampus-dependent encoding, and therefore are not ideally suited to control for the reduced sensory stimulation of sleep.

Sleep and quiet rest participants reported "trying to remember" the learning tasks more often during retention period, relative to the active wake group. It is therefore possible that sleep and rest benefitted memory as a result of intentional rehearsal, rather than spontaneous offline consolidation. However, several factors argue against this possibility. First, performance in the sleep and quiet rest groups remained significantly better than in the active wake group on both tasks even when statistically controlling for self-reported rehearsal. Also, in line with our previously published observations (Brokaw et al. 2016), rehearsal did not predict performance in any experimental group. Furthermore, we note that prior research has argued that quiet rest benefits memory even for nonrecallable, difficult to rehearse stimuli (Dewar et al. 2014).

During the brief nap in this study, there was little opportunity for participants to enter slow wave sleep (SWS), and no participants entered REM sleep. Both stages have been argued to contribute to consolidation (Plihal and Born 1997; Stickgold et al. 2000; Alger et al. 2012; Boyce et al. 2016), and therefore it is possible that a full night of sleep would have conferred a greater performance advantage than either the nap or rest conditions did here. We chose to focus on a brief nap so that it would be feasible for the task-free rest interval to be equivalent in duration to the sleep interval. However, despite its brief duration, we note that the nap did have medium-to-large sized effects on memory, relative to active wakefulness. This suggests that the nap was sufficient to replicate the memory enhancement effects reported in the prior sleep literature.

Only four sleep participants obtained SWS during the nap. This may be important in light of prior evidence that naps benefit memory optimally when SWS is present (Durrant et al. 2011; Alger et al. 2012). Indeed, in our current data, sleep participants who entered SWS performed marginally better on the Icelandic word pairs

task compared with those who did not. However, our sample size was insufficient to provide a powerful test of the hypothesis that naps with SWS lead to a superior memory outcome than those without. Additionally, there was no relationship between δ or slow oscillation EEG power during sleep and memory. Thus, our observations do not provide strong support for the notion that a longer nap containing more SWS would have enhanced memory to a greater degree than rest. Still, this hypothesis would be worth continuing to pursue in future research.

Two of our hypotheses about the consolidation-promoting features of quiet rest were not supported. First, we anticipated that rest periods high in slow oscillation power would be especially beneficial for memory, given the slow oscillation's proposed role in hippocampal–cortical communication (Mölle and Born 2011). Although this association did not reach statistical significance, the analogous correlation reported in our 2016 paper ($r = 0.64$ in Brokaw et al. 2016) does lie within the 95% confidence interval of the current effect. Our current observations therefore cannot rule out an effect of the magnitude reported by Brokaw et al. (2016). If the true association between resting slow oscillations and memory is smaller than reported by Brokaw et al. (2016), we may not have been well-powered to detect it. Second, because even internally generated cognitive activities may inhibit consolidation (Craig et al. 2014; Collins and Wamsley 2020), we expected that participants high on trait daydreaming would show worse memory retention across the 30-min interval. However, we found no association between trait daydream frequency and memory performance, contrasting with both Humiston et al. (2019) and Wamsley and Summer (2020). Again, the current study could have been underpowered to detect weaker-than-anticipated association between daydream propensity and memory retention.

Unexpectedly, we found that $n = 8$ participants who entered N1 for at least one epoch during quiet rest showed less improvement on the word pairs task across the retention interval, but more improvement on the motor sequence task, in comparison with quiet wake participants who did not enter N1. Although subjective sleepiness was not itself significantly associated with performance, this correlation between N1 sleep and performance could possibly be driven by the fact that this subset of participants was sleepier than others, at both the training and testing time points. Importantly, we found that excluding these 8 participants from our main analysis did not alter the results.

While the current study shows that rest provides the same memory benefit as sleep under these particular circumstances, the boundaries and duration of this effect remain undefined. First, we tested only for simple changes in memory strength over time, assessing how postlearning state affects the number of words recalled or the speed of typing. However, sleep is thought to also aid in complex, qualitative changes in the form of memories over time, such as in solving problems (Wagner et al. 2004; Beijamini et al. 2014), selectively strengthening important memories (Payne et al. 2008), and extracting gist across stimulus sets (Payne et al. 2009; Lewis and Durrant 2011). It is possible that sleep could be required for these more complex transformations of memory over time, as opposed to the simple improvements tested in the current study (though see Craig et al. (2018)). Second, it remains unclear whether the memory benefits of quiet rest are as long-lasting as those following sleep. While several studies demonstrate that a short period of quiet rest can boost memory for at least a week (e.g., Dewar et al. 2012), here we did not use any delayed testing time points. Future research should continue to probe the potential for nonsleep resting states to facilitate the type of long-lasting benefits and qualitative memory transformations that have so far been attributed to sleep-dependent consolidation.

In summary, these observations demonstrate that eyes-closed, stimulus-free rest can boost both declarative and pro-

cedural memory to the same extent as a nap, at least across the short term. Thus, previously reported effects of short (≤30 min) naps on memory may not be attributable to sleep-specific neurobiological mechanisms, but instead to mechanisms that sleep and eyes-closed rest share in common.

The iterative offline reactivation of memory networks in the hippocampus and cortex could explain the observed effects of both sleep and rest on memory. Memory reactivation and associated hippocampal sharp-wave ripples have been linked to consolidation during sleep, yet these phenomena are also strongly prevalent during resting wakefulness (Foster and Wilson 2006; Karlsson and Frank 2009; O'Neill et al. 2010; Carr et al. 2011). Furthermore, inhibition of sharp-wave ripples during wakefulness impairs memory (Girardeau et al. 2009; Jadhav et al. 2012). During sleep, sharp-wave ripples and memory reactivation are associated with other electrophysiological features proposed to support memory, including spindles and slow oscillations (Clemens et al. 2007; Staresina et al. 2015). While slow oscillations do occur during resting wakefulness and have been associated with memory (Brokaw et al. 2016; Sattari et al. 2019), sleep spindles are notably absent in wake. Here we find that a period of resting wake, in the absence of spindles, can benefit memory to the same degree as a period of spindle-rich NREM sleep. This suggests that while spindles cooccur with memory reactivation during sleep, they may not be causally required for offline consolidation in all brain states.

Finally, this work highlights the importance of accounting for the memory effect of resting with one's eyes closed in future research, which invariably occurs in all studies of full-night sleep. Even in long-duration overnight studies, some portion of sleep's apparent memory benefit may be initiated during the first few minutes of eyes-closed rest, before participants fall asleep. Thus, while the current study by no means establishes that rest can account for all reported aspects of sleep's effect on memory performance, it should urge us to seriously consider the effect of rest in future studies.

Materials and Methods

Participants

Participants were $n = 94$ current and recently graduated college students (65 females; mean age 19.9 ± 1.2 SD years, range 18–23) who were fluent English speakers. Participants were compensated either $10 per hour or by receiving research credits for an introductory psychology course. $N = 1$ participant was excluded from all data analyses due to sleep deprivation (either slept for <5 h per night on average across the three nights prior to the study or slept for <4 h on the night immediately prior to the study). $n = 2$ participants were excluded from all analyses for technical problems with task training. Finally, one participant was selectively excluded from analyses of MST performance, and one participant was selectively excluded from analyses of word pair task performance, due to extreme outlying scores (more than three interquartile ranges above or below the median).

Procedure

The experimental timeline is illustrated in Figure 3. Participants reported to the laboratory for testing between 8:30 a.m. and 6:30 p.m. There was no difference between experimental groups in the time of day that testing took place ($P = 0.32$ in a one-way ANOVA). After being instructed about the procedures and signing informed consent, participants completed initial forms including a demographics form, the Epworth Sleepiness Scale (Johns 1991), a three-night retrospective sleep log, and the Daydream Frequency subscale of the Imaginal Processes Inventory (Singer and Antrobus 1972). Participants were also queried about their experience playing musical instruments using the method of Tucker et al. (2016), who reported that musical experience predicts faster
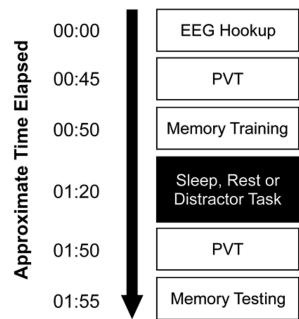
Figure 3. Experimental timeline. (00:00) Study start time, (PVT) psychomotor vigilance task. During memory training and testing, participants completed the Icelandic word pairs and MST tasks in counterbalanced order.

learning and better consolidation of the motor sequence task. For purposes of analysis, participants were classified according to whether or not they play a musical instrument that requires finger movements and have last played that instrument within the previous year.

Participants were wired for polysomnographic (PSG) recording using six EEG electrodes placed according to the 10–20 system (C3, C4, F3, F4, O1, and O2, referenced to the contralateral mastoid). Additionally, EOG (electrooculography) electrodes were placed at the left and right outer canthus, and EMG (electromyography) was recorded from the chin.

Before both the learning and the testing phases of the memory tasks, participants completed the psychomotor vigilance task (PVT; a standardized measure of alertness) (Dinges and Powell 1985), in which they pressed the spacebar as quickly as possible every time a red dot appeared on the computer screen. Following the PVT, participants performed the two memory tasks described below, with the order counterbalanced across participants. There was 2-min break between tasks.

Participants then began a 30-min retention interval in one of three pseudorandomly assigned conditions: sleep, quiet rest, or active wake. In the sleep group, participants lay in bed with the lights off and were instructed to attempt to fall asleep. To assist participants in falling and staying asleep, after the first $n = 34$ participants, a white noise machine was used to block out external noise from the hallway. In the quiet rest condition, participants were instructed to stay awake for 30 min as they rested in a lit room with their eyes closed. The first $n = 34$ participants enrolled sat in a chair, and the remaining $n = 60$ participants sat on a stool. If participants appeared sleepy (as defined by EEG slowing and/or the presence of slow-rolling eye movements), technicians provided up to four verbal reminders over the intercom system to help participants stay awake. Participants in the active wake condition played a nonverbal distractor game, Snood, on the computer for 30 min while sitting in a chair with the lights on, following the same procedures used in (Brokaw et al. 2016).

Participants in the sleep condition were required to obtain at least 5 min of total sleep to be included in analysis, while participants in the wake conditions were excluded from analysis if they obtained ≥2 min of N1 sleep, or if they entered N2 or N3 sleep for any duration. Based on our prior work (Tucker et al. 2020), we anticipated that a substantial number of sleep participants would have difficulty reaching the 5-min sleep criterion. Therefore, participants were assigned to the sleep condition at a ratio of six sleep participants to every five quiet rest and active wake participants. Prior to sleep time exclusions, group sizes were $n = 34$ in sleep, $n = 28$ in quiet rest, and $n = 29$ in active wake. Following sleep time exclusions, the final group sizes were $n = 24$ in sleep, $n = 22$ in quiet rest, and $n = 29$ in active wake. During the retention period, participants' EEG, EOG, and EMG were recorded at 500 Hz using a BrainAmp system (BrainProdcuts, GmbH).

Afterwards, participants were tested again on the two memory tasks in the same order as at training, again with a 2-min break be-

tween the tasks. Finally, an exit questionnaire was administered to evaluate participants' mental activities during the retention period. This included questions measuring rehearsal, asking if participants had "thought about," "imagined," or "tried to remember" the learning tasks during the retention interval (rated on a five-point scale). Participants also rated the proportion of the retention interval they spent engaged in one or more of 11 predefined mental categories: "thinking about the past" (something else earlier today/yesterday to a week ago/past year or several years ago), "imagining the future" (later today/tomorrow to next week/next year or several years), "thinking about the memory tasks from earlier," "mind was blank," "focusing on breath," "thinking about something else," and "other." Following our prior work (Brokaw et al. 2016), for purposes of analyses these items were collapsed into four categories: thinking about the memory tasks from earlier, thinking about that past (something else earlier today/yesterday to a week ago/past year or several years ago), imagining the future (later today/tomorrow to next week/next year or several years), and other (all other categories combined).

Memory tasks

Icelandic word pairs task
During the learning phase, 20 Icelandic–English word pairs (e.g., "hundur–dog") were presented individually on a computer screen for 5 sec each, with a 1-sec interstimulus interval. Immediately following learning, and again during the delayed testing phase, participants were asked to recall the English translation for each of the 20 Icelandic words, which were presented simultaneously as a list on the screen. Performance was assessed as the number of English translations correctly recalled. Performance improvement was defined as the number of words correctly recalled at test minus the number of words correctly recalled at training. This task was adapted from that used by Mercer (2015).

Motor sequence task
In both the learning and the testing phases of the motor sequence task (MST), participants were instructed to repeatedly type a five-digit sequence, 4–1–3–2–4, using their nondominant hand, as quickly and accurately as possible. Learning and testing each consisted of 12 trials. Each trial consisted of 30 sec of typing, followed by a 30-sec rest period. The target number sequence was displayed on screen the entire time.

For the MST, performance was measured as the number of correct sequences typed per trial. Baseline performance at training was defined as the mean number of correct sequences typed across the last three training trials. We assessed both initial percent improvement from baseline to the first three test trials after the break, and also final percent improvement from baseline to the last three test trials after the break. Initial percent improvement was therefore defined as [(mean correct sequences on first three test trials – mean correct sequences on last three training trials)/mean correct sequences on last three training trials]. Final percent improvement was defined as [(mean correct sequences on last three test trials – mean correct sequences on last three training trials)/mean correct sequences on last three training trials].

Sleep scoring and EEG analysis
For participants in the sleep and quiet rest groups, sleep was scored in 30-sec epochs according to the AASM scoring manual (Iber et al. 2007). After artifact rejection by visual inspection and applying a 0.3–35 Hz band pass filter to the EEG, we conducted spectral analysis using Brainstorm (Tadel et al. 2011). Welch's method was applied to all artifact-free 4-sec segments of N2 and N3 sleep, with 50% overlap, in five a priori frequency bands: slow oscillation (0.3–1 Hz), δ (1–4 Hz), θ (4–7 Hz), α (8–12 Hz), and β (13–35 Hz). Correlational analyses considered only the mean spectral power across all electrode sites in each of these frequency bands. Spindles during N2 sleep were counted automatically at C3, using a validated automated detector based on the characteristics of 11–

16 Hz σ activity (Lacourse et al. 2019). In brief, the detector marks a spindle when the following four parameters exceed threshold for between 0.3–2.5 sec: relative σ power (threshold [z-score] = 1.6), absolute σ power (threshold ($\log_{10}\mu V^2$) = 1.25), the covariance between the σ-filtered and broadband EEG signal (threshold [z-score] = 1.3), and the correlation between the σ-filtered and broadband EEG signal (threshold [r] = 0.69). This detection method has recently been demonstrated to outperform other commonly used methods and shows a high correspondence with expert hand scoring (Lacourse et al. 2019). We calculated both the total number of spindles detected during N2, as well as "spindle density," defined as the number of spindles per minute of N2 sleep.

Statistical analysis

Our primary hypotheses were tested using one-way analyses of variance, followed by uncorrected pairwise comparisons (Fisher's LSD). Pearson's correlations were used to test for associations between sleep features (sleep architecture, mean spectral power in each frequency band, and spindles) and memory performance, except in the case of correlations with amount of N3 sleep. For N3 sleep, we instead present Spearman rank order correlations, due to the nonnormal distribution of time in N3.

Acknowledgments

References

Alger SE, Lau H, Fishbein W. 2012. Slow wave sleep during a daytime nap is necessary for protection from subsequent interference and long-term retention. *Neurobiol Learn Mem* **98:** 188–196. doi:10.1016/j.nlm.2012.06.003

Bailey CH, Kandel ER. 2008. Synaptic remodeling, synaptic growth and the storage of long-term memory in Aplysia. *Prog Brain Res* **169:** 179–198. doi:10.1016/S0079-6123(07)00010-6

Beijamini F, Pereira SIR, Cini FA, Louzada FM. 2014. After being challenged by a video game problem, sleep increases the chance to solve it. *PLoS One* **9:** e84342. doi:10.1371/journal.pone.0084342

Boyce R, Glasgow SD, Williams S, Adamantidis A. 2016. Causal evidence for the role of REM sleep θ rhythm in contextual memory consolidation. *Science* **352:** 812–816. doi:10.1126/science.aad5252

Brokaw K, Tishler W, Manceor S, Hamilton K, Gaulden A, Parr E, Wamsley EJ. 2016. Resting state EEG correlates of memory consolidation. *Neurobiol Learn Mem* **130:** 17–25. doi:10.1016/j.nlm.2016.01.008

Buckner RL, Vincent JL. 2007. Unrest at rest: default activity and spontaneous network correlations. *Neuroimage* **37:** 1091–1096. doi:10.1016/j.neuroimage.2007.01.010

Carr MF, Jadhav SP, Frank LM. 2011. Hippocampal replay in the awake state: a potential substrate for memory consolidation and retrieval. *Nat Neurosci* **14:** 147–153. doi:10.1038/nn.2732

Clemens Z, Molle M, Eross L, Barsi P, Halasz P, Born J. 2007. Temporal coupling of parahippocampal ripples, sleep spindles and slow oscillations in humans. *Brain* **130:** 2868–2878. doi:10.1093/brain/awm146

Cohen DA, Pascual-Leone A, Press DZ, Robertson EM. 2005. Off-line learning of motor skill memory: a double dissociation of goal and movement. *Proc Natl Acad Sci* **102:** 18237–18241. doi:10.1073/pnas.0506072102

Collins MB, Wamsley EJ. 2020. Effect of postlearning meditation on memory consolidation: level of focused attention matters. *Learn Mem* **27:** 250–253. doi:10.1101/lm.051151.119

Craig M, Della Sala S, Dewar M. 2014. Autobiographical thinking interferes with episodic memory consolidation. *PLoS One* **9:** e93915. doi:10.1371/journal.pone.0093915

Craig M, Ottaway G, Dewar M. 2018. Rest on it: awake quiescence facilitates insight. *Cortex* **109:** 205–214. doi:10.1016/j.cortex.2018.09.009

de Sousa AF, Cowansage KK, Zutshi I, Cardozo LM, Yoo EJ, Leutgeb S, Mayford M. 2019. Optogenetic reactivation of memory ensembles in the retrosplenial cortex induces systems consolidation. *Proc Natl Acad Sci* **116:** 8576. doi:10.1073/pnas.1818432116

Dewar M, Alber J, Butler C, Cowan N, Della Sala S. 2012. Brief wakeful resting boosts new memories over the long term. *Psychol Sci* **23:** 955–960. doi:10.1177/0956797612441220

Dewar M, Alber J, Cowan N, Della Sala S. 2014. Boosting long-term memory via wakeful rest: intentional rehearsal is not necessary, consolidation is sufficient. *PLoS One* **9:** e0109542. doi:10.1371/journal.pone.0109542

Diekelmann S, Born J. 2010. The memory function of sleep. *Nat Rev Neurosci* **11:** 114–126. doi:10.1038/nrn2762

Diekelmann S, Biggel S, Rasch B, Born J. 2012. Offline consolidation of memory varies with time in slow wave sleep and can be accelerated by cuing memory reactivations. *Neurobiol Learn Mem* **98:** 103–111. doi:10.1016/j.nlm.2012.07.002

Dinges DF, Powell JW. 1985. Microcomputer analyses of performance on a portable, simple visual RT task during sustained operations. *Behav Res Methods Instrum Comput* **17:** 652–655. doi:10.3758/BF03200977

Durrant SJ, Taylor C, Cairney S, Lewis PA. 2011. Sleep-dependent consolidation of statistical learning. *Neuropsychologia* **49:** 1322–1331. doi:10.1016/j.neuropsychologia.2011.02.015

Ego-Stengel V, Wilson MA. 2010. Disruption of ripple-associated hippocampal activity during rest impairs spatial learning in the rat. *Hippocampus* **20:** 1–10. doi:10.1002/hipo.20707

Foster DJ, Wilson MA. 2006. Reverse replay of behavioural sequences in hippocampal place cells during the awake state. *Nature* **440:** 680–683. doi:10.1038/nature04587

Frankland PW, Bontempi B. 2005. The organization of recent and remote memories. *Nat Rev Neurosci* **6:** 119–130. doi:10.1038/nrn1607

Genzel L, Wixted JT. 2017. Cellular and systems consolidation of declarative memory. In *Cognitive neuroscience of memory consolidation* (ed. Axmacher N, Rasch B), pp. 3–16. Springer International Publishing, Cham

Girardeau G, Benchenane K, Wiener SI, Buzsáki G, Zugaro MB. 2009. Selective suppression of hippocampal ripples impairs spatial memory. *Nat Neurosci* **12:** 1222–1223. doi:10.1038/nn.2384

Gottselig JM, Hofer-Tinguely G, Borbély AA, Regel SJ, Landolt H-P, Rétey JV, Achermann P. 2004. Sleep and rest facilitate auditory learning. *Neuroscience* **127:** 557–561. doi:10.1016/j.neuroscience.2004.05.053

Hasselmo ME, McGaughy J. 2004. High acetylcholine levels set circuit dynamics for attention and encoding and low acetylcholine levels set dynamics for consolidation. *Prog Brain Res* **145:** 207–231. doi:10.1016/S0079-6123(03)45015-2

Huber R, Ghilardi MF, Massimini M, Tononi G. 2004. Local sleep and learning. *Nature* **430:** 78–81. doi:10.1038/nature02663

Humiston G, Tucker MA, Summer T, Wamsley EJ. 2019. Resting states and memory consolidation: a preregistered replication and meta-analysis. *Sci Rep* **9:** 1–9. doi:10.1038/s41598-019-56033-6

Iber C, Ancoli-Israel S, Chesson A, Quan S. 2007. *The AASM manual for the scoring of sleep and associated events: rules, terminology, and technical specifications*. American Academy of Sleep Medicine, Westchester, IL.

Jadhav SP, Kemere C, German PW, Frank LM. 2012. Awake hippocampal sharp-wave ripples support spatial memory. *Science* **336:** 1454–1458. doi:10.1126/science.1217230

Ji D, Wilson MA. 2007. Coordinated memory replay in the visual cortex and hippocampus during sleep. *Nat Neurosci* **10:** 100–107. doi:10.1038/nn1825

Johns MW. 1991. A new method for measuring daytime sleepiness: the Epworth Sleepiness Scale. *Sleep* **14:** 540–545. doi:10.1093/sleep/14.6.540

Kaefer K, Nardin M, Blahna K, Csicsvari J. 2020. Replay of behavioral sequences in the medial prefrontal cortex during rule switching. *Neuron* **106:** 154–165.e6. doi:10.1016/j.neuron.2020.01.015

Karlsson MP, Frank LM. 2009. Awake replay of remote experiences in the hippocampus. *Nat Neurosci* **12:** 913–918. doi:10.1038/nn.2344

Karni A, Tanne D, Rubenstein BS, Askenasy JJ, Sagi D. 1994. Dependence on REM sleep of overnight improvement of a perceptual skill. *Science* **265:** 679–682. doi:10.1126/science.8036518

Lacourse K, Delfrate J, Beaudry J, Peppard P, Warby SC. 2019. A sleep spindle detection algorithm that emulates human expert spindle scoring. *J Neurosci Methods* **316:** 3–11. doi:10.1016/j.jneumeth.2018.08.014

Laventure S, Fogel S, Lungu O, Albouy G, Sévigny-Dupont P, Vien C, Sayour C, Carrier J, Benali H, Doyon J. 2016. NREM2 and sleep spindles are instrumental to the consolidation of motor sequence memories. *PLoS Biol* **14:** e1002429. doi:10.1371/journal.pbio.1002429

Lee AK, Wilson MA. 2002. Memory of sequential experience in the hippocampus during slow wave sleep. *Neuron* **36:** 1183–1194. doi:10.1016/S0896-6273(02)01096-6

Lewis PA, Durrant SJ. 2011. Overlapping memory replay during sleep builds cognitive schemata. *Trends Cogn Sci* **15:** 343–351. doi:10.1016/j.tics.2011.06.004

Marshall L, Helgadóttir H, Mölle M, Born J. 2006. Boosting slow oscillations during sleep potentiates memory. *Nature* **444:** 610–613. doi:10.1038/nature05278

Martini M, Sachse P. 2020. Factors modulating the effects of waking rest on memory. *Cogn Process* **21:** 149–153. doi:10.1007/s10339-019-00942-x

Martini M, Martini C, Bernegger C, Sachse P. 2018. Post-encoding wakeful resting supports the retention of new verbal memories in children aged 13–14 years. *Br J Dev Psychol* **37:** 199–210. doi:10.1111/bjdp.12267

McDevitt E, Rowe K, Brady M, Duggan K, Mednick S. 2014. The benefit of offline sleep and wake for novel object recognition. *Exp Brain Res* **232:** 1487–1496. doi:10.1007/s00221-014-3830-3

McDevitt E, Duggan KA, Mednick SC. 2015. REM sleep rescues learning from interference. *Neurobiol Learn Mem* **122:** 51–62. doi:10.1016/j.nlm.2014.11.015

McGaugh JL. 2000. Memory:a century of consolidation. *Science* **287:** 248–251. doi:10.1126/science.287.5451.248

Mednick SC, Nakayama K, Cantero JL, Atienza M, Levin AA, Pathak N, Stickgold R. 2002. The restorative effect of naps on perceptual deterioration. *Nat Neurosci* **5:** 677–681. doi:10.1038/nn864

Mednick SC, Makovski T, Cai DJ, Jiang YV. 2009. Sleep and rest facilitate implicit memory in a visual search task. *Vision Res* **49:** 2557–2565. doi:10.1016/j.visres.2009.04.011

Mednick SC, Cai DJ, Shuman T, Anagnostaras S, Wixted JT. 2011. An opportunistic theory of cellular and systems consolidation. *Trends Neurosci* **34:** 504–514. doi:10.1016/j.tins.2011.06.003

Mednick SC, McDevitt E, Walsh JK, Wamsley E, Paulus M, Kanady JC, Drummond SPA. 2013. The critical role of sleep spindles in hippocampal-dependent memory: a pharmacology study. *J Neurosci* **33:** 4494–4504. doi:10.1523/JNEUROSCI.3127-12.2013

Mercer T. 2015. Wakeful rest alleviates interference-based forgetting. *Memory* **23:** 127–137. doi:10.1080/09658211.2013.872279

Mölle M, Born J. 2011. Slow oscillations orchestrating fast oscillations and memory consolidation. *Prog Brain Res* **193:** 93–110. doi:10.1016/B978-0-444-53839-0.00007-7

O'Neill J, Pleydell-Bouverie B, Dupret D, Csicsvari J. 2010. Play it again: reactivation of waking experience and memory. *Trends Neurosci* **33:** 220–229. doi:10.1016/j.tins.2010.01.006

Payne JD, Stickgold R, Swanberg K, Kensinger EA. 2008. Sleep preferentially enhances memory for emotional components of scenes. *Psychol Sci* **19:** 781–788. doi:10.1111/j.1467-9280.2008.02157.x

Payne JD, Schacter DL, Propper RE, Huang L-W, Wamsley EJ, Tucker MA, Walker MP, Stickgold R. 2009. The role of sleep in false memory formation. *Neurobiol Learn Mem* **92:** 327–334. doi:10.1016/j.nlm.2009.03.007

Peyrache A, Khamassi M, Benchenane K, Wiener SI, Battaglia FP. 2009. Replay of rule-learning related neural patterns in the prefrontal cortex during sleep. *Nat Neurosci* **12:** 919–926. doi:10.1038/nn.2337

Piosczyk H, Holz J, Feige B, Spiegelhalder K, Weber F, Landmann N, Kuhn M, Frase L, Riemann D, Voderholzer U, et al. 2013. The effect of sleep-specific brain activity versus reduced stimulus interference on declarative memory consolidation. *J Sleep Res* **22:** 406–413. doi:10.1111/jsr.12033

Plihal W, Born J. 1997. Effects of early and late nocturnal sleep on declarative and procedural memory. *J Cogn Neurosci* **9:** 534–547. doi:10.1162/jocn.1997.9.4.534

Redondo RL, Morris RGM. 2011. Making memories last: the synaptic tagging and capture hypothesis. *Nat Rev Neurosci* **12:** 17–30. doi:10.1038/nrn2963

Sattari N, Whitehurst LN, Ahmadi M, Mednick SC. 2019. Does working memory improvement benefit from sleep in older adults? *Neurobiol Sleep Circadian Rhythms* **6:** 53–61. doi:10.1016/j.nbscr.2019.01.001

Simor P, Zavecz Z, Horvath K, Elteto N, Török C, Pesthy O, Gombos F, Janacsek K, Nemeth D. 2018. Deconstructing procedural memory: different learning trajectories and consolidation of sequence and statistical learning. *Front Psychol* **9:** 2708. doi:10.3389/fpsyg.2018.02708

Singer JL, Antrobus JS. 1972. Daydreaming, imaginal processes, and personality: a normative study. In *The function and nature of imagery* (ed. Sheehan P), pp. 175–202. Academic Press, New York.

Staresina BP, Alink A, Kriegeskorte N, Henson RN. 2013. Awake reactivation predicts memory in humans. *Proc Natl Acad Sci* **110:** 21159–21164. doi:10.1073/pnas.1311989110

Staresina BP, Bergmann TO, Bonnefond M, van der Meij R, Jensen O, Deuker L, Elger CE, Axmacher N, Fell J. 2015. Hierarchical nesting of slow oscillations, spindles and ripples in the human hippocampus during sleep. *Nat Neurosci* **18:** 1679–1686. doi:10.1038/nn.4119

Stickgold R, Whidbee D, Schirmer B, Patel V, Hobson JA. 2000. Visual discrimination task improvement: a multi-step process occurring during sleep. *J Cogn Neurosci* **12:** 246–254. doi:10.1162/089892900562075

Tadel F, Baillet S, Mosher J, Pantazis D, Leahy R. 2011. Brainstorm: a user-friendly application for MEG/EEG analysis. *Comput Intell Neurosci* **2011:** 1–13. doi:10.1155/2011/879716

Tucker MA, Fishbein W. 2009. The impact of sleep duration and subject intelligence on declarative and motor memory performance: how much is enough? *J Sleep Res* **18:** 304–312. doi:10.1111/j.1365-2869.2009.00740.x

Tucker MA, Nguyen N, Stickgold R. 2016. Experience playing a musical instrument and overnight sleep enhance performance on a sequential typing task. *PLoS One* **11:** e0159608. doi:10.1371/journal.pone.0159608

Tucker MA, Humiston G, Summer T, Wamsley E. 2020. Comparing the effects of sleep and rest on memory consolidation. *Nat Sci Sleep* **12:** 79–91. doi:10.2147/NSS.S223917

Wagner U, Gais S, Haider H, Verleger R, Born J. 2004. Sleep inspires insight. *Nature* **427:** 352–355. doi:10.1038/nature02223

Walker MP, Brakefield T, Morgan A, Hobson JA, Stickgold R. 2002. Practice with sleep makes perfect: sleep-dependent motor skill learning. *Neuron* **35:** 205–211. doi:10.1016/S0896-6273(02)00746-8

Wamsley EJ. 2019. Memory consolidation during waking rest. *Trends Cogn Sci* **23:** 171–173. doi:10.1016/j.tics.2018.12.007

Wamsley EJ, Summer T. 2020. Spontaneous entry into an 'offline' state during wakefulness: a mechanism of memory consolidation? *J Cogn Neurosci* **32:** 1714–1734. doi:10.1162/jocn_a_01587

Wamsley EJ, Tucker MA, Shinn AK, Ono KE, McKinley SK, Ely AV, Goff DC, Stickgold R, Manoach DS. 2012. Reduced sleep spindles and spindle coherence in schizophrenia: mechanisms of impaired memory consolidation? *Biol Psychiatry* **71:** 154–161. doi:10.1016/j.biopsych.2011.08.008