Title:

All Memories Are Equal at Night: Sleep Protects Without Preference for Strength

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Abstract

Objectives: Sleep benefits memory, but whether this benefit depends on initial memory strength remains heavily debated. We asked whether overnight sleep preferentially stabilizes weakly vs. strongly encoded declarative items, and whether classical sleep oscillations account for any benefit.

Methods: Ninety healthy adults (n=30/group) learned 80 unrelated word pairs; half were presented twice (S-, weak), while the other half was studied three times (S+, strong). Memory retention was tested after (i) 9hrs containing nocturnal sleep (n= 30), (ii) a comparable daytime waking period (n= 30), or (iii) immediately (~40-min) after encoding. Accuracy (cued recall) and reaction times (RT) indexed memory accessibility. In the sleep group, polysomnography was used to quantify slow oscillation (SO) density as well as fast spindle intensity to study potential relations to memory performance.

Results: Strongly encoded items (S+) were recalled better than weak items (S-) in all three groups. An interaction indicated that WAKE disproportionately forgot more weak items S- relative to strong S+ items, whereas SLEEP showed no differential benefit for weak versus strong items, with performance more closely resembling that of the *immediate recall* group. Reaction-time analyses echoed this pattern with WAKE responding more slowly than SLEEP and IMMEDIATE, and there is no RT difference between SLEEP and IMMEDIATE. S+ were retrieved faster than S- (with no group interaction). Finally, classical sleep markers did not account for overnight retention: spindle and slow-oscillation metrics showed no stronger associations on the learning night than on the adaptation night and did not differ by item strength, suggesting largely trait-like rather than state-dependent relationships between these oscillations and declarative memory.

Conclusions: Sleep protects declarative memories irrespective of initial strength and matches immediate recall performance. Traditional sleep metrics, such as slow oscillation density and spindle intensity, did not predict overnight retention performance but instead reflected more trait-like relationships.

1. Introduction

Sleep is widely recognized as beneficial for memory consolidation (Rasch & Born, 2013). Behaviorally, the most consistent finding is that sleep reduces time-dependent forgetting compared to wakefulness, an effect first noted by Ebbinghaus (1885) and is often attributed to reduced interference during sleep (Drosopolus et al., 2007; Ellenbogen et al., 2006; Müller & Pilzecker, 1900). Beyond this protective role, physiological processes have been proposed to actively support consolidation. Synaptic downscaling during deep sleep restores cortical homeostasis and may incidentally aid memory consolidation (Tononi & Cirelli, 2014), whereas the active systems consolidation framework highlights hippocampal reactivation and redistribution into cortical stores (Diekelmann & Born, 2010). Both views link consolidation to characteristic oscillations—slow oscillations and sleep spindles—which are thought to play a central role and may even act in complementary ways (Feld & Born, 2017).

Yet, the beneficial effects of sleep on memory do not seem to be uniform. Rather, several studies have reported sleep benefits only for subsets of the learned material, or particularly strong effects for specific types of memories. Sleep therefore appears to be selective, prioritizing the consolidation of certain memory traces over others depending on features such as salience or expected future relevance (Stickgold & Walker, 2013). Other than salience and future relevance, a range of candidate features have been discussed in this context, including emotional valence and, most fundamentally, initial memory strength. However, the literature remains inconsistent regarding the role of memory strength in sleep-dependent consolidation. For instance, some studies report that sleep preferentially stabilizes weakly encoded items (Drosopoulos et al., 2007; Denis et al., 2021), others conclude that strongly encoded items are favored for sleep-dependent consolidation (Tucker et al., 2008; Ellenbogen et al., 2009). Furthermore, Petzka et al. (2021) showed that under “standard” testing conditions without interference, a sleep-dependent consolidation effect is indeed only seen for weaker memories. Critically though, the authors report that with increased retrieval demands (i.e., learning new temporospatial arrangements of the same objects directly before final retrieval), sleep-dependent consolidation effects were seen for both weaker and stronger memories. These interesting results suggest that all memories may be consolidated during sleep, but that memories of different strengths benefit of sleep depending on the exact conditions before retrieval such as testing with or without retroactive interference before.

To complete the picture regarding the relevance of memory strength for sleep-dependent consolidation, Stickgold (2009, p. 306) proposed an inverted U-shaped curve of sleep benefit,

suggesting that especially memories of intermediate strength profit from sleep, whereas extremely weak or strong items may not.

One possible reason for such divergent findings - besides the usual caveats of small sample sizes, varying tasks, and heterogeneous materials, which have hampered replication in the sleep-and-memory field (for critical review see Nemeth et al., 2024) - is methodological. In many studies, memory strength is manipulated by a mixture of repeated study ("re-study") and retrieval practice before sleep. Yet these two routes to strengthening are not equivalent: retrieval practice induces distinct neural responses (van den Broek et al., 2016), enhances retention more than re-study (Roediger & Butler, 2011), and in some cases even eliminates subsequent sleep effects (Bäuml et al., 2014). Retrieval may thus constitute a form of consolidation, thereby diminishing or masking the additional role of sleep. This complicates the isolation of sleep's direct contribution to memory stabilization.

In the present study, we therefore examined sleep's impact on memory consolidation when initial strength is manipulated exclusively by re-study, without retrieval practice. We tested three independent groups: a sleep group with overnight retention, a wake group with equivalent daytime retention, and a short-delay group. The latter group not only serves as a control for circadian influences but also provides a benchmark for the level of recall performance shortly after encoding, against which forgetting across the longer retention intervals (either filled with wake or sleep) can then be compared. Memory strength was assessed as (1) overall accessibility of memory traces (cued recall) and (2) the response time required for successful retrieval.

2. Methods

2.1. Participants

We recorded 92 participants. Two participants were excluded as their initial recall performance was too low (lower than 10%). The final sample included 90 healthy participants (70 females) aged between 18-30 years (M = 22.88, SD = 2.64). All participants were native German speakers, with no history of psychological or sleep disorders. We divided the participants randomly into 3 experimental groups. The study was conducted in accordance with the ethical principles in the Declaration of Helsinki and was approved by the local research ethics committee (University of Salzburg Ethics Committee). All participants gave their written informed consent before the start of the experiment.

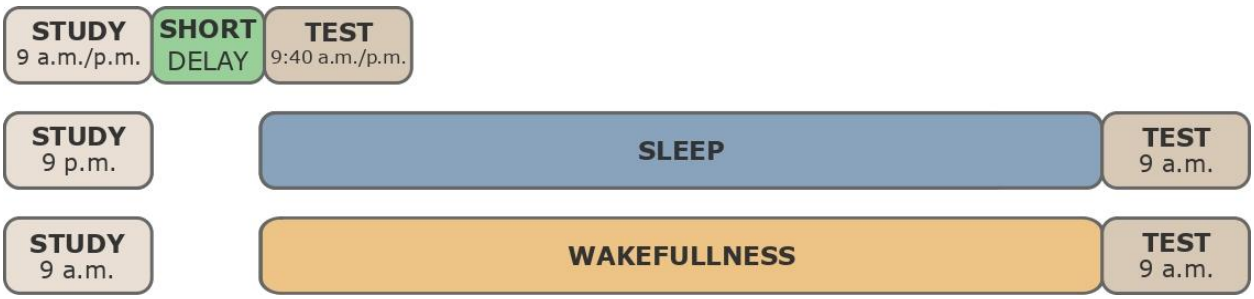

Figure 1. Experimental design. Following initial screening tests, 90 healthy participants were recruited to the experiment and were divided into 3 groups, Sleep, Wake, and Immediate (N=30/group). Participants learned a list of unrelated word pairs and were tested after varying retention intervals: 9 hours containing nocturnal sleep (~8h), 9 hours of wakefulness, or 40 minutes post-encoding. In total, 80 word-pairs were presented during the encoding phase, half of which (N=40) were presented twice (S-, weakly encoded) and the other half (N=40) was presented three times (S+, strongly encoded). Memory performance was assessed using a cued-recall test, measuring recall accuracy and response times for each word pair.

2.2. Experiment

The study employed a 3 x 2 mixed-factorial design, featuring a between-subjects factor of GROUP comprising three levels (n=30/group): SLEEP (SG), WAKE (WG), and SHORT (IG). The within-subjects factor of memory STRENGTH had two levels: weak (S-) and high (S+). Participants across all RETENTION groups learned a list of word pairs before undergoing a retention interval, which contained either nocturnal sleep or daytime wakefulness, followed by a memory performance test (TEST). The SLEEP group studied the word pairs in the evening and completed a memory test the next morning after 9 hours and filled with 8 hours of sleep opportunity in the laboratory. Two or three days earlier, participants came for an adaptation and screening night without performing the learning task. The WAKE group learned the word pairs in the morning and took the memory test later that evening after 9 hours of wakefulness. The SHORT group was tested 40 minutes post-encoding, matching the interval between the end of training and "lights off" in the sleep group, serving as a proxy for memory strength just before the sleep or wake retention interval. To control for circadian confounds, half of the subjects in the SHORT group encoded the word pairs in the evening, while the other half studied them in the morning.

2.3. Word Pair Task

The study material consisted of a list of 80 unrelated word-pair associations. During the learning phase, half of the word pairs were presented twice (S-) and the other half three times (S+) (see

Fig. 2). Each word-pair was shown for 7500 ms, followed by a white fixation cross for 1500 ms and a red fixation cross for 1000 ms, indicating the end of encoding (white cross) and the start of the next word-pair presentation (red cross). The word-pair list was randomized for each participant, ensuring that identical word-pair repetitions were separated by the presentation of at least three other word pairs.

Memory performance was assessed using a cued-recall test, where participants were given the first word of each pair as a cue (for a maximum of 5000 ms) and asked to recall the corresponding second word. Participants were instructed to press a button on the keyboard as soon as they recalled the word, followed by their verbal response. Test performance was measured by recall rates (%) and response times (RT).

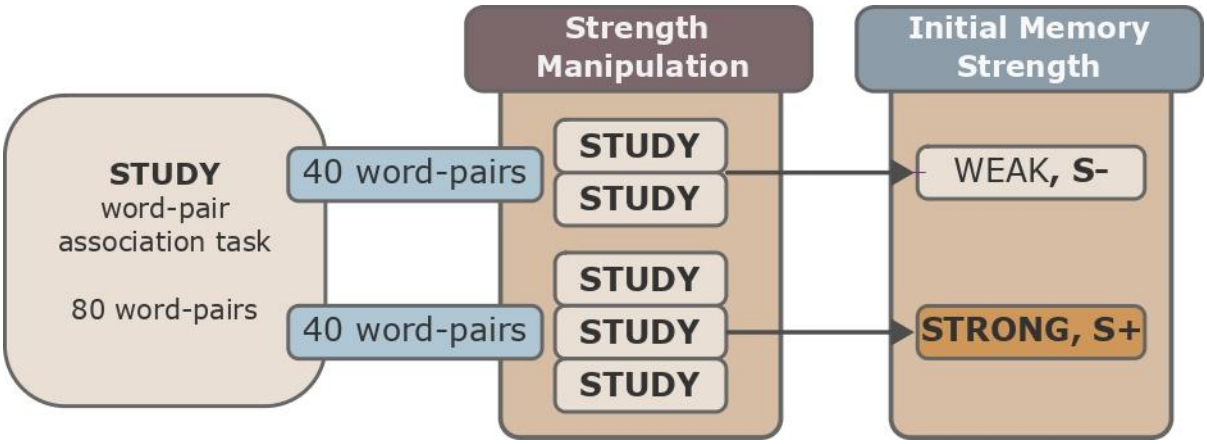

Figure 2. Word-pair learning task. Half of the word pairs was studied twice (S-) and the other half was studied three times (S+). Each word-pair was shown for 7500 ms, followed by a white fixation cross for 1500 ms, then a red fixation cross for 1000 ms, indicating the end of encoding (white cross) and the start of the next word-pair presentation (red cross). The word-pair list was randomized for each participant.

2.4. EEG acquisition and analysis

EEG was recorded using Synamps EEG amplifiers (Neuro-Scan, Inc., El Paso, TX). EEG data were acquired using 16 Ag/AgCl electrodes (F7, F3, Fz, F4, F8, C5, C3, Cz, C4, C6, P3, Pz, P4, O1, Oz, and O2 as well as A1 and A2 for later re-referencing) attached to participants' scalps according to the 10-20 system (Jasper, 1958). In addition, a number of physiological channels were recorded: one bipolar submental EMG channel, one bipolar electrocardiogram channel, one

bipolar respiratory channel (chest wall movements), and two horizontal EOG channels. All channels were recorded using a sampling rate of 1000Hz, a high-pass filter (0.10 Hz) and a 50Hz notch filter. Monopolar channels were recorded using FCz as the online reference.

2.5. Sleep staging

Sleep was scored semi-automatically using an algorithm developed by the SIESTA Group (SIESTA GmbH) and described in (Anderer et al., 2005; 2010), following the standard criteria recommended by the American Association for Sleep Medicine (AASM; Berry et al., 2017).

2.6. Sleep spindle detection

Sleep spindles were detected using an algorithm developed by the SIESTA Group (AskAnalyzer; Gruber et al., 2015). First, we filtered the raw data between 11 and 16 Hz and then detected spindle events at electrodes re-referenced to the average of mastoids using the criteria described in Schimicek et al. (1994). Only events with an amplitude >12 μV and a duration between 500 and 2000 ms were considered. Further validation of the detected spindles was done using LDA in which the detected spindles were compared with a template that is generated based on the visual scoring of sleep spindles in 8730 min of PSG data from 189 healthy participants and 90 participants with sleep disorders. For our analyses, we detected sleep spindles at electrode C3 and only considered events that occurred during N2 and N3 sleep. We defined fast spindles as sleep spindles that occurred in the frequency range between 13-15 Hz, and we calculated sleep spindle intensity using the classical measure as described in Schabus et al. (2004), which is a measure quantifying the average of spindle duration x spindle amplitude.

2.7. Slow Oscillations detection

To detect slow oscillations, we applied standard detection criteria (Mölle et al., 2004) using custom-built Matlab routines (MathWorks®, Natick, MA). The criteria were as follows: (1) a positive zero crossing follows a negative zero crossing within a time window of 0.3-1s; (2) the peak negativity between these zero crossings must exceed -80μV; and (3) the amplitude difference between the peak negativity and the subsequent positive peak must be at least 140μV. We measured slow oscillation density (at FCz) as the number of slow oscillations per minute in NREM (N2+N3).

3. Results

We included 90 healthy participants in our study (70 females, age = 22.8 ± 2.64). All participants performed a classical word-pair task. In each group, the word pairs were presented either 2 times (S-) or 3 times (S+) to account for difference in memory strength. In this section, we present the behavioral memory performance data as well as the association with slow oscillations and sleep spindles (for the sleeping group).

3.1. Memory performance:

We assessed memory performance as the percentage of correctly recalled word-pairs in the retrieval session. That is, we performed a mixed 3x2 repeated measures analysis of variance (ANOVA) with a between-subjects factor GROUP (SG, WG, IG), and a within-subject factor: Strength (S- and S+). Our analysis revealed significant main effects for the within factor STRENGTH ($F_{1,87} = 172.87$, $p < 0.001$, $\eta 2 = 0.17$) and the between factor GROUP ($F_{2,87} = 28.99$, $p < 0.001$, $\eta 2 = 0.37$) on test performance (Figure 3). The interaction GROUP x STRENGTH ($F_{2,87} = 5.75$, $p < .005$) was likewise significant with the wake group forgetting a proportionally greater number of S- items, although with a small effect size ($\eta 2 = 0.01$). More specifically, the performance was as follows: $WG_{S-} = 15.7$, $SG_{S-} = 26.1$ (difference 10.4), $WG_{S+} = 24$, $IG_{S+} = 31.1$ (difference 7.1) and $SG_{S-} = 29.7$ (14.0 difference to WG_{S-}), $SG_{S+} = 34.6$ (difference 10.6 to WG_{S+}).

Post-hoc pairwise comparisons (Bonferroni adjusted) revealed superior performance levels for S+ compared to S- in all three GROUPS (SHORT: $M_{S-} = 26.$, $SD_{S-} = 9.0$; $M_{S+} = 31.1$, $SD_{S-} = 7.28$, $p < 0.001$; SLEEP: $M_{S-} = 29.7$, $SD_{S-} = 6.6$; $M_{S+} = 34.6$, $SD_{S-} = 3.9$, $p < 0.001$; WAKE: $M_{S-} = 15.7$, $SD_{S-} = 6.8$; $M_{S+} = 24.0$, $SE_{S+} = 6.3$, $p < 0.001$).

Moreover, TEST performance of subjects in the WAKE group ($M = 19.8$, $SD = 7.7$) was poorer than in both the SLEEP and the SHORT groups. Specifically, participants in the wake group forgot more items that those in the Sleep group ($M = 32.2$, $S = 6.0$, $p < 0.001$), and the SHORT group ($M = 28.6$, $SD = 8.5$, $p < 0.001$). In contrast, no performance difference was found between subjects in the SLEEP and SHORT group ($p = 0.49$), indicating that no forgetting occurred over a retention period filled with sleep as compared to immediate testing.

In addition, we assessed the reaction times (RT), defined as the time between word presentation and the button press, only for the correctly recalled word-pairs. Also here we performed a mixed

3x2 ANOVA with the factors GROUP and STRENGTH and revealed significant main effects for both the within factor STRENGTH ($F_{1,77} = 57.04$, $p < 0.01$, $\eta 2 = 0.07$ and the between factor GROUP ($F_{2,77} = 12.86$, $p < 0.001$, $\eta 2 = 0.23$) on test performance (Figure 3). However, the interaction GROUP x STRENGTH ($F_{2,77} = 0.01$, $p = .90$, $\eta 2 < 0.01$) was not significant for reaction times.

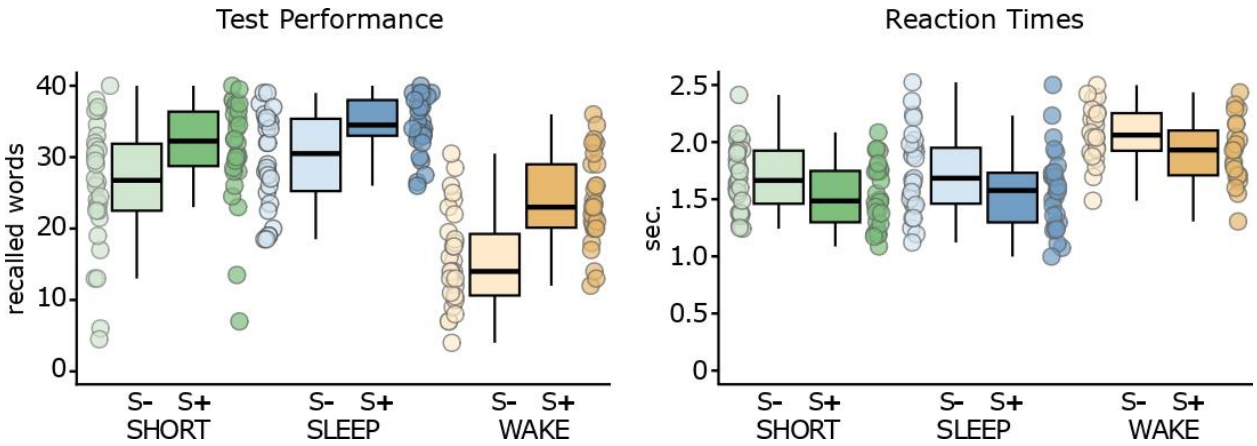

Figure 3. Behavioral performance for correctly retrieved items (HITS) and associated reaction times. Displayed are the 3 groups with immediate recall (SHORT), overnight sleep (SLEEP) and WAKE between learning and final retrieval. S- denotes items that were studied twice whereas S+ denotes items studied thrice in the encoding face. Note that the SLEEP and WAKE groups did not have a recall following immediately upon learning and reveals that S+ items are always superior in recall to S- items independent of the group assignment. Sleep group performance is identical to immediate recall after learning whereas the wake group demonstrates behavioral decrements with respect to both immediate recall and sleeping after learning. Sleep-dependent consolidation mechanisms.

3.2. Influence of Sleep microstructure on memory performance:

For the 30 people in the sleep group, we additionally correlated the recall performance of S- and S+ items with classical metrics that have been associated with declarative learning in the past. We focused on slow oscillation density (at FCz) as well as fast sleep spindle intensity (13-15Hz spindle amplitude x duration at C3).

Spearman correlations (2-tailed) revealed that fast spindle intensity showed non-significant positive correlations with recall performance of S- and S+ items (for S- items: $r_{27} = 0.25$, $p = .20$ in the adaptation night; $r_{28} = 0.22$, $p = .24$ in the learning night). For S+ items, positive correlations

were revealed in the adaptation (r_{27}= 0.39, p= .04) as well as the learning night (r_{28}= 0.37, p= .04) (cf. Figure 4, upper panels). Spearman correlations were then compared between conditions (S- vs. S+) using a percentile bootstrap method for paired-samples (twoDcorR function from Wilcox's robust statistics toolbox (Rallfun-v35)) as described by Wilcox & Muska (2002). Analysis reveals that correlations of the adaptation nights (p= .33) as well as the experimental learning nights (p= .30) do not statistically differ. These findings indicate that learning before sleep did not alter the association of studied sleep metrics and memory performance. Similarly, the numerical stronger correlations in the learning as compared to the adaptation night are not statistically different for S- (p= .82) as well as S+ (p= .82) items.

Spearman correlations (2-tailed) revealed that for slow oscillation density recall performance of S- and S+ items both showed non-significant positive correlations (for S- items: r_{27}= 0.33, p= .08 in the adaptation night; r_{27}= 0.30, p= .12 in the learning night). For S+ items, similar non-significant correlations were revealed (r_{27}= 0.34, p= .11 in the adaptation night; r_{27}= 0.27, p= .16 in the learning night) (cf. Figure 4 A-B). Both the correlations for weak S- items (p= .77) as well as strong S+ items (p= .62) were statistically not different between adaptation and learning nights.

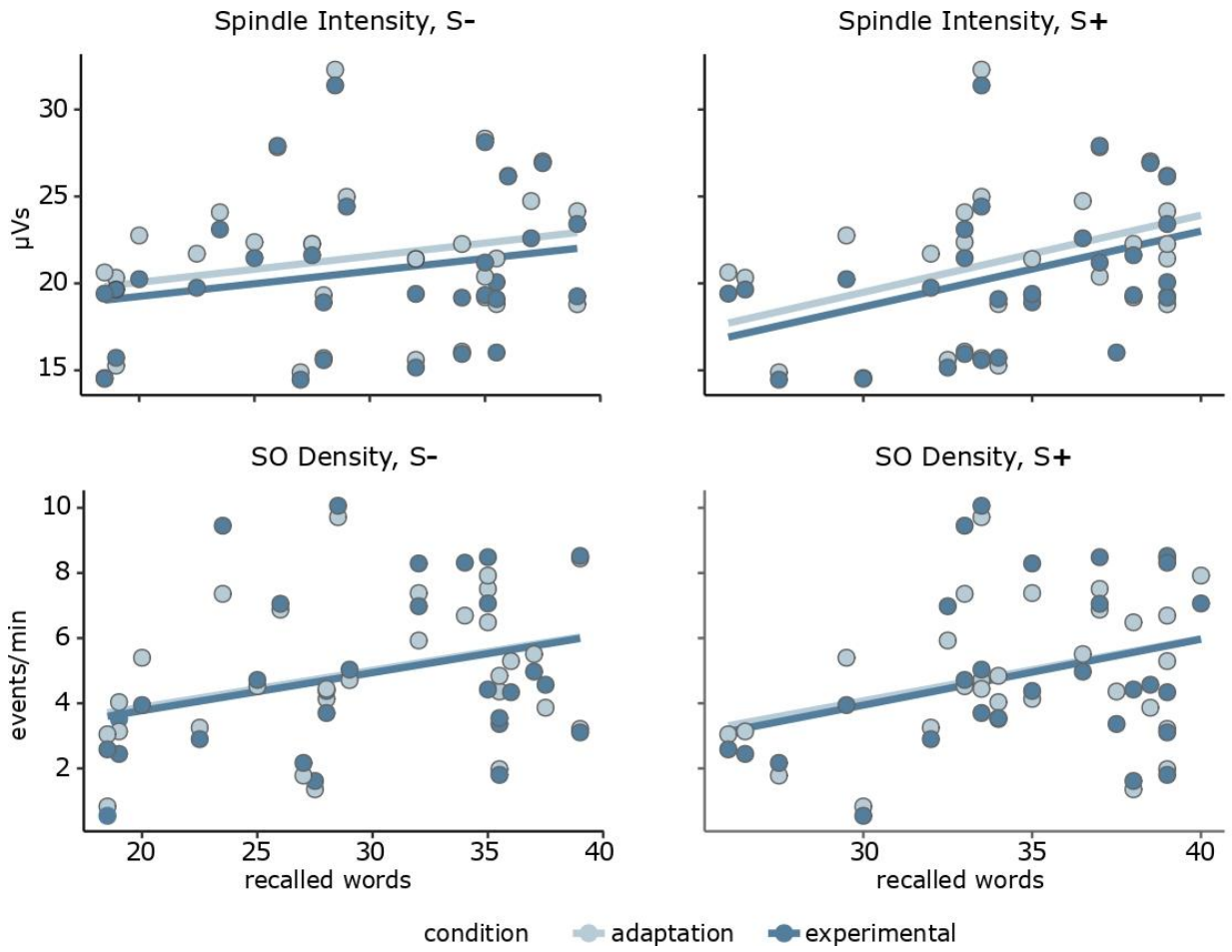

Figure 4. Correlations of fast spindle intensity and slow oscillation density with recall performance (sleep group). The upper left panel depicts the correlation between recall performance of weakly encoded items (S-) with spindle intensity in the adaptation (light blue color) as well as the learning night (dark blue color), with the right panel highlighting the associations for S+ items. The lower two panels illustrate positive associations of weak S- and strong S+ items with slow oscillation density. Note that these associations are already present in the non-learning adaptation nights and are statistically not different from the association in the learning night.

4. Discussion

We show that sleep prevents the forgetting of declarative memories regardless of encoding strength, with slightly more pronounced forgetting of weak items during wakefulness. Memory performance on word-pairs following a full night of sleep matches performance immediately after learning.

Interestingly, we also failed to detect any state-dependent relation between this protective effect of sleep on memory and the classical electrophysiological signatures previously associated with sleep-dependent memory consolidation, namely sleep spindles and slow oscillations;

While both measures showed mostly positive, although non-significant correlations with overnight forgetting, these associations were already present in the non-learning adaptation night and did not differ between nights. This suggests that the observed relationships are not specific to memory consolidation processes.

These traditional sleep metrics therefore did not predict overnight retention performance but indicate much more a general trait-like relationship (Bodizs et al., 2025; Schabus et al., 2006) with better memory performers tending to have more sleep spindle activity (e.g., Wislowska et al., 2016) and/or slow oscillations (e.g., Qin et al., 2025).

These findings indicate that sleep's impact on retention–at least in the used declarative word-pair paradigm-is not modulated by nor selectively tuned to the strength of the memory engrams before falling asleep. Since memory strength exists on a continuous spectrum, future work may need to probe a wider range of encoding conditions, strength manipulations of items before sleep, as well as manipulations to challenge the memory traces before retrieval such as interference tasks before retrieval following sleep. Additionally, in this study, we only measured memory after 9 hours following initial encoding but not at later time points where effects could vary dramatically. Moreover, we only focused on the "usual suspects" that were earlier associated to sleep-dependent declarative memory consolidation; such as slow oscillations and sleep spindles. It is possible that other sleep markers are better at indexing the mechanisms needed to strengthen declarative memories at night.

Future research should aim to move beyond the classical oscillatory markers examined here and explore a broader spectrum of neural and physiological signatures that may underlie the protective effects of sleep on memory. High-density EEG, intracranial recordings, or multimodal imaging could reveal finer-grained interactions between hippocampal and cortical networks that remain hidden in conventional scalp measures. Moreover, expanding the temporal window beyond a single night—particularly through continuous, real-world monitoring approaches as for example demonstrated by Topalidis et al. (2023)—may uncover delayed or cumulative effects of sleep on differently encoded memories, offering insights into how consolidation unfolds dynamically across multiple nights. The demonstrated feasibility of accurate daily sleep staging

using low-cost wearable devices opens the door for large-scale, longitudinal studies linking nightly physiological fluctuations to memory outcomes. Experimental manipulations of interference, reactivation, and targeted stimulation could further clarify whether sleep's stabilizing role is merely passive protection or reflects active integration of memories into long-term memory networks. Ultimately, understanding why sleep preserves all memories equally in some contexts—but selectively in others—will help refine theoretical models of memory consolidation and bridge trait-like and state-dependent perspectives on how the sleeping brain shapes our cognitive architecture.

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