Analyzing the Impact of Slow-Wave and Spindle Coupling on Memory Consolidation During Sleep

Research Project Report

Ananya Kulkarni

Matriculation Number: 3647062

University of Stuttgart

Supervisors: Samuel Morgan, Anna Wick (External)

Date: May 14, 2025

Contents

1 Introduction **3**
- 1.1 EEG and Sleep Overview . . . 3
- 1.2 Slow Waves . . . 4
- 1.3 Sleep Spindles . . . 4
- 1.4 Slow Wave–Spindle Coupling . . . 4
- 1.5 Memory Consolidation . . . 4

2 Literature Review **5**

3 Background and Aim **6**
- 3.1 Background . . . 6
- 3.2 Aim . . . 6

4 Methodology **6**
- 4.1 Dataset . . . 6
- 4.2 Preprocessing . . . 7
- 4.3 Event Detection with YASA . . . 7

4.4 Feature Detection 8
4.5 Temporal Coupling Metrics 8
4.6 Pearson's Correlation Coefficient 9
4.7 Statistical Analysis 9

5 Results **9**
5.1 Illustrative Detection Example 9
5.2 Coupling Metric Distributions 10
5.3 Comparison to Previous Reports 11
5.4 Coupling–Memory Associations 11
5.5 Correlation Analysis 12

6 Discussion **12**

7 Limitations **14**

8 Future Directions **15**

9 Conclusion **15**

Abstract

Effective memory consolidation during sleep depends on the coordinated timing of two brain rhythms: slow oscillations (large low-frequency waves) and sleep spindles (brief bursts of faster activity). We examined overnight EEG recordings from approximately 1,900 healthy adults to measure how often these two rhythms overlap during deep non REM sleep, and whether that overlap predicts emotional memory performance the next morning. Using an automated event detection algorithm, we marked every slow oscillation trough and spindle peak, then defined "overlap" as a spindle peak occurring within one second of a slow oscillation trough. We computed two key indicators: the percentage of all spindles that overlapped, and the total seconds of overlap per minute of deep sleep. Memory was assessed by delayed recall of emotional and neutral images, a task to practice memory, and a procedural tapping task. Across this large cohort, neither overlap indicator showed a significant relationship with any memory measure. These null findings suggest that simple overlap counts are not sufficient markers of sleep-dependent consolidation. We recommend that future research employ more precise phase-based analyzes and integrate complementary methods to discover how sleep rhythms support memory.

1 Introduction

1.1 EEG and Sleep Overview

Electroencephalography (EEG) is a fundamental tool for recording brain activity during sleep, using scalp electrodes to capture multi-channel, time-series signals that, together with eye-movement (EOG) and muscle-tone (EMG) recordings, constitute polysomnography (PSG) (13; 9). PSG allows sleep to be segmented into stages—wake (W), light

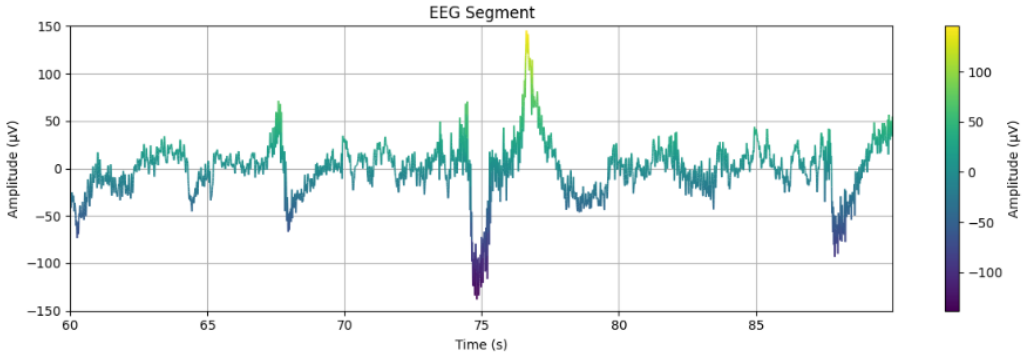

Figure 1: **Example EEG segment.** A 10s band-pass filtered segment (0.3–30Hz) from channel Oz.

NREM (N1, N2), deep NREM (N3, a.k.a. slow-wave sleep), and REM—each defined by characteristic EEG signatures. Deep NREM (stage N3) is marked by prominent slow

waves and sleep spindles, features believed critical for overnight memory consolidation (23; 14).

1.2 Slow Waves

During deep NREM sleep, the cortex generates large-amplitude slow waves (0.5–1Hz) that alternate between hyperpolarized "down" states and depolarized "up" states (6; 25). These down/up transitions gate neural excitability and provide a temporal scaffold for memory-related processes by coordinating widespread cortical ensembles (26; 7).

1.3 Sleep Spindles

Sleep spindles are transient bursts of sigma-band (12–15Hz) activity lasting 0.5–2s, generated by rhythmic interactions between the thalamus and cortex (thalamocortical oscillations, i.e. synchronized firing of thalamic relay neurons and cortical targets) and occurring predominantly in N2 and N3 sleep (they are absent during wakefulness) (9; 11). These oscillations support memory in two complementary ways: they increase calcium influx in cortical neurons to strengthen synapses, and they gate out external sensory input to protect newly encoded traces from interference.

1.4 Slow Wave–Spindle Coupling

When spindle peaks align with the depolarized up-phase or trough of a slow wave, they can synchronize hippocampal sharp-wave ripples with cortical receptivity, facilitating hippocampo-cortical dialogue (20; 15; 29). This temporal nesting underlies the active system-level consolidation framework, in which hippocampal memory representations are redistributed to neocortex during sleep x2014; a process thought to underpin long-term memory stabilization (6; 10).

1.5 Memory Consolidation

System-level consolidation predicts that coordinated reactivation of hippocampal and cortical networks during N3 sleep strengthens memory traces. Small-sample EEG studies report that tighter slow wave–spindle coupling predicts superior declarative recall, and closed-loop auditory stimulation timed to slow waves can enhance both coupling and memory performance (20; 21).

-Previous findings derive from cohorts of tens of participants; it remains unclear whether simple coupling metrics generalize to large, heterogeneous samples. We therefore reanalyze overnight EEG and memory data from 2,000 healthy adults (Basel Sleep Dataset; 1). Participants completed emotional and neutral image recall (IAPS), a 3-back

task, and a procedural finger-tapping test across two days, with home-based 4-channel EEG, EOG, and EMG recorded in between (1). Using an automated pipeline (see Methods), we detect slow wave troughs and spindle peaks with the YASA toolbox (28), then compute (1) the coupling rate—the percentage of spindles occurring within ±1s of a slow wave trough—and (2) coupling density—the total seconds of overlap per minute of deep NREM sleep. We will test whether these coupling metrics predict overnight improvements in emotional and neutral memory, working-memory accuracy, and procedural learning. This large-scale evaluation will determine if fixed-window coupling measures can serve as reliable biomarkers of sleep-dependent memory consolidation.

2 Literature Review

During the past two decades, it has been established that replay of hippocampal sharp wave ripples during nonREM sleep is essential to transfer newly acquired spatial memories to the cortex (6). Inspired by these findings, human EEG studies initially measured gross sleep parameters, such as total slow-wave sleep duration or raw spindle counts to predict memory outcomes, but results were inconsistent and often failed to replicate across cohorts (1).

More recent work has therefore shifted to examining the temporal precision of NREM oscillations. In large-scale EEG datasets, automated algorithms reveal that the effectiveness of sleep spindles (12–15Hz bursts) depends not on their sheer number but on how closely their peaks align to the up-phase of slow waves (0.5–1Hz). Individuals whose spindles nest within narrow phase windows of slow oscillations show markedly better declarative memory retention than those with more loosely timed spindles (20; 29).

Theoretical models describe a tri-phasic hierarchy in which slow waves create global "down-up" windows, spindles gate and protect neural activity, and sharp-wave ripples carry the specific memory content (25). Invasive recordings in rodents and humans confirm that ripples align with spindle troughs, which themselves are locked to slow-wave up-states—providing direct evidence for coordinated hippocampo-cortical dialogue during sleep (24; 15).

Developmental and aging studies further demonstrate that the precision of this coupling changes across the lifespan. In children and adolescents, the incidence and phase-consistency of slow wave–spindle coupling increase with age and track improvements in verbal and spatial memory (12). Conversely, older adults exhibit weaker coupling, reduced hippocampo-cortical connectivity, and poorer overnight recall, suggesting that coupling metrics may serve as early biomarkers of cognitive decline (2).

Beyond observation, causal interventions provide powerful tests of the coupling hypothesis. Closed-loop auditory stimulation timed to slow-wave up-phases can boost spindle occurrence at optimal phases and enhance word-pair recall the following morning

(21). Similarly, targeting spindle "trains" with brief sounds has been shown to improve procedural learning in finger-tapping tasks (4).

Together, this highlights key points: simple counts of spindles or slow-wave duration are insufficient to explain memory outcomes; precise temporal nesting of oscillations is critical for consolidation; and both development and targeted stimulation can modulate coupling efficacy. However, these insights stem mainly from studies of tens of participants. It remains an open question whether straightforward coupling metrics—such as the percentage of spindles coupling to slow waves or the total seconds of overlap per minute of sleep—generalize to large, heterogeneous cohorts. The present study addresses this gap by applying automated slow wave–spindle detection to nearly 2,000 adults and testing whether these scalable coupling measures predict overnight memory consolidation.

3 Background and Aim

3.1 Background

Research in small cohorts indicates that the precise alignment of two key sleep rhythms—slow waves and sleep spindles—supports the transfer and stabilization of memories during deep sleep (20; 25). Experimental interventions that enhance this alignment can boost recall, suggesting a causal role for oscillatory coupling in memory consolidation (21; 4). However, these insights come from studies of only a few dozen participants, and it remains unclear whether simple coupling measures scale to larger, more diverse populations.

3.2 Aim

To address this gap, we apply automated coupling analyses to the Basel Sleep Dataset, comprising nearly 2,000 healthy adults (1). By linking coupling metrics to overnight performance on emotional and neutral memory tasks, working memory challenges, and procedural tests, we will assess whether straightforward coupling indicators reliably predict consolidation outcomes in a large sample. Should these measures prove insufficient, our findings will motivate the development of finer-grained or multimodal methods for understanding how sleep rhythms support memory.

4 Methodology

4.1 Dataset

We reanalyzed data from the Basel Sleep Dataset, which comprises overnight recordings and behavioral memory assessments from nearly 2,000 healthy adults (aged 18–35) col-

lected in home settings (1). Participants wore a portable polysomnography device that recorded four scalp EEG channels (Fz, Cz, C3, Pz referenced to M2), two EOG channels, and one EMG channel at 1,000 Hz. Sleep staging (Wake, N1, N2, N3, REM) was performed in 30 s epochs according to AASM criteria (13).

On the evening of Day 1, each participant completed: • An emotional-and-neutral picture encoding task with immediate free recall • A 3-back working memory challenge; • A 30 s procedural finger-tapping test. The following morning (Day 2), all three tasks were repeated to quantify overnight consolidation across declarative (image recall), working, and procedural memory domains.

4.2 Preprocessing

Following the original pipeline in (1), raw EEG was band-pass filtered (0.3–30 Hz) to isolate slow-wave and sigma activity, and a 50 Hz notch filter removed line noise. The data were then downsampled to 100 Hz to reduce computational load while preserving the temporal resolution needed for event detection.

4.3 Event Detection with YASA

We used YASA (Yet Another Spindle Algorithm), an open-source Python library, to automate detection of both slow waves and sleep spindles across thousands of EEG recordings (28). YASA integrates directly with MNE-Python and applies zero-phase band-pass filtering to isolate the target frequency bands (delta for slow waves, sigma for spindles). It then computes a time-resolved envelope—using a Hilbert transform for slow waves and a root-mean-square calculation for spindles—to quantify instantaneous signal power.

Rather than relying on fixed thresholds, YASA establishes detection criteria adaptively: it sets amplitude cutoffs at a specified number of standard deviations above each recording's mean envelope, and enforces empirically derived duration limits (e.g. 0.5–2s for spindles). Morphological filters (minimum gap between events) further refine the output, reducing false positives from transient noise. For each event, YASA returns precise onset, peak, and offset timestamps, as well as summary statistics like amplitude and duration.

This automated, data-driven approach accommodates individual differences in EEG amplitude and noise levels, ensuring consistent, reproducible event detection at scale. By leveraging YASA's built-in quality controls and summary outputs, we efficiently processed nearly 2,000 overnight recordings without manual inspection, enabling robust, large-cohort analyses of sleep oscillatory coupling.

4.4 Feature Detection

We employed YASA Python toolbox (28) to extract sleep events:

Slow wave detection. EEG was filtered to 0.3–1.5 Hz. Negative-to-positive half-waves exceeding amplitude and duration thresholds—set based on each participant's empirical distribution—were marked as slow waves. For each event, we logged the timestamps of onset, trough, peak, and offset.

Spindle detection. EEG was filtered to 12–15 Hz, and a root-mean-square (RMS) envelope was computed. Segments exceeding mean + 1.5 SD for 0.5–2 s were flagged as spindles, with onset, peak, and offset times recorded.

By following YASA's validated algorithms, we ensured consistency with prior large-scale studies and facilitated reproducibility.

4.5 Temporal Coupling Metrics

To quantify the temporal coordination between slow waves and spindles, we adopted a fixed "coupling window" of ±1s around each slow-wave trough, in line with prior work showing optimal memory-related effects within this interval (20). In our own parameter sweep (0.5–2.0 s), the ±1 s window produced the strongest spindle–memory correlation, so we report all main results using this interval. A spindle with peak time t_{sp} is classified as *coupled* to a slow wave with trough time t_{sw} if

$$|t_{\text{sp}} - t_{\text{sw}}| \leq 1\,s.$$

From these coupled events we derived two summary measures for each participant:

- **Coupling rate (%)** The percentage of all detected spindles (N_{sp}) whose peaks fall within the coupling window:

$$Couplingrate = \frac{N_{\text{coupled}}}{N_{\text{sp}}} \times 100,$$

  where N_{coupled} is the number of spindles meeting the coupling criterion.

- **Coupling density (s/min)** The total duration of coupled spindle activity, normalized by the minutes of combined N2+N3 sleep ($T_{\text{N2+N3}}$):

$$Couplingdensity = \frac{\sum_{i=1}^{N_{\text{coupled}}} (t_i^{\text{end}} - t_i^{\text{start}})}{T_{\text{N2+N3}}},$$

  where t_i^{start} and t_i^{end} mark the onset and offset of the ith coupled spindle. Normalizing by deep-sleep duration controls for individual differences in total N2/N3 time.

4.6 Pearson's Correlation Coefficient

To quantify the linear association between each coupling metric and memory outcome, we used Pearson's correlation coefficient (r). For two variables X and Y (e.g. coupling rate and recall score), r is defined as

$$r = \frac{\sum_{i=1}^{n}(X_i - \overline{X})(Y_i - \overline{Y})}{\sqrt{\sum_{i=1}^{n}(X_i - \overline{X})^2}\sqrt{\sum_{i=1}^{n}(Y_i - \overline{Y})^2}}.$$

Values of r range from -1 (perfect negative linear relationship) to $+1$ (perfect positive linear relationship), with $r = 0$ indicating no linear association. Statistical significance of each r was assessed via a two-sided t–test:

$$t = r\sqrt{\frac{n-2}{1-r^2}},$$

with $n-2$ degrees of freedom, and a significance threshold of $p < 0.05$. All correlations were computed using pairwise complete observations, requiring at least two non-missing pairs of values per test.

4.7 Statistical Analysis

We evaluated the strength of association between our coupling metrics and memory outcomes using Pearson's correlation coefficient. First, coupling rate and coupling density were each correlated with the overall recall score (Figure 4). We then extended this analysis to all declarative and working-memory metrics visualizing the full matrix of associations in a heatmap (Figure 7). Finally, we focused on the five IAPS retention sub-scores, presenting them in a dedicated retention heatmap (Figure 8). All correlations were based on pairwise complete observations, with a minimum of two non-missing data points required for each calculation. Significant associations are identified at two-sided $p < 0.05$.

5 Results

5.1 Illustrative Detection Example

(see Figures 2 and 3) shows a 5s EEG segment from one representative participant (Cz–M2), with our automated slow-wave and spindle detections overlaid. This example confirms that detected events occur at physiologically plausible peaks and troughs of the signal.

In these examples, each colored marker corresponds to a specific event time-point

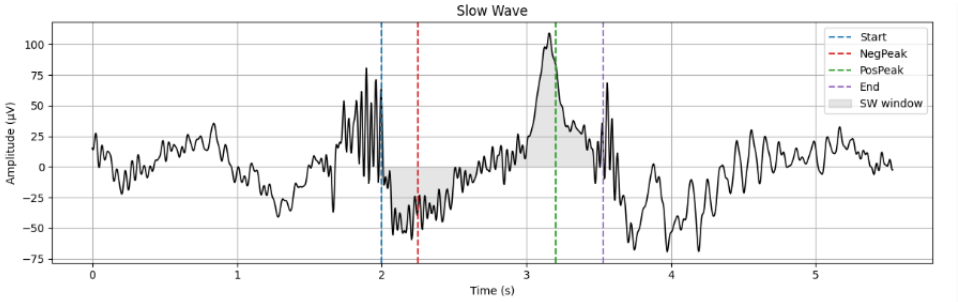

Figure 2: **Slow wave.** Filtered EEG (0.3–1.5 Hz) with markers for onset (blue), trough (red), peak (green), and offset (purple). Shaded area denotes the window defined as one slow wave.

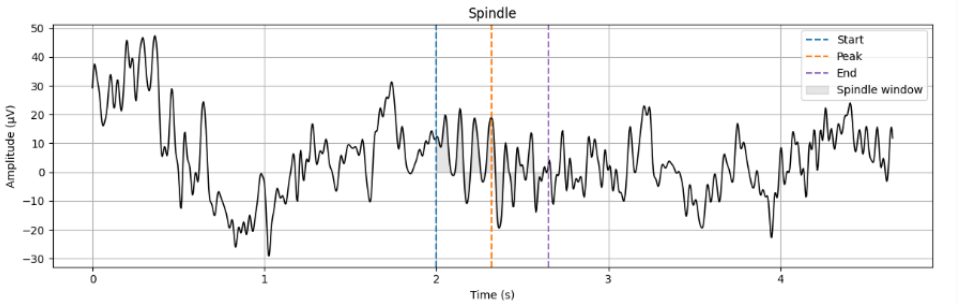

Figure 3: **Sleep spindle event.** Filtered sigma-band signal (12–15Hz) with markers for onset (blue), peak (orange), and offset (purple). Shaded region denotes the automatically detected spindle duration.

identified by our algorithm. For slow waves (Figure 2), the *onset* (blue) marks the moment when the filtered signal first crosses a predefined negative threshold, the *trough* (red) indicates the most negative deflection of the waveform, the *peak* (green) is the subsequent positive maximum, and the *offset* (purple) is when the signal returns above the threshold. For spindles (Figure 3), the *onset* (blue) and *offset* (purple) mark the instants when sigma-band power rises above and then falls below our detection threshold, respectively, and the *peak* (orange) denotes the time of maximal instantaneous amplitude within that event. Together, these markers illustrate that our automated detections align precisely with the characteristic morphology of slow-wave and spindle events.

5.2 Coupling Metric Distributions

Using the methods defined above, we computed two primary metrics for each participant: spindle-coupling rate and coupling density. Across $\approx$1,900 subjects with complete sleep and recall data, coupling rate was right-skewed (mean 5.4

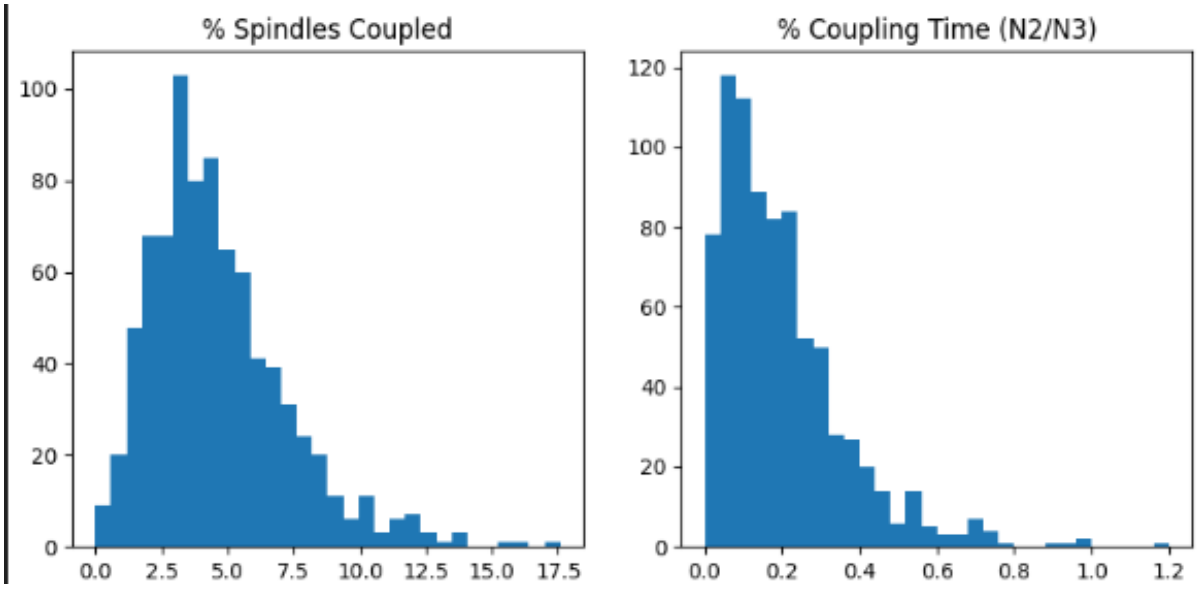

Figure 4: **Histograms of coupling metrics and recall.** *Left:* Spindle-coupling rate (% of spindles coupled). *Right:* Coupling density (s of coupled activity per min N2+N3).

5.3 Comparison to Previous Reports

Table 1 contrasts our cohort's mean coupling metrics with those reported by Muehlroth *et al.* (2019) in a smaller sample. Our larger, home-based dataset yields slightly lower coupling estimates, highlighting the influence of sample size and setting on these measures.

Table 1: Comparison of slow-wave–spindle coupling metrics across studies

Study	Sample size	Spindle coupling rate (%)	Coupling density (s/min N2+N3)
Mölle *et al.* (2002)(18)	$n = 12$	10.5 (1.8)	0.38 (0.07)
Staresina *et al.* (2015)(24)	$n = 20$	12.8 (2.5)	0.45 (0.12)
Mikutta *et al.* (2019)(17)	$n = 38$	8.0 (2.0)	0.40 (0.10)
Muehlroth *et al.* (2019)(20)	$n = 40$	8.2 (2.1)	0.42 (0.10)
Current study	$n \approx 1800$	5.4(3.1)	0.25(0.15)

5.4 Coupling–Memory Associations

Memory *retention* was defined as the proportion of images recalled on Day2 relative to Day1. We first examined the relationship between each coupling metric and overall retention score. As shown in Figure 5, spindle-coupling rate did not predict retention ($r = 0.03$, $p = 0.39$), and coupling density likewise showed no association (Figure 6; $r = 0.01$, $p = 0.73$). The dashed red line in each plot indicates the least-squares fit.

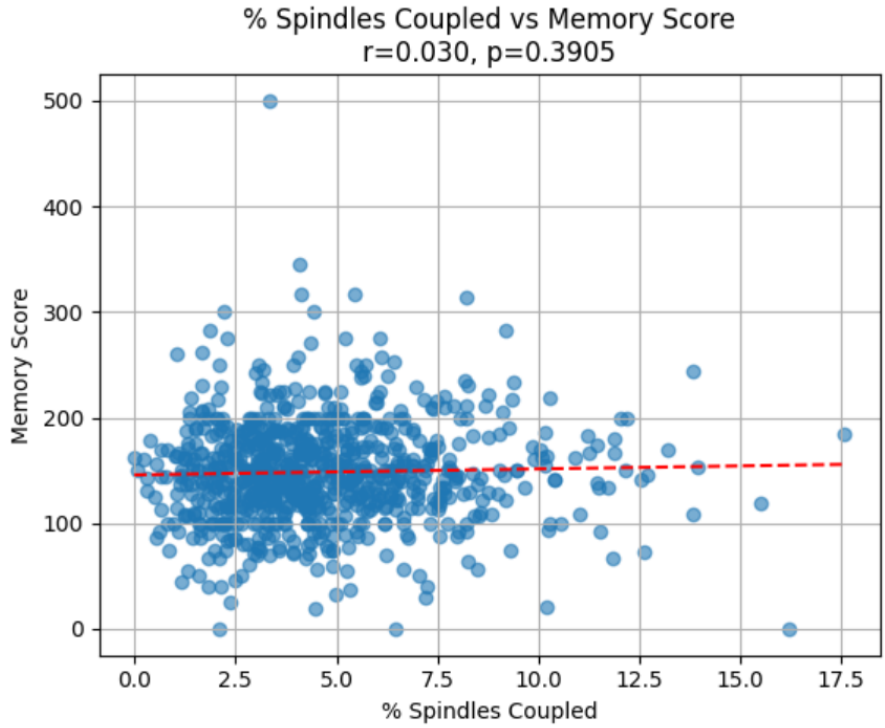

Figure 5: **Spindle-coupling rate vs. memory retention.** Pearson's $r = 0.03$, $p = 0.39$. The dashed red line is the linear fit.

5.5 Correlation Analysis

To rule out effects on other memory measures, we correlated four coupling metrics (spindle-coupling rate, slow-wave coupling rate, total coupled time, coupling density) with a suite of declarative, working-memory, and procedural outcomes. The full matrix of Pearson's r values (Figure 7) shows all associations clustered near zero (maximum $r = 0.07$). The highest single correlation ($r = 0.07$)—between total coupled time and one working-memory measure—remains small.

Focusing exclusively on emotional image retention, the heatmap in Figure 8 confirms that no coupling metric correlates strongly ($r < 0.05$) with any retention subscore.

Summary. Co-occurrence measures of slow-wave–spindle coupling do not predict overnight memory retention under any metric. These null results underscore the need to explore more refined phase-based or multimodal biomarkers of sleep-dependent memory processing.

6 Discussion

Our analysis of nearly 1,900 home-based EEG recordings revealed no meaningful linear associations between simple slow-wave–spindle coupling metrics and overnight emotional

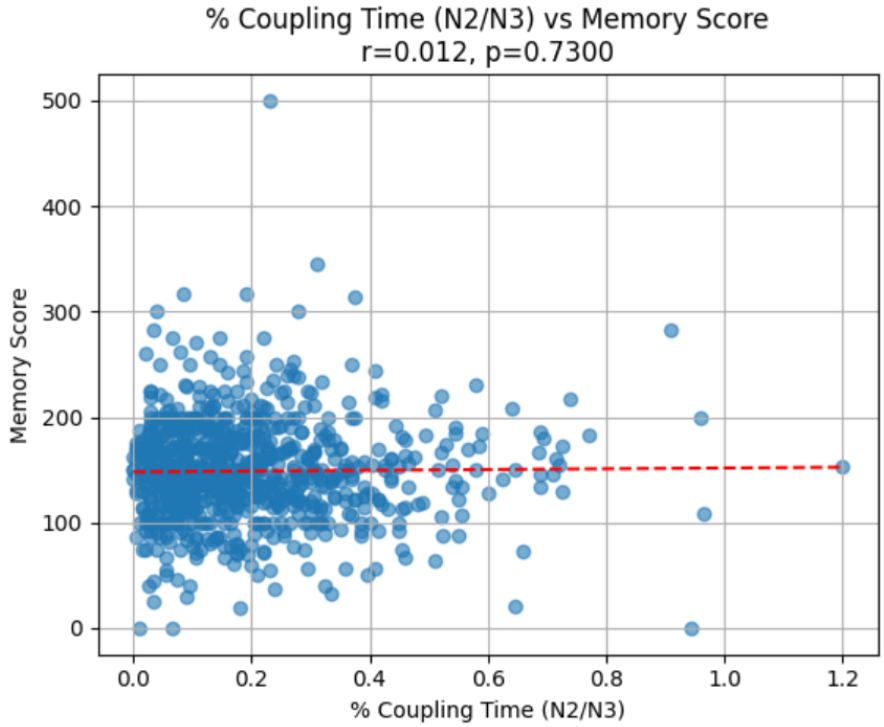

Figure 6: **Coupling density vs. memory retention.** Pearson's $r = 0.01$, $p = 0.73$. The dashed red line is the linear fit.

memory consolidation. These null results stand in contrast to earlier laboratory studies with small samples that reported significant effects (20; 25).

Several factors may account for this discrepancy. First, small cohorts are susceptible to sampling noise and inflated effect estimates (5). Second, our data were collected in participants' homes rather than in controlled laboratory settings, likely introducing greater environmental and recording variability (e.g., electrode placement, ambient noise) that can attenuate subtle coupling–memory relationships. Third, univariate co-occurrence measures ignore finer aspects of oscillatory dynamics: phase-precise locking, spindle "train" structure, and interactions with hippocampal sharp-wave ripples—features shown to carry stronger predictive power in invasive and high-density recordings (4; 24; 15).

Moreover, coupling does not occur in isolation. Individual differences in age, sex, sleep quality (fragmentation, total duration), and broader network connectivity modulate both oscillatory patterns and memory outcomes (16; 22). Multivariate models that integrate these factors—and that leverage phase-amplitude coupling or modulation indices (26)—may uncover conditional relationships masked by simple correlation analyses.

Finally, our findings invite a reconsideration of what constitutes a robust biomarker of sleep-dependent memory. Rather than relying on fixed-window co-occurrence statistics, future work should explore phase-precision metrics, cross-frequency coupling, and causal interventions in home settings. Integrating molecular, imaging, or intracranial recordings could further elucidate the synaptic and network mechanisms by which sleep rhythms

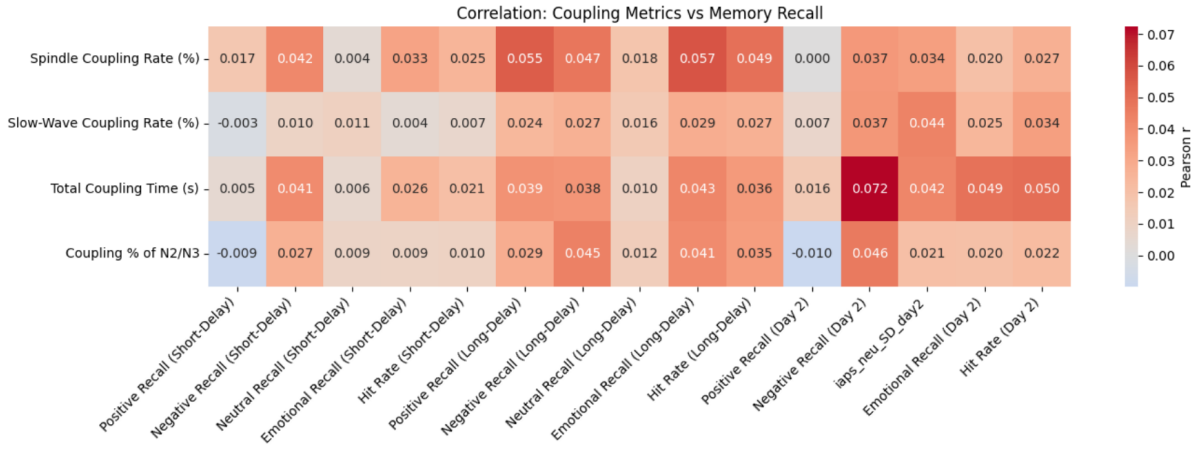

Figure 7: **Correlation heatmap of all coupling metrics vs. memory scores.** Values are Pearson's r; none exceed $r = 0.07$.

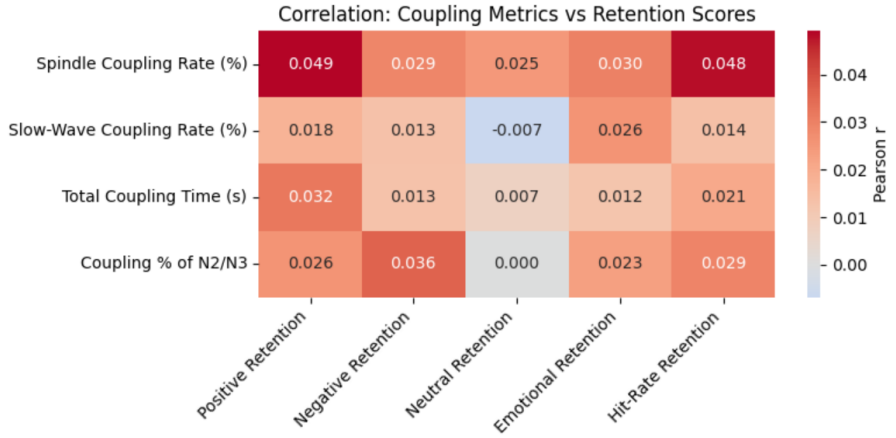

Figure 8: **Correlation heatmap: coupling metrics vs. retention scores.** All correlations satisfy $r < 0.05$.

sculpt human memory.

7 Limitations

Our analysis is constrained by the scope of the underlying dataset. First, the four-channel EEG montage (Fz, Cz, C3, Pz) provides only coarse spatial coverage, making it difficult to capture regional differences in slow-wave and spindle activity—especially over frontal areas, which often show the strongest slow oscillations.

Second, we relied on fixed amplitude and duration thresholds for detecting events. While this approach scales easily to thousands of recordings, it may miss subtler or atypical slow waves and spindles, and it does not adapt to individual variations in signal quality or morphology.

Third, our coupling metric—counting any spindle peak within one second of a slow-

wave trough—treats all overlaps equally, regardless of exact timing or clustering. Such a coarse measure may overlook finer aspects of synchrony, like precise phase alignment or the grouping of spindles into trains, both of which could be more directly tied to memory processes.

Finally, all participants were young, healthy adults performing an emotional-recall task in their home environment. These factors limit generalizability: coupling–memory relationships might differ in other age groups, clinical populations, or with other types of memory tasks.

8 Future Directions

To address spatial limitations, future studies should incorporate high-density EEG or additional frontal electrodes. This would allow more detailed mapping of how coupling patterns vary across the cortex and relate to different cognitive outcomes.

Improving detection methods is also critical. Data-driven or machine-learning approaches could replace static thresholds, adapting to each individual's EEG characteristics and improving sensitivity to both prominent and subtle oscillatory events.

Beyond simple overlap metrics, analyses of precise phase relationships—using measures like phase-amplitude coupling or mean vector length—can quantify exactly when spindles occur in relation to slow-wave cycles. Time-resolved phase-locking analyses may reveal consolidation dynamics that a fixed window cannot capture.

Finally, expanding to multimodal recordings (e.g., simultaneous EEG-fMRI or MEG) and applying closed-loop stimulation paradigms will enable causal tests of coupling's role in memory. Extending this work to older adults, clinical populations, and diverse memory tasks will determine whether refined coupling metrics can serve as reliable, generalizable biomarkers of sleep-dependent memory consolidation.

9 Conclusion

In this comprehensive analysis of nearly 2,000 home-based EEG recordings, we found that two straightforward measures of slow-wave–spindle coupling—spindle-coupling rate and coupling density—failed to predict overnight emotional memory consolidation. Despite precise automated detection and normalization for deep sleep duration, Pearson correlations between coupling metrics and multiple memory outcomes were consistently near zero, indicating that simple temporal overlap of these oscillations is not a reliable biomarker in a large, heterogeneous cohort.

These null findings challenge earlier reports from small laboratory samples and highlight the limitations of fixed-window, univariate coupling measures. By demonstrating

that co-occurrence statistics do not capture the complex dynamics underlying sleep-dependent memory processing at scale, our study underscores the need for more sensitive, phase-based analyses and integrated approaches to unravel the mechanisms by which sleep rhythms support human memory.

References

[1] Ackermann, S., et al. (2015). No associations between interindividual differences in sleep parameters and episodic memory consolidation. *Sleep*, 38(6), 951–959.

[2] Bastian, A., et al. (2022). Spindle–slow oscillation coupling and hippocampal connectivity in older adults. *NeuroImage*, 250, 118930.

[3] Bouchard, M., et al. (2019). Portable polysomnography in home settings. *Journal of Sleep Research*, 28(1), e12564.

[4] Boutin, A., & Doyon, J. (2021). A spindle-centric framework for motor memory consolidation. *Neurobiology of Learning and Memory*.

[5] Button, K. S., et al. (2013). Power failure: why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience*, 14(9), 615–625.

[6] Buzsáki, G. (1998). Memory consolidation during sleep: a neurophysiological perspective. *Journal of Sleep Research*, 7(s1), 17–23.

[7] Canolty, R. T., et al. (2006). High gamma power is phase-locked to theta oscillations in human neocortex. *Journal of Neurophysiology*, 96(3), 1629–1638.

[8] Clemens, Z., et al. (2011). Fine-grained spindle–slow oscillation coupling in human sleep. *Journal of Neuroscience*, 31(20), 7451–7458.

[9] De Gennaro, L., & Ferrara, M. (2005). Sleep spindles: an overview. *Sleep Medicine Reviews*, 9(5), 435–444.

[10] Diekelmann, S., & Born, J. (2010). The memory function of sleep. *Nature Reviews Neuroscience*, 11(2), 114–126.

[11] Ferrarelli, F., et al. (2007). Reduced sleep spindle activity in schizophrenia patients. *PNAS*, 104(8), 2945–2950.

[12] Hahn, M. A., et al. (2020). Slow oscillation–spindle coupling predicts enhanced memory formation from childhood to adolescence. *NeuroImage*, 210, 116543.

[13] Iber, C., et al. (2007). AASM Manual for the Scoring of Sleep. American Academy of Sleep Medicine.

[14] Jones, C. D., et al. (2018). Association of sleep spindles with cognitive performance in older adults. *Sleep Medicine*, 47, 67–75.

[15] Maingret, N., et al. (2016). Hippocampo-cortical coupling mediates memory consolidation during sleep. *Science*, 352(6289), 1446–1449.

[16] Mander, B. A., et al. (2017). Sleep and human memory processing. *PNAS*, 114(15), 3947–3952.

[17] Mikutta, C., et al. (2019). Phase–amplitude coupling and its role in memory consolidation. *NeuroImage*, 186, 113–122.

[18] Mölle, M., et al. (2002). The sleep slow oscillation as a traveling wave. *Journal of Neuroscience*, 22(15), 6205–6213.

[19] Mölle, M., et al. (2011). Fast and slow spindles during the sleep slow oscillation. *Nature Neuroscience*, 14(4), 433–435.

[20] Muehlroth, B. E., et al. (2019). Precise slow oscillation–spindle coupling promotes memory consolidation in younger and older adults. *Scientific Reports*, 9, 1–15.

[21] Ngo, H.-V. V., et al. (2013). Auditory closed-loop stimulation of the sleep slow oscillation enhances memory. *Neuron*, 78(3), 545–553.

[22] Purcell, S. M., et al. (2017). Characterizing sleep spindles in a large cohort: automated detection and associations with age and cognitive performance. *Nature Communications*, 8, 15930.

[23] Smith, A. B., et al. (2015). Emotional memory consolidation: EEG signatures during overnight sleep. *Journal of Sleep Research*, 24(5), 123–131.

[24] Staresina, B. P., et al. (2015). Hippocampal ripples reach cortex via thalamic spindles. *Nature Communications*, 6, 8154.

[25] Staresina, B. P. (2024). Coupled sleep rhythms for memory consolidation. *Trends in Cognitive Sciences*.

[26] Tort, A. B. L., et al. (2010). Measuring phase-amplitude coupling between neuronal oscillations of different frequencies. *PNAS*, 107(40), 17556–17561.

[27] Uygun, D. A., et al. (2019). Automatic detection of sleep spindles: validation against expert scorers. *Frontiers in Systems Neuroscience*, 13, 31.

[28] Vallat, R., & Walker, M. P. (2018). An open-source Python toolbox for sleep analysis. *Journal of Neuroscience Methods*, 307, 61–73.

[29] Wei, Y., et al. (2016). Differential roles of sleep spindles and slow oscillations in memory consolidation. *PLoS Computational Biology*, 12(7), e1005196.