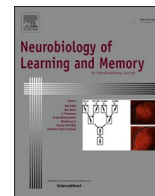




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Short communication

The role of sleep for episodic memory consolidation: Stabilizing or rescuing?

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ABSTRACT

Prior studies suggest a role for sleep in memory consolidation, with specific contributions from slow oscillations and sleep spindles (Rasch & Born, 2013). However, recent studies failed to replicate sleep's superiority over wake in strengthening memory against interference (Cordi & Rasch, 2021). The goal of the current study is to investigate whether sleep protects newly formed memory from unspecific interference induced by daytime experiences over 24 h, as well as to elucidate the sleep features that are involved. 56 healthy adults were randomly assigned to either the Sleep First or Wake First group. The Sleep First group encoded word pairs at night before sleep, while the Wake First group encoded word pairs in the morning before a day of wakefulness. Memory was tested 30 min, 12 h, and 24 h after encoding for both groups. The Sleep First group performed significantly better 12 h after encoding, replicating prior findings that memory is better after a period of sleep compared to wake. However, after 24 h, the two groups performed similarly. The Wake First group showed a positive correlation between overnight memory improvement and the theta and delta band power during slow wave sleep, an effect not found in the Sleep First group. These correlations suggest the possibility that after a day of waking interference, the brain recruits extra sleep resources to rescue memories from further forgetting. Our results are not consistent with prior studies showing a significant role for sleep in stabilizing memory from future interference, but they may suggest that sleep rescues memories after interference has occurred.

1. Introduction

Memory consolidation refers to the process of transforming a vulnerable memory trace into an enduring state by increasing its resistance to interference (Müller & Pilzecker, 1900). Since the 1920s, sleep has been implicated in this process, as Jenkins and Dallenbach reported that experimental subjects remembered more non-sensical syllables after a period of sleep compared to a period of wake, leading the authors to suggest that sleep passively facilitates episodic memory via reduced interference (Jenkins & Dallenbach, 1924). Similarly, other studies have reported that memory performance was superior following a period of sleep compared to wake (Gais et al., 2006; Rasch & Born, 2013; Talamini et al., 2008). This enhancement has been reported to last up to 24 h after initial learning (Benson & Feinberg, 1977).

In the early 2000 s, more studies emerged to suggest that sleep not only passively sheltered memory from waking experience, but also actively stabilized memory against future interference induced by competing encoding traces (Ellenbogen, Hulbert, et al., 2006). In other

words, the memory trace is more resistant to decline from interference once it has gone through a period of sleep-dependent consolidation. To explore the question of whether sleep passively or actively contributes to episodic memory consolidation, researchers had subjects learn a word list with a subsequent retrieval test after a night of sleep or a day of wake (Ellenbogen, Hulbert, et al., 2006). Interference was introduced by having half the subjects learn a new word list immediately before retrieval of the old word list. Researchers found that retroactive interference, when new learning hinders memory for previously learned material, was present for both wake and sleep. However, sleep provided more protection from interference than wake. These results suggested that sleep actively stabilized memories by making them more resistant to interference (Ellenbogen, Hulbert, et al., 2006).

The active role of sleep in memory consolidation gained further support with the elucidation of neural mechanisms that may contribute to the consolidation process during sleep (Diekelmann & Born, 2010; Feld & Diekelmann, 2015). The active systems consolidation hypothesis states that during non-rapid eye movement (NREM) sleep, newly

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encoded memories are strengthened through a dialogue between the neocortex and hippocampus mediated by specific sleep features (Born & Wilhelm, 2012). The temporal coupling of neocortical slow oscillations (SOs), with sharp wave-ripples and thalamo-cortical spindles, has been hypothesized to drive the repeated reactivation of hippocampal memory representations, which facilitates their transformation into long-term memories (Born & Wilhelm, 2012; Staresina et al., 2015).

Even still, some studies have failed to demonstrate sleep's superiority over wake in stabilizing memories (Cordi & Rasch, 2021). Specifically, using a laboratory interference paradigm similar to Ellenbogen and colleagues (2006), other groups have reported no differences between sleep and wake on protecting memories from later interference over a night of sleep (Bailes et al., 2020) and a daytime nap (Pöhlchen et al., 2021). Moreover, a study reported retroactive interference after sleep, but not after sleep deprivation, suggesting that memories become more labile and vulnerable to interference with sleep, further contradicting sleep's role in stabilizing memories (Deliens et al., 2013). Additionally, studies typically test sleep's role in resilience to future interference, but whether sleep serves to rescue memories that have occurred the previous day is rarely studied. Specifically, does information learned in the morning, prior to a day of waking, get selectively recovered during the subsequent night of sleep?

The goal of the current study was to determine if sleep serves to stabilize (strengthen new memory against later waking experiences) or rescue (recover previous memory after waking experiences) memory over a 24-hour period. One group (Wake First) learned a list of word pair-associates in the morning followed by three recall tests: Test 1 (30 min after encoding), Test 2 (delayed over a day of wake, 12 h after encoding), and Test 3 (delayed over a night of sleep in the lab, 24 h after encoding). Another group (Sleep First) learned the word-pairs at night followed by three tests: Test 1 (30 min after encoding), Test 2 (over a night of sleep in the lab, 12 h after encoding), Test 3 (delayed over a day of wake, 24 h after encoding). We tested the hypothesis that memory performance should be greater at Test 3 in the Sleep First group, compared with the Wake First group, because a night of sleep immediately after learning would stabilize memories against interference caused by daytime experiences between Test 2 and Test 3. We also tested the hypothesis that sleep would rescue memories after a day of wakefulness, with overnight memory improvement correlated with sleep features in the Wake First group.

2. Methods

2.1. Subjects and study protocol

A total of 56 subjects (age: 20.67 ± 2.52 , 26 females) provided informed consent, which was approved by the University of California, Riverside Human Research Review Board. All subjects were healthy, college-aged adults without any sleep disorders. Participants were randomly assigned to two groups, Wake First and Sleep First. All groups were tested three times, with approximately 12 h in between each test session. For the Wake First group, memory encoding occurred in the morning followed by 12 h of wakefulness. For the Sleep First group, memory encoding occurred just before nighttime sleep.

The study procedure is outlined in Fig. 1. In the Wake First condition ($n = 28$, 14 females), participants reported to the laboratory in the morning. They completed the word paired associates (WPA) task encoding and immediate testing (Test 1) at around 8:30 am. Then, participants left the lab to continue their day. At around 9 pm, participants returned to the lab for a second memory testing (Test 2). Then, participants went to sleep in a standardized bedroom. Participants were woken up at 9 am the next morning and provided breakfast. At 10:30 am, participants completed the memory task (Test 3) and were permitted to leave the lab. In the Sleep First condition ($n = 28$, 12 females), participants reported to the laboratory in the evening. They completed the WPA task encoding and immediate testing (Test 1) at around 9 pm before being prepared for nighttime sleep. Participants were woken up at 9 am the next morning and provided breakfast. At 10:30 am, participants completed the memory task (Test 2) and were permitted to leave the lab. At around 9 pm, participants returned to the lab for a third memory test session (Test 3).

2.2. Task

The word-paired associates (WPA) task consisted of an encoding session and three testing sessions (Fig. 2). During encoding, participants passively viewed 60 pairs of words, each presented vertically stacked and shown twice in random order. Every word pair was presented for 1000 ms followed by a fixation cross for 100 ms. We trained subjects to criterion using a test in which participants were shown the upper word of the pair and were required to type in the missing word. Participants had to achieve 70% accuracy for all 60 pairs to finish the training. Feedback was provided after each trial to let participants know if the entry was correct or incorrect, and the correct word pair was displayed. Retrieval was identical to the training to criterion except no feedback

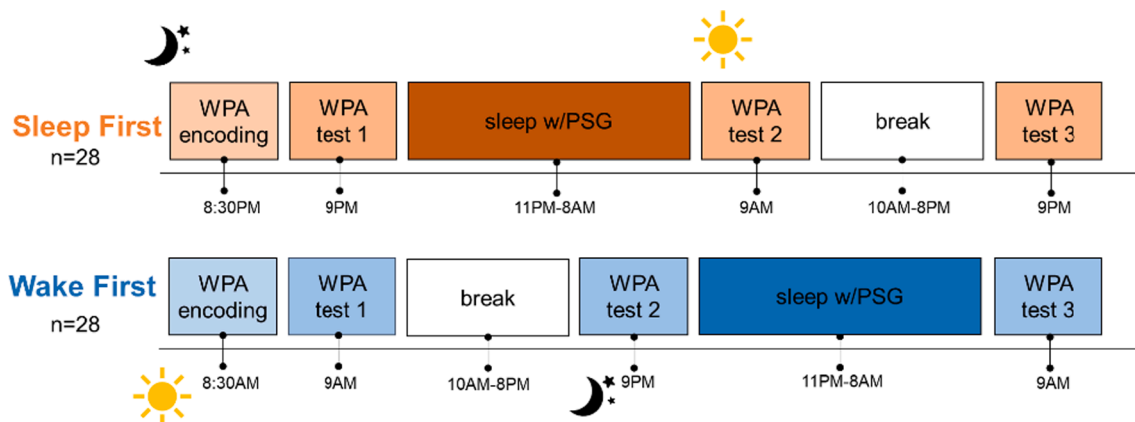


Fig. 1. The study protocol. The Sleep First group performed the WPA encoding at 8:30 PM, followed by an immediate test (Test 1) and PSG-monitored sleep. In the morning, participants were tested on the word pairs (Test 2) before leaving the laboratory. In the evening, participants returned to the laboratory and were tested on the word pairs for the 3rd time (Test 3). The Wake First group performed the WPA encoding at 8:30 AM followed by an immediate test (Test 1) and left the laboratory. They returned at 9 pm and got tested on the word pairs (Test 2) before PSG-monitored sleep. In the morning, participants were tested on the word pairs for the 3rd time (Test 3).

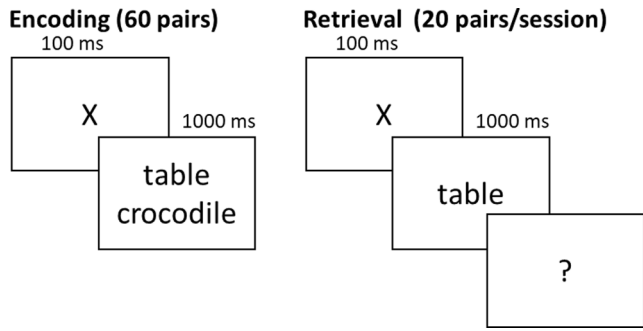


Fig. 2. The word paired-associates task. During encoding, subjects viewed 60 word pairs and trained to 70% criterion. During retrieval, subjects view one word of the pair and were required to type in the missing word. Feedback was not given.

was given. The word pairs were divided into three sets of 20 pairs; one set was tested at each test session and the order was counterbalanced. Three retrieval tests were conducted: 1) 30 min after encoding (Test 1), 2) 12 h after encoding (Test 2), and 3) 24 h after encoding (Test 3). The accuracy score was calculated for each test.

2.3. Sleep recording and scoring

EEG data were acquired using a 32-channel cap (EASYCAP GmbH) with Ag/AgCl electrodes placed according to the international 10–20 System. Twenty-two electrodes were scalp recordings, and the remaining electrodes were used for electrocardiogram (ECG), electromyogram (EMG), electrooculogram (EOG), ground, an online common reference channel (at FCz location, retained after re-referencing), and mastoid (A1 & A2) recordings. The EEG was recorded with a 1000 Hz sampling rate and was re-referenced to the contralateral mastoid (A1 & A2) and downsampled to 256 Hz post-recording. Eight scalp electrodes (F3, F4, C3, C4, P3, P4, O1, O2), the EMG, and EOG were used in the scoring of the nighttime sleep data. High pass filters were set at 0.3 Hz and low pass filters at 35 Hz for EEG and EOG. Raw data were visually scored in 30-sec epochs into Wake, Stage 1, Stage 2, Slow Wave Sleep (SWS) and rapid eye movement (REM) sleep according to the AASM scoring manual (Iber et al., 2007).

2.4. Power spectra estimation

To examine which sleep frequency bands might account for memory changes, we analyzed the following sleep frequency bands: sigma (11–15 Hz), theta (4–7 Hz), delta (1–4 Hz), and slow oscillation (SO) (0–1 Hz). Sleep spindles were detected using the same method published previously (Zhang et al., 2020). The EEG epochs that were contaminated by muscle and/or other artifacts were rejected using a simple out-of-bounds test (with a $\pm 200 \mu\text{V}$ threshold) on high-pass filtered (0.5 Hz) version of the EEG signals. All epochs with artifacts and arousals were identified rejected by visual inspection before spectral analyses. The EEG power spectra were computed using the Welch method (4 sec Hanning windows with 50 % overlap) on the artifact-free 30-sec epochs. Then, the estimated power spectra were averaged within each sleep stage/electrode/subject.

2.5. Statistical analysis

Our primary hypothesis was that the memory improvement would be higher for the Sleep First condition compared to the Wake First condition. To test this hypothesis, we conducted a mixed ANOVA test with the within-subject factor being time (Test 1 and Test 3) and the between-subjects factor being groups (Wake First and Sleep First).

To examine the hypothesis that sleep rescues memory, we compared

the relevant sleep features associated with overnight improvement (Test 2- Test 1 for the Sleep First group; Test 3- Test 2 for the Wake First group) between two groups. If sleep rescues memory, specific sleep features would be correlated with overnight improvement for the Wake First group but not the Sleep First group. To this end, we calculated Pearson’s *r* between each frequency band and the memory difference scores for each group separately. Benjamini-Hochberg correction with a false discovery rate set as 5% was used to control for multiple comparisons.

3. Results

3.1. Behavioral

For the Sleep First Group, participants took 1.60 ± 0.48 trials to reach the 70% criterion during encoding, and the average accuracy during encoding was $85.00 \pm 6.43\%$. For the Wake First Group, participants took 1.64 ± 0.62 trials to reach the 70% criterion, and the average accuracy during encoding was $87.44 \pm 6.16\%$. Participants took similar number of trials to reach the criterion between groups, $t_{54} = 0.23, p = 0.55$, and the performance during learning was not significantly different $t_{54} = 1.44, p = 0.15$.

As shown in Fig. 3, the baseline performance was similar between the two groups ($t_{54} = -0.55, p = 0.59$), suggesting the differences in encoding and test times between the two groups had minimal impact on immediate recall. At Test 2, the Sleep First group performed significantly better than the Wake First group ($t_{54} = 3.78, p < 0.001$), showing that memory performance was better after a night of sleep compared to a day of wakefulness. At Test 3, however, the two groups showed similar recall levels ($t_{54} = 1.33, p = 0.19$), suggesting sleeping immediately after learning did not stabilize memory against further interference. There was a main effect of time, $F_{(1,54)} = 216.17, p < 0.001$, indicating that both groups showed significant forgetting across the three sessions. The main effect of group was not statistically significant ($F_{(1,54)} = 0.78, p = 0.38$), providing additional evidence that sleeping immediately after learning did not protect new memories from waking experiences following a night of sleep. When comparing overnight performance changes, the Sleep First group had significantly less forgetting across sleep compared to the Wake First group ($t_{54} = 2.50, p = 0.02$, supplemental material Fig. 1). There was significantly less forgetting across sleep compared to wake for both Sleep First and Wake First group ($p < 0.05$).

3.2. Sleep

The two groups showed similar sleep architecture except for the

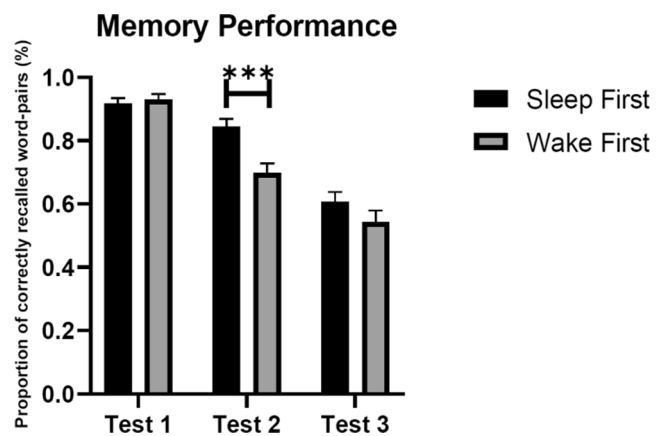


Fig. 3. Memory performance. Two groups performed similarly during Test 1 ($t_{54} = -0.55, p = 0.59$) and Test 3 ($t_{54} = 1.33, p = 0.19$). At Test 2, the Sleep First group scored higher than the Wake First group ($t_{54} = 3.78, p < 0.001$).

Total Sleep Time (TST), sleep onset latency, and time spent in SWS (Table 1). Specifically, the WASO, and percent time spent in each stage, and time spent in N1, N2 and REM were not statistically different between the two groups ($p > 0.05$). The Wake First group had significantly more Total Sleep Time (TST) ($p < 0.001$) and time spent in SWS ($p = 0.03$) than the Sleep First group. When correlating with memory performance, TST was positively related to overnight memory improvement for the Wake First group (Test 3-Test 2) ($r = 0.43$, $p = 0.03$), but not for the Sleep First group (Test 2 – Test 1) ($r = 0.01$, $p = 0.95$). Time spent in SWS and sleep onset latency was not correlated with any performance measure for either group ($p > 0.05$).

3.3. Power performance correlation

Overnight memory performance change for the Wake First group (Test 3 – Test 2) was positively correlated with spectra power in theta and delta frequency during SWS (Fig. 4, top panel). Specifically, for delta band, 16 electrodes located over parietal, occipital and temporal lobes showed a positive correlation with overnight memory change (Test 3 - Test2) in SWS after Benjamini-Hochberg correction for multiple comparisons. For theta band, 3 electrodes located at prefrontal, left temporal and left occipital areas showed a positive correlation with overnight memory change (Test 3 - Test2) in SWS after Benjamini-Hochberg correction for multiple comparisons. The same correlation was not observed in the Sleep First group (Fig. 4, bottom panel). In fact, no statistically significant correlation was found between any frequency band and memory performance for the Sleep First group. Fisher's r to z transformation reflected that the correlations between EEG features and memory performance in two groups are significantly different. Specifically, there are significantly different correlations at 7 electrodes for delta power and at 7 electrodes for theta power during SWS ($ps < 0.05$) supplemental Fig. 2).

4. Discussion

Prior studies have demonstrated that sleep protects and stabilizes memories against future interference, suggesting an active role of sleep in memory consolidation (Ellenbogen, Payne, et al., 2006). In addition, studies report that sleep must occur shortly after learning to optimize consolidation for episodic memories (Payne et al., 2012), associative memory (Talamini et al., 2008) and motor skills (Van Der Werf et al., 2009). However, whether sleep stabilizes memory is still a debate as other studies show similar memory performance after a period of sleep and wake (Bailes et al., 2020; Deliens et al., 2013; Pöhlichen et al., 2021). The goal of the current study was to investigate if sleep plays a stabilizing or rescuing role in memory consolidation and the specific features involved.

Consistent with prior studies, we found better memory over a night of sleep compared to a day of wake (Diekelmann & Born, 2010; Gais et al., 2006; Jenkins & Dallenbach, 1924). However, the memory was

similar between the two groups after 24-hours containing both sleep and wake. The null result in sleep's stabilizing effect on memory contradicts previous findings utilizing a similar study design (Talamini et al. 2008, Payne et al. 2012). Specifically, using a face-location association task, Talamini et al reported less forgetting in a 24-hr interval when learning was followed by sleep immediately compared to a delayed sleep condition. One potential explanation for the difference between our null result and this positive result is that the cross-domain association process in the face-location task invokes hippocampal processing more strongly (Borders et al., 2017), creating a stronger memory that is more resilient to interference. However, the study conducted by Payne et al., 2012 used a similar word-pair association task as our study and they reported that memory was better after 24hrs containing both sleep and wake if sleep occurred immediately after learning. In the current study, we compared the 24hr change in performance and, similar to Payne et al., 2012, the Sleep First group had less forgetting ($M = -0.31 \pm 0.03$) compared to the Wake First group ($M = -0.39 \pm 0.04$), but it was not statistically significant ($p = 0.11$, supplemental Fig. 1). It is possible that the current study was under powered. Another potential difference was that we controlled participants' sleep environment, and re-tested within a strict 12-hr interval, whereas participants in the previous study slept at home and only got tested 24 h after learning.

Moreover, participants slept longer when the waking experiences occurred before compared to after sleep. Importantly, we only observed an association between memory performance and overnight sleep features when a night of sleep followed a day of wake (Wake First group), which suggests that sleep could be optimally positioned to rescue memories after daytime experiences has occurred. Specifically, the rescue effect was associated with increased power in theta and delta frequency during SWS. However, we found similar memory performance levels between the two groups at 24-hours, which would not be expected if sleep only rescued memories from prior interference. The correlations between spectra power and memory improvement were in favor of the rescue argument but not definitive. Thus, our results do not exclude the possibility that sleep both protects memory against interference and rescues memory after interference.

Our findings are aligned with Drosopoulos and colleagues who also showed that sleep recovered memory of an older word list when an interference list was learned before sleep (Drosopoulos et al., 2007). Similarly, a study conducted by Abel and Bäuml (2014) showed that sleep after interference recovered prior memory of word pairs. Specifically, subjects learned two lists of word pairs before 12-hour of wake or sleep, and those who slept performed better for both lists compared to those who were awake (Abel & Bäuml, 2014). Backhaus and colleagues reported that both immediate and delayed post-learning sleep enhanced episodic memory (Backhaus et al., 2008). However, they also showed a stabilizing effect of sleep with less forgetting across wakefulness in the Sleep First group compared to the Wake First group, which was not observed in the current study.

The rescuing effect of sleep on memory has been shown in a non-declarative, perceptual learning task with the amount of REM sleep positively associated with the magnitude of memory recovery (McDevitt et al., 2015). The current study suggests that the rescuing effect of sleep may extend to episodic memory, with TST, theta and delta power during SWS being correlated to the amount of memory recovery. Sleep-dependent declarative memory consolidation has been associated with SWS duration (Cairney et al., 2015; Fowler et al., 1973; Plihal & Born, 1997; Tucker et al., 2006) and specific features during SWS such as SOs (Dang-Vu et al., 2008, p.; Farhadian et al., 2021; Marshall et al., 2006; Ruch et al., 2012). The current study shows that theta power during SWS may be implicated in this process as well. Theta power has been associated with the redistribution of memory from the hippocampus to the neocortex, (Headley & Paré, 2017), and studies have shown that theta power is correlated with successful memory reactivation during NREM sleep (Choi et al., 2021; Schreiner et al., 2018).

Studies of forgetting have historically defined interference as a

Table 1

Sleep architecture. TST = total sleep time; N1 = stage 1; N2 = stage 2; N3 = stage 3; WASO = Wake Time After Sleep Onset; SE = sleep efficiency.

Sleep Stage	Wake First	Sleep First	P values
Sleep Latency (min)	6.87(6.04)	20.36(19.40)	0.001*
TST (min)	534.90(49.73)	482.32(41.08)	0.001*
N1 (min)	14.96(8.60)	14.38(13.15)	0.85
N1(%)	2.83(1.65)	3.11(3.10)	0.69
N2 (min)	283.06(54.17)	259.57(36.82)	0.07
N2(%)	52.88(8.71)	53.93(7.14)	0.63
N3 (min)	108.75(39.10)	89.34(24.79)	0.03*
N3(%)	20.46(7.59)	18.56(5.06)	0.28
REM(min)	128.12(34.02)	119.00(43.20)	0.40
REM(%)	23.76(5.26)	24.40(7.99)	0.99
WASO	31.63(28.50)	34.05(37.86)	0.79
SE	92.20(5.78)	89.58(7.46)	0.16

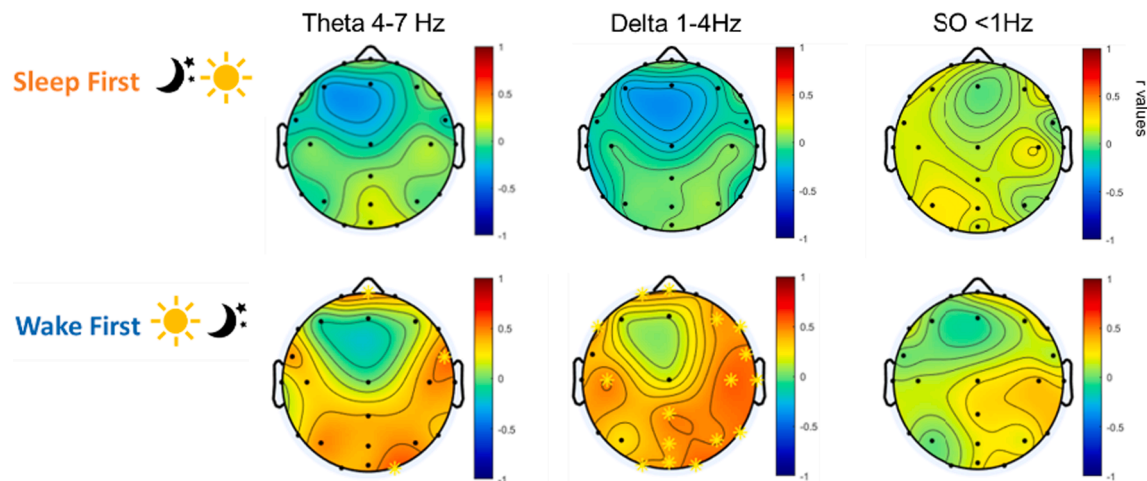


Fig. 4. . Topographic plots of Pearson's r between overnight memory performance change and power spectra in theta, delta and SO bands for the Sleep First group (top panel) and the Wake First group (bottom panel). * statistically significant at this electrode following Benjamini-Hochberg correction for multiple comparisons.

condition in which the mind remains biologically active, compared with a non-interference state in which the mind is quiescent where no new learning can interfere with prior learning (Wixted, 2004). Given these standards, a 12-hour period in which the experimental subject is awake and going about her daily business would constitute an interference state, compared with an overnight sleep period. However, without direct experimental manipulation of interference there is less certainty regarding the magnitude and duration of interference. Follow-up studies should implement experimental tests of interference to further isolate the effect of sleep on memory against retroactive interference.

In summary, the current study shows similar memory performance after 24 h containing both sleep and wake. Interestingly, when there was a delay between learning and sleep, subjects recruited more resources during sleep to rescue the earlier memories, as shown by increased TST, theta and delta power. Taken together, our results are not consistent with the hypothesis that sleep right after learning significantly stabilizes memory against future interference, but it may suggest that extra brain resources recruited during sleep rescue damaged memories after a day of activities.

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CRedit authorship contribution statement

Jing Zhang: Conceptualization, Methodology, Software, Data curation, Formal analysis, Writing – original draft, Visualization. **Lauren N. Whitehurst:** Conceptualization, Methodology, Investigation, Resources, Validation, Data curation, Writing – review & editing, Project administration, Funding acquisition. **Sara C. Mednick:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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