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A Brief Period of Eyes-Closed Rest Enhances Motor Skill Consolidation

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Abstract

Post-training sleep benefits both declarative and procedural memory consolidation. However, recent research suggests that eyes-closed waking rest may provide a similar benefit. Brokaw et al. (2016), for example, recently demonstrated that verbal declarative memory improved more following a 15min period of waking rest, in comparison to 15min of active wake. Here, we used the same procedures to test whether procedural memory similarly benefits from waking rest. Participants were trained on the Motor Sequence Task (MST), followed by a 15min retention interval during which they either rested with their eyes closed or completed a distractor task. Rest significantly enhanced MST performance, mirroring the effect observed in Brokaw et al. (2016) and demonstrating that waking rest benefits the early stages of procedural memory. An additional group of participants tested 4hrs later displayed no effect of rest. Overall, these results suggest that the early MST performance “boost” described in prior studies may depend on post-learning state.

Keywords

memory consolidation; procedural memory; learning and memory; finger-tapping; resting state

Introduction

Rest is often considered a waste of time, when productivity ceases and we do nothing. Yet new evidence suggests this is far from the case. Our minds are hard at work during periods of unoccupied rest – replaying past memories, creating imagined scenarios, and planning for the future (Andrews-Hanna, 2012; Brokaw et al., 2016; Carr, Jadhav, & Frank, 2011; Dewar, Alber, Butler, Cowan, & Della Sala, 2012; Dewar, Alber, Cowan, & Della Sala, 2014; Foster & Wilson, 2006; Jadhav, Kemere, German, & Frank, 2012; Mednick, Cai, Shuman, Anagnostaras, & Wixted, 2011; Schacter, Addis, & Buckner, 2007, 2008). Rather than being a waste of time, these “offline” periods may serve a critical role in the initial stages of memory consolidation. For example, recent evidence shows that just 15min of eyes-closed rest following learning can significantly boost declarative memory for up to one week

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(Brokaw et al., 2016; Dewar et al., 2012, 2014). Here, we tested whether a brief post-training period of waking rest similarly benefits procedural memory.

A century of research has established that sleep protects, stabilizes and, at times, enhances memory (Ekstrand, 1967; Jenkins & Dallenbach, 1924; Plihal & Born, 1997; Stickgold, 2005; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002). Early studies demonstrated that memory is enhanced after a period of sleep, relative to an equivalent period of wake (Ekstrand, 1967; Jenkins & Dallenbach, 1924; Plihal & Born, 1997), an effect now thought to result from active neuronal processes facilitating the reactivation and consolidation of memory (Clemens et al., 2007; Diekelmann & Born, 2010; Frank, Issa, & Stryker, 2001; Marshall & Born, 2007; Marshall, Helgadóttir, Mölle, & Born, 2006; Mednick et al., 2013; Stickgold, 2005). The specific neurobiology of sleep has been proposed to be essential for these consolidation processes (Diekelmann & Born, 2010; Stickgold, 2005). But is sleep, *per se*, really required for these memory benefits to occur? Some key features of sleep thought to benefit memory consolidation are also present during waking rest (Carr et al., 2011; Foster & Wilson, 2006; Mednick et al., 2011). Relative to active wake, dominated by beta EEG rhythms (>13Hz), both rest and sleep are characterized by EEG slowing. During rest, beta EEG rhythms give way to the slower, more synchronous alpha rhythm (8–12 Hz). As we enter sleep, theta (4–7 Hz), and then delta (1–4 Hz) and slow oscillations (<1 Hz) increasingly dominate the EEG.

Waking rest and sleep are also both accompanied by a dramatic reduction in sensory input, reducing interference and potentially enabling memory consolidation by diminishing new encoding demands on the hippocampus (Mednick et al., 2011). On the neurochemical level, decreased acetylcholine levels during both sleep and waking rest may facilitate hippocampal-neocortical dynamics that favour consolidation over encoding (Hasselmo, 1999, 2006). Finally, the cellular-level “reactivation” of memory during sharp-wave ripple complexes in the hippocampus occurs during waking rest at rates similar to those observed during NREM sleep (Carr et al., 2011; Clemens et al., 2007; Foster & Wilson, 2006; Jadhav et al., 2012).

The potential benefit of waking rest for memory has not been adequately tested. Many studies examining the effect of sleep on memory conclude that sleep benefits memory more than an equivalent period of wake, but wake control conditions are often confounded by interfering activities, as wake participants may be permitted to leave the laboratory (Ellenbogen, Hulbert, Stickgold, Dinges, & Thompson-Schill, 2006; Payne, Stickgold, Swanberg, & Kensinger, 2008; Witt, Margraf, Bieber, Born, & Deuschl, 2010), or else are directed to complete an activity such as watching videos (Tucker et al., 2006; Wamsley, Tucker, Payne, & Stickgold, 2010; Wilhelm et al., 2011), or listening to music (Mednick, Makovski, Cai, & Jiang, 2009; Rieth, Cai, McDevitt, & Mednick, 2010). To be free of these confounds, the ideal waking control would have participants resting quietly with their eyes closed without engaging in any task, matching the behavioural conditions present during sleep. Although this is difficult for participants to achieve across long durations, such a control is possible for brief intervals (Brokaw et al., 2016; Dewar et al., 2012).

A handful of recent studies utilizing an eyes-closed waking rest condition have established that rest confers a benefit for declarative memory similar to that of sleep when compared to active wake (Brokaw et al., 2016; Craig, Dewar, Della Sala, & Wolbers, 2015; Dewar et al., 2012, 2014). In two recent studies, participants listened to a short story, then either rested with their eyes closed or played a simple computer game for 15 minutes (Brokaw et al., 2016; Dewar et al., 2012). Those who rested remembered significantly more details of the story when tested later. EEG recordings revealed that cortical slow oscillations (<1Hz), which have been associated with hippocampus-dependent memory consolidation during sleep, predicted improved memory following rest (Brokaw et al., 2016).

These studies demonstrate that waking rest benefits hippocampus-dependent verbal and spatial memory, but have not examined the effect on procedural memory, also repeatedly shown to benefit from sleep (Hotermans, Peigneux, Maertens de Noordhout, Moonen, & Maquet, 2006; Plihal & Born, 1997; Walker et al., 2002). Here, for the first time, we tested whether the memory benefit of eyes closed rest extends to procedural learning, using the Motor Sequence Task (MST). This task has been used extensively in past research (Hotermans, Peigneux, De Noordhout, Moonen, & Maquet, 2008; Hotermans et al., 2006; Kuriyama, Stickgold, & Walker, 2004; Nishida & Walker, 2007; Tucker & Fishbein, 2009; Tucker, McKinley, & Stickgold, 2011; Walker et al., 2002), and is especially notable in that multiple studies have observed a “boost” in task performance following a short break (Albouy et al., 2006; Hotermans et al., 2008, 2006; Schmitz et al., 2009), appearing 5–30min after training and dissipating by 4hrs (Hotermans et al., 2008, 2006). Although a number of prior studies have reported enhancement of MST performance following sleep (Walker et al., 2002), the extent to which sleep is necessary for offline performance gains remains controversial (Rickard, Cai, Rieth, Jones, & Ard, 2008).

In the current study, participants were trained on the MST prior to either resting with their eyes closed or completing a distractor task. We hypothesized that waking rest would benefit performance on the test administered immediately afterwards. Subsequently, an additional group of participants was retested after a 4hr delay, in which timeframe the MST “boost” effect is thought to dissipate (Hotermans et al., 2008, 2006).

Methods

Participants

To evaluate whether rest improves procedural memory, participants were trained on the MST and tested immediately following a 15min retention interval of either rest or active wake. To explore the time course of rest’s effect, we subsequently tested an additional group following a 4hr delay. The immediate test group was run three months before the delayed test group. Participants were excluded from analysis if they fell asleep during the retention interval, defined as at least one 30sec epoch of N2 sleep or more than five minutes of N1 sleep (n=4 in the immediate test group, and n=7 in the 4hr delay group; all instances occurred during waking rest; mean N1=3.36min $\pm$ 2.35 S.D., mean N2= 5.23min $\pm$ 3.56 S.D.), or if they scored higher than 4 on the Stanford Sleepiness Scale (n=3 in the immediate test group, n=2 in the 4hr delay group).

Following exclusions, the immediate test group was comprised of 18 college students (7 males, mean age 20.50 ± 1.10 S.D., range 19–24), and the delayed test group of 17 college students (4 males, mean age of 19.29 ± 1.31 S.D., range 18–21). N=6 participants included in analysis obtained a mean of 2.67 ± 1.66 S.D. min N1 sleep. All participants signed informed consent and were compensated \$10/hour or received course credit in an introductory psychology course. Participants were instructed not to consume caffeine after 10am on the day of their session.

Procedure

Procedures closely followed those of Brokaw et al., with the exception of the memory task used (Brokaw et al., 2016) (Fig 1). Upon arrival at the laboratory (which occurred at variable times of day), participants completed demographics forms, the Epworth Sleepiness scale (ESS; a measure of trait sleepiness) (Johns, 1991), a questionnaire about experience playing musical instruments (Tucker, Nguyen, & Stickgold, 2016), the Stanford Sleepiness Scale (SSS, a measure of state sleepiness; n=10 participants in the delayed test group had incomplete SSS data) (Hoddes, Zarcone, Smythe, Phillips, & Dement, 1973), and two visual analogue scales rating alertness and concentration. Additionally, participants completed an exit questionnaire about their thoughts and activities during the 15min retention intervals, depicting on a pie chart the proportion of time spent thinking about a range of selected topics (see Tables S1-S3). Those in the 4hr delay group completed this questionnaire twice, once after each 15min retention interval. Those in the immediate test group completed the questionnaire once, at the conclusion of the study.

Six EEG electrodes were attached to the scalp (F3/4, C3/4, O1/2), referenced to the contralateral mastoid. Eye and chin electrodes were also applied, in order to facilitate the detection of sleep onset. Impedance was kept to $<10\text{k}\Omega$ and signals were digitally acquired at 400Hz.

Following electrode attachment, participants completed 12 training trials for the MST (see below). Participants were then randomly assigned either to rest with their eyes closed (“rest” condition) or play the computer game “Snood” (<http://snoodworld.com>) (“distractor task” condition) for 15min. Participants completed both conditions in counterbalanced order, with a 5min break between sessions. EEG was recorded throughout the retention interval.

In the waking rest condition, participants were semi-recumbent and were instructed to keep their eyes closed, minimize movement, and stay awake until the experimenter returned to end the retention interval. In the distractor condition, the experimenter explained the rules of Snood and told participants to continue playing for the entire 15min, and to minimize movement. Difficulty level was set to “medium”. No instruction was given in either condition about what participants should be doing mentally. After the retention interval, participants again completed the SSS and visual analogue scales rating their alertness and concentration.

Those in the immediate test group were tested on MST performance immediately following the retention interval, and then after a 5min break proceeded to complete the other experimental condition (order of conditions counterbalanced across participants).

Participants in the 4hr delay condition took a 5min break after their first retention interval, then proceeded to the training and retention interval for the other condition (order of conditions counterbalanced across participants). They returned to the lab 4hrs later to complete both of the tests.

Motor Sequence Task (MST).—Participants typed a 5-digit sequence using their non-dominant hand, as quickly and accurately as possible. Training and testing each consisted of 12 trials, beginning with 30 seconds of typing, followed by 30 seconds of rest. The two possible sequences were 41324 and 23142. The sequence was displayed on the screen, and assignment of sequence to experimental condition was counterbalanced. The experimenter remained in the testing room at the beginning of the task to ensure participants were correctly following instructions; if they were not, the experimenter reiterated the instructions. Raw change in MST performance was calculated by subtracting the average score of the first three training trials from the average score of the final three test trials. Percent change was calculated by dividing the raw change by the average score of the first three training trials.

Snood.—We chose “Snood” as the distractor task because it has little content overlap with the MST (Snood is a visuospatial task with minimal motor components), is engaging, and requires only minimal hand and eye movement, minimizing artifact in the EEG recording. The objective is to clear the screen of “Snoods” by joining three or more icons of the same color and design. The window displaying the game was reduced in size to minimize participants’ eye movements.

EEG Analysis.—PSG (polysomnographic) records were scored for sleep stage following the standardized criteria established by the American Academy of Sleep Medicine (Iber, Ancoli-Israel, Chesson, & Quan, 2007). Following artifact rejection via visual inspection, rest recordings were then subjected to spectral analysis via Welch’s method, conducted on all artifact-free 4sec epochs using Hamming windowing with 50% segment overlap. Analysis focused on 5 a priori frequency bands of interest: beta (13–35Hz), alpha (8–12Hz), theta (4–7Hz), delta (1–4Hz), and slow oscillation (<1Hz).

Results

Post-Training Rest Enhances MST Performance at Immediate Test, But Not After a 4hr Delay

Post-training rest improved MST performance significantly more than the distractor task at the immediate test (raw change: $t(17)=2.28$, $p=.036$, $d=.67$; % change: $t(17)=2.17$, $p=.045$, $d=.58$) (Table 1). This effect was no longer present in the 4hr delay group (raw change: $t(16)=.13$, $p=.90$; % change: $t(16)=.07$, $p=.94$; Condition x Delay interaction effect for raw change: $F(1,33)=3.01$, $p=.092$; % change: $F(1,33)=2.47$, $p=.13$) (Table 1; Fig 2).

The Effect of Sleep on Performance

When the combined performance of the $n=8$ participants from both groups who fell asleep but met all other inclusion criteria (mean number of minutes asleep 9.19 ± 2.17 S.D.; mean

minutes of N1 3.56 ± 2.67 S.D.; mean minutes of N2 5.63 ± 3.18 S.D.), were included in the above analyses, there was no significant difference between the rest and distractor task conditions in either delay group. The only significant effect remaining was that participants in the immediate test group still improved more after the retention interval than those in the 4hr delay group (Main effect of delay for MST raw change: $F(1,42)=38.14$, $p=.00000022$, $\eta_p^2=.48$; MST percent change: $F(1,42)=29.66$, $p=.000002$, $\eta_p^2=.41$).

Although low statistical power prohibits meaningful tests of significance, we note that among the participants who fell asleep but met all other inclusion criteria (immediate and delayed participants combined), performance was actually numerically *worse* in the rest condition (raw change: $M=1.09 \pm 3.78$ S.D.; % change: $M=6.2\% \pm 20\%$ S.D.) than in the distractor task condition (raw change: $M=4.31 \pm 3.91$ S.D.; % change: $M=25.6\% \pm 28.6\%$ S.D.). Overall, participants who fell asleep improved a similar amount at test (raw change: $M=2.70 \pm 3.08$ S.D.; % change: $M=14.3\% \pm 17.0\%$ S.D.), relative to those who did not (raw change: $M=3.55 \pm 3.10$ S.D.; % change: $M=16.9\% \pm 15.1\%$ S.D.). Participants who slept had similar average SSS scores (2.81 ± 1.16 S.D.) to participants who did not sleep ($2.67 \pm .85$ S.D.), with average total ESS scores somewhat higher in those who slept (10.5 ± 3.42 S.D.) than in those who did not (8.4 ± 3.31 S.D.).

Confirmation of an MST “Boost” Effect Present at Immediate Test, Dissipated by 4hrs

As reported in prior literature (Hotermans et al., 2008, 2006), immediate test participants showed a very large performance improvement following the 15min retention interval ($t(17)=10.09$, $p=0.000000014$, $d=2.38$) much greater in magnitude than has typically been reported after longer waking durations (Walker et al., 2002) (Fig 3). We ran the 4hr delay participants expecting that this “boost” in performance would have dissipated after 4hrs. Indeed, participants tested after a 4hr delay showed significantly less improvement than those tested immediately following the 15min break (main effect of delay on raw change: $F(1,33)=30.86$, $p=.000004$, $\eta_p^2=.48$; percent change: $F(1,33)=23.00$, $p=.000034$, $\eta_p^2=.41$). However, at 4hrs, improvement above baseline remained significant ($t(16)=2.62$, $p=0.019$, $d=.38$).

Neither Subjective Experience nor EEG Spectral Power during the Retention Interval Correlates with MST Performance

In contrast to Brokaw et al. (Brokaw et al., 2016), neither subjective experience nor EEG spectral power during the retention interval meaningfully correlated with MST improvement in either group (see Supplementary Results). In the immediate test group, thinking about the next day during waking rest positively correlated with MST percent improvement ($r_s=.47$, $p=.047$). In the 4hr delay group, reports of meditating during waking rest positively correlated with MST improvement (raw change: $r_s=.53$, $p=.042$; % change: $r_s=.53$, $p=.042$). Both counting time ($r_s=.52$, $p=.049$) and sleeping (self-reported; $r_s=.52$, $p=.049$) during waking rest also positively correlated with MST % change in the delayed group. Thinking about the past year during the distractor task positively correlated with MST raw change ($r_s=.59$, $p=.022$). However, each of these correlations were due to a single outlier, and when the outlier was removed none remained significant.

Order Effects and Participant Characteristics

Condition order did not affect MST performance in either group. There was no main effect of condition counterbalancing order ($p > .22$), and there were no significant interactions involving condition order (all p -values $> .09$). In both the immediate and delayed test groups, baseline MST performance was equivalent between conditions (rest vs. distractor at immediate test: $t = .76$, $p = .46$; rest vs. distractor at delayed test: $t = .13$, $p = .90$) and was equivalent between the first and second sessions (1st vs. 2nd condition completed at immediate test: $t = 1.20$, $p = .25$; 1st vs. 2nd condition completed at delayed test: $t = .92$, $p = .37$). Participants in the immediate test and 4hr delay groups did not differ in their sex, SSS scores, experience with playing instruments, or their baseline MST performance (see Table 2).

There were statistically significant group differences in age, ($t(33) = 2.96$, $p = .01$; Table 2, and ESS scores ($t(33) = 2.21$, $p = .03$; Table 2). ESS scores were not related to MST improvement in either the rest (correlation with raw improvement: $r = -.07$, $p = 0.69$; % improvement: $r = -.01$, $p = 0.95$) or distractor task conditions (correlation with raw improvement: $r = .12$, $p = .51$; % improvement: $r = .11$, $p = .54$). However, there was an association between age and MST improvement across the distractor task condition (raw improvement: $r = .36$, $p = .04$; % improvement: $r = .34$, $p = .048$), as well as trend-level associations between age and improvement across the rest condition (raw improvement: $r = .29$, $p = .09$; % improvement: $r = .27$, $p = .11$).

We therefore repeated statistical comparison of the immediate vs. delayed groups controlling for age as a covariate. Controlling for age, MST improvement was still greatly reduced after a 4hr delay (raw change: $F(1,32) = 21.7$, $p = 0.00005$; % change: $F(1,32) = 16.13$, $p = .00033$). Controlling for age, the Delay (immediate vs. delayed) $\times$ Condition (rest vs. snood) interactions remained near-significant for both raw change ($F(1,32) = 4.11$, $p = 0.051$) and % change in MST performance ($F(1,32) = 3.51$, $p = 0.07$). Together, these analyses demonstrate that group differences in age do not account for the above-reported effects.

Discussion

Consistent with our hypothesis, waking rest benefited MST performance at immediate test. This concurs with prior research from our lab and others showing that a brief period of rest following learning benefits declarative memory (Brokaw et al., 2016; Dewar et al., 2012, 2014). Here, for the first time, we extend this observation to motor-procedural learning. However, in contrast to the long-lasting effects of rest reported for declarative memory (Dewar et al., 2012, 2014), our data suggest that this effect of rest on motor-procedural performance may be short-lived.

In agreement with prior reports (Debarnot, Clerget, & Olivier, 2011; Hotermans et al., 2008, 2006; Nettersheim, Hallschmid, Born, & Diekelmann, 2015; Schmitz et al., 2009), we observed a large “boost” in MST performance present 15min after the completion of training. This early performance boost was modulated by rest, but 4hrs later, rest no longer significantly benefited performance. A possible interpretation of the apparently transient nature of rest’s effect is that rest facilitates the early, synaptic-level consolidation thought to

underlie initial offline performance gains on the MST (Hotermans et al., 2008), but may not influence later stages of consolidation.

A short-lasting effect of rest on motor-procedural memory may also be explained by the divergent mechanisms underlying systems-level consolidation for procedural, as opposed to declarative memory. Across longer timescales, consolidation of declarative memory relies on hippocampal-cortical communication dynamics that are less relevant to procedural memory (Buzsáki, 1996; Frankland & Bontempi, 2005; Mölle & Born, 2011; Wang & Morris, 2010). In the case of declarative memory, waking rest's long-term benefit may be due to a reduction of encoding demands that allows for the hippocampus to engage in consolidation of new declarative memories, rather than encoding of new information (Mednick et al., 2011). This hippocampus-specific mechanism would not be expected to confer a similar long-term benefit on procedural memory.

The lack of association between MST performance and EEG activity during rest may similarly be explained by the differing brain systems supporting declarative vs. procedural memory consolidation. Brokaw et al. reported that cortical slow oscillations during rest predicted declarative memory improvement (Brokaw et al., 2016). Slow oscillations during sleep are believed to facilitate communication between the hippocampus and neocortex (Buzsáki, 1996; Clemens et al., 2007; Marshall et al., 2006; Mölle & Born, 2011), a mechanism which again may impact only declarative memory consolidation.

Although our data are consistent with an effect of rest on procedural memory consolidation, alternative explanations are possible. For example, motor performance improvement following a short break is also consistent with recovery from fatigue. However, it is not clear why the rest condition would allow greater dissipation of fatigue than the distractor task, if “fatigue” is taken to result from use of the specific finger muscles and associated brain regions engaged during the MST. These would not necessarily be utilized more while playing Snood than during quiet rest, and therefore both conditions would be expected to allow recovery from motor fatigue.

In summary, we report that a brief period of post-training rest benefits procedural memory at immediate test. Similar effects have previously been reported for declarative memory (Brokaw et al., 2016; Dewar et al., 2012, 2014), but the present study is the first to report this observation for a procedural learning task. However, rest's effect on procedural memory may be transient, influencing early but not later phases of memory consolidation. Sleep-specific mechanisms may thus be required for long-lasting offline gains in motor performance to emerge.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

- Albouy G, Ruby P, Phillips C, Luxen A, Peigneux P, & Maquet P (2006). Implicit oculomotor sequence learning in humans: Time course of offline processing. *Brain Research*, 1090(1), 163–171. 10.1016/j.brainres.2006.03.076 [PubMed: 16677617]
- Andrews-Hanna JR (2012). The brain's default network and its adaptive role in internal mentation. *The Neuroscientist: A Review Journal Bringing Neurobiology, Neurology And Psychiatry*, 18(3), 251–270. 10.1177/1073858411403316
- Brokaw K, Tishler W, Manceor S, Hamilton K, Gaulden A, Parr E, & Wamsley EJ (2016). Resting state EEG correlates of memory consolidation. *Neurobiology of Learning and Memory*, 130, 17–25. [PubMed: 26802698]
- Buzsáki G (1996). The hippocampo-neocortical dialogue. *Cerebral Cortex (New York, N.Y.: 1991)*, 6(2), 81–92.
- Carr MF, Jadhav SP, & Frank LM (2011). Hippocampal replay in the awake state: A potential substrate for memory consolidation and retrieval. *Nature Neuroscience*, 14(2), 147–153. 10.1038/nn.2732 [PubMed: 21270783]
- Clemens Z, Mölle M, Eross L, Barsi P, Halász P, & Born J (2007). Temporal coupling of parahippocampal ripples, sleep spindles and slow oscillations in humans. *Brain: A Journal of Neurology*, 130(Pt 11), 2868–2878. 10.1093/brain/awm146 [PubMed: 17615093]
- Craig M, Dewar M, Della Sala S, & Wolbers T (2015). Rest boosts the long-term retention of spatial associative and temporal order information. *Hippocampus*, n/a-n/a. 10.1002/hipo.22424
- Debnart U, Clerget E, & Olivier E (2011). Role of the primary motor cortex in the early boost in performance following mental imagery training. *PloS One*, 6(10), e26717 10.1371/journal.pone.0026717 [PubMed: 22046337]
- Dewar M, Alber J, Butler C, Cowan N, & Della Sala S (2012). Brief wakeful resting boosts new memories over the long term. *Psychological Science*, 23(9), 955–960. 10.1177/0956797612441220 [PubMed: 22829465]
- 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(10), e109542 10.1371/journal.pone.0109542 [PubMed: 25333957]
- Diekelmann S, & Born J (2010). The memory function of sleep. *Nature Reviews. Neuroscience*, 11(2), 114–126. 10.1038/nrn2762 [PubMed: 20046194]
- Ekstrand BR (1967). Effect of sleep on memory. *Journal of Experimental Psychology*, 75(1), 64–72. [PubMed: 6065839]
- Ellenbogen JM, Hulbert JC, Stickgold R, Dinges DF, & Thompson-Schill SL (2006). Interfering with theories of sleep and memory: Sleep, declarative memory, and associative interference. *Current Biology*, 16(13), 1290–1294. [PubMed: 16824917]
- Foster DJ, & Wilson MA (2006). Reverse replay of behavioural sequences in hippocampal place cells during the awake state. *Nature*, 440(7084), 680–683. 10.1038/nature04587 [PubMed: 16474382]
- Frank MG, Issa NP, & Stryker MP (2001). Sleep enhances plasticity in the developing visual cortex. *Neuron*, 30(1), 275–287. [PubMed: 11343661]
- Frankland PW, & Bontempi B (2005). The organization of recent and remote memories. *Nature Reviews. Neuroscience*, 6(2), 119–130. 10.1038/nrn1607 [PubMed: 15685217]
- Hasselmo. (1999). Neuromodulation: Acetylcholine and memory consolidation. *Trends in Cognitive Sciences*, 3(9), 351–359. [PubMed: 10461198]
- Hasselmo ME (2006). The role of acetylcholine in learning and memory. *Current Opinion in Neurobiology*, 16(6), 710–715. 10.1016/j.conb.2006.09.002 [PubMed: 17011181]
- Hoddes E, Zarcone V, Smythe H, Phillips R, & Dement WC (1973). Quantification of sleepiness: A new approach. *Psychophysiology*, 10(4), 431–436. [PubMed: 4719486]
- Hotermans C, Peigneux P, De Noordhout AM, Moonen G, & Maquet P (2008). Repetitive transcranial magnetic stimulation over the primary motor cortex disrupts early boost but not delayed gains in performance in motor sequence learning. *European Journal of Neuroscience*, 28(6), 1216–1221. 10.1111/j.1460-9568.2008.06421.x [PubMed: 18783369]

- Hotermans C, Peigneux P, Maertens de Noordhout A, Moonen G, & Maquet P (2006). Early boost and slow consolidation in motor skill learning. *Learning & Memory* (Cold Spring Harbor, N.Y.), 13(5), 580–583. 10.1101/lm.239406
- 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*. Westchester, IL: American Academy of Sleep Medicine.
- Jadhav SP, Kemere C, German PW, & Frank LM (2012). Awake hippocampal sharp-wave ripples support spatial memory. *Science*, 336(6087), 1454–1458. 10.1126/science.1217230 [PubMed: 22555434]
- Jenkins JG, & Dallenbach KM (1924). Obliviscence during sleep and waking. *The American Journal of Psychology*, 35(4), 605–612.
- Johns MW (1991). A new method for measuring daytime sleepiness: The Epworth Sleepiness Scale. *Sleep*, 14(6), 540–545. 10.1093/sleep/14.6.540 [PubMed: 1798888]
- Kuriyama K, Stickgold R, & Walker MP (2004). Sleep-dependent learning and motor-skill complexity. *Learning & Memory*, 11(6), 705–713. 10.1101/lm.76304 [PubMed: 15576888]
- Marshall L, & Born J (2007). The contribution of sleep to hippocampus-dependent memory consolidation. *Trends in Cognitive Sciences*, 11(10), 442–450. 10.1016/j.tics.2007.09.001 [PubMed: 17905642]
- Marshall L, Helgadóttir H, Mölle M, & Born J (2006). Boosting slow oscillations during sleep potentiates memory. *Nature*, 444(7119), 610–613. 10.1038/nature05278 [PubMed: 17086200]
- Mednick SC, Cai DJ, Shuman T, Anagnostaras S, & Wixted JT (2011). An opportunistic theory of cellular and systems consolidation. *Trends in Neurosciences*. 10.1016/j.tins.2011.06.003
- Mednick SC, Makovski T, Cai DJ, & Jiang YV (2009). Sleep and rest facilitate implicit memory in a visual search task. *Vision Research*, 49(21), 2557–2565. 10.1016/j.visres.2009.04.011 [PubMed: 19379769]
- Mednick SC, McDevitt EA, Walsh JK, Wamsley E, Paulus M, Kanady JC, & Drummond SPA (2013). The critical role of sleep spindles in hippocampal-dependent memory: A pharmacology study. *The Journal Of Neuroscience: The Official Journal Of The Society For Neuroscience*, 33(10), 4494–4504. 10.1523/JNEUROSCI.3127-12.2013 [PubMed: 23467365]
- Mölle M, & Born J (2011). Slow oscillations orchestrating fast oscillations and memory consolidation. *Progress in Brain Research*, 193, 93–110. 10.1016/B978-0-444-53839-0.00007-7 [PubMed: 21854958]
- Nettersheim A, Hallschmid M, Born J, & Diekelmann S (2015). The role of sleep in motor sequence consolidation: Stabilization rather than enhancement. *The Journal of Neuroscience*, 35(17), 6696–6702. 10.1523/JNEUROSCI.1236-14.2015 [PubMed: 25926448]
- Nishida M, & Walker MP (2007). Daytime naps, motor memory consolidation and regionally specific sleep spindles. *Plos One*, 2(4), e341–e341. [PubMed: 17406665]
- Payne JD, Stickgold R, Swanberg K, & Kensinger EA (2008). Sleep preferentially enhances memory for emotional components of scenes. *Psychological Science*, 19(8), 781. [PubMed: 18816285]
- Plihal W, & Born J (1997). Effects of early and late nocturnal sleep on declarative and procedural memory. *Journal of Cognitive Neuroscience*, 9(4), 534–547. [PubMed: 23968216]
- Rickard TC, Cai DJ, Rieth CA, Jones J, & Ard MC (2008). Sleep does not enhance motor sequence learning. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 34(4), 834–842. 10.1037/0278-7393.34.4.834
- Rieth CA, Cai DJ, McDevitt EA, & Mednick SC (2010). The role of sleep and practice in implicit and explicit motor learning. *Behavioural Brain Research*, 214(2), 470–474. 10.1016/j.bbr.2010.05.052 [PubMed: 20553972]
- Schacter DL, Addis DR, & Buckner RL (2007). Remembering the past to imagine the future: The prospective brain. *Nature Reviews. Neuroscience*, 8(9), 657–661. [PubMed: 17700624]
- Schacter DL, Addis DR, & Buckner RL (2008). Episodic simulation of future events. *Annals of the New York Academy of Sciences*, 1124(1), 39–60. 10.1196/annals.1440.001 [PubMed: 18400923]
- Schmitz R, Schabus M, Perrin F, Luxen A, Maquet P, & Peigneux P (2009). Recurrent boosting effects of short inactivity delays on performance: An ERPs study. *BMC Research Notes*, 2, 170. 10.1186/1756-0500-2-170 [PubMed: 19709401]

- Stickgold R (2005). Sleep-dependent memory consolidation. *NATURE-LONDON*-, 7063, 1272.
- Tucker MA, & Fishbein W (2009). The impact of sleep duration and subject intelligence on declarative and motor memory performance: How much is enough? *Journal of Sleep Research*, 18(3), 304–312. 10.1111/j.1365-2869.2009.00740.x [PubMed: 19702788]
- Tucker MA, Hirota Y, Wamsley EJ, Lau H, Chaklader A, & Fishbein W (2006). A daytime nap containing solely non-REM sleep enhances declarative but not procedural memory. *Neurobiology of Learning and Memory*, 86(2), 241–247. [PubMed: 16647282]
- Tucker MA, McKinley S, & Stickgold R (2011). Sleep optimizes motor skill in older adults. *Journal of the American Geriatrics Society*, 59(4), 603–609. 10.1111/j.1532-5415.2011.03324.x [PubMed: 21410442]
- 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(7), e0159608 10.1371/journal.pone.0159608 [PubMed: 27472398]
- Walker MP, Brakefield T, Morgan A, Hobson JA, & Stickgold R (2002). Practice with sleep makes perfect: Sleep-dependent motor skill learning. *Neuron*, 35(1), 205–211. [PubMed: 12123620]
- Wamsley EJ, Tucker MA, Payne JD, & Stickgold R (2010). A brief nap is beneficial for human route-learning: The role of navigation experience and EEG spectral power. *Learning & Memory*, 17(7), 332. [PubMed: 20581255]
- Wang S-H, & Morris RGM (2010). Hippocampal-neocortical interactions in memory formation, consolidation, and reconsolidation. *Annual Review of Psychology*, 61, 49–79, C1–4. 10.1146/annurev.psych.093008.100523
- Wilhelm I, Diekelmann S, Molzow I, Ayoub A, Mölle M, & Born J (2011). Sleep selectively enhances memory expected to be of future relevance. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 31(5), 1563–1569. 10.1523/JNEUROSCI.3575-10.2011 [PubMed: 21289163]
- Witt K, Margraf N, Bieber C, Born J, & Deuschl G (2010). Sleep consolidates the effector-independent representation of a motor skill. *Neuroscience*, 171(1), 227–234. 10.1016/j.neuroscience.2010.07.062 [PubMed: 20691764]

Fig1. Study timeline.

00:00 represents study start time. Following EEG hookup, participants completed MST training, and then a 15min retention interval during which they either rested or completed the distractor task. The MST test occurred immediately after the retention interval in the immediate test group, and 4hrs later in the 4hr delay group.

Fig2. Rest benefits immediate, but not delayed test performance.

Rest significantly benefitted performance at immediate test, but not after a 4hr delay.

Fig3. MST improvement by group.

Participants in the immediate test group showed greater improvement between training and test than participants in the 4hr delay group. P-values represent increase in MST performance from training to testing.

Table 1.

MST Performance in Immediate Test and 4hr Delay Groups.

		Immediate Test (n=18)		4hr Delay Test (n=17)	
		<i>mean</i>	<i>±SD</i>	<i>mean</i>	<i>±SD</i>
Distractor Task	Raw Change	4.6	3.4	1.4	2.5
	% Change	22%	17%	7.4%	13%
Rest	Raw Change	6.6	2.5	1.3	3.0
	% Change	31%	14%	7.7%	14%

Notes. Raw and % change in the number of sequences correctly typed per 30sec trial, (mean of last 3 test trials - mean of first 3 training trials).

Table 2.

Participant Characteristics by Condition.

	Immediate Test (n=18)		4hr Delay Test (n=18)		t/χ^2	p
	<i>mean</i>	$\pm SD$	<i>mean</i>	$\pm SD$		
Age (yrs)	20.5	1.10	19.3	1.31	3.0	.01*
ESS	7.28	3.21	9.62	3.05	-2.2	.03*
SSS	2.56	.86	2.89	.86	-.95	.35
Baseline MST	23.5	7.3	20.5	3.49	1.6	.13
Sex (% male)	39%		24%		.96	.47
% Play Instrument	44%		41%		.04	1.0

Notes. P-values derived from independent-samples t-tests (with the exception of chi square tests for sex and instruments) comparing the immediate test and 4hr delay groups.

*
p < .05.

SSS=Stanford Sleepiness Scale; ESS=Epworth Sleepiness Scale; MST=Motor Sequence Task.