



Decoding spatiotemporal dynamics of neural oscillations during sleep and their age-related effects on emotional memory consolidation

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INTRODUCTION:

Slow oscillations (SOs) and sleep spindles (SPs) are crucial for sleep-dependent memory consolidation, yet their role in coordinating long-range cortical communication and how aging affects this function remains poorly understood. Prior studies focused on local dynamics due to limited electrode coverage. Using high-density polysomnography (PSG), this study explores the spatiotemporal dynamics of SOs and SPs, specifically their repeated directional propagation across the cortex and how these propagations are modulated across different frequency ranges, which may represent a potential mechanism to support long-range memory transfer. We also investigate how aging alters the stability of this cortical connectivity during sleep. By applying computational modeling, we further aim to clarify the relevance of SO and SP metrics to memory processes.

METHODS:

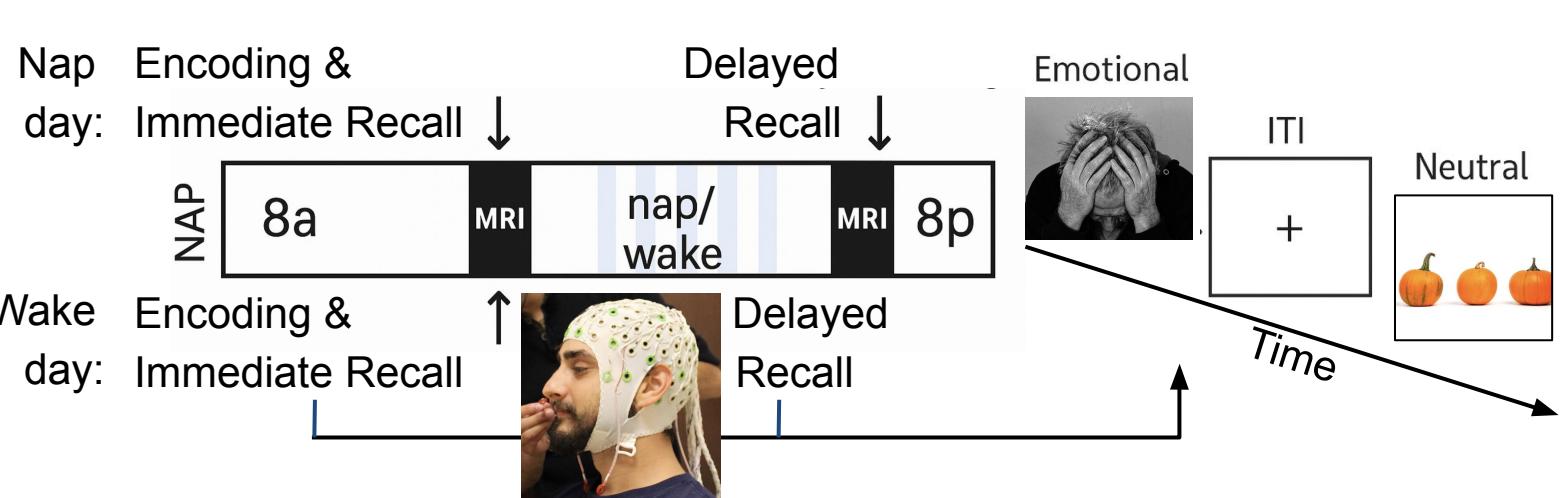


Fig. 1. Experimental paradigm and memory task design

- Experiment:** Healthy young (N=15, YA) and older adults (N=15, OA) completed immediate and delayed recall tasks for emotional recognition memory on both nap and wake days. High-density PSG (122 electrodes; Fs = 500 Hz) was collected between tests.
- Behavioral Analysis:** Unequal variance signal detection and drift-diffusion models (DDM) modeled the mechanism underlying memory consolidation. Sensitivity (D_A) and drift rate (V) were used as measure of memory strength in each model.

- Spectral Analysis:** Multi-Gaussian curve fitting improved topographical measurements in SO and SP peak frequencies and powers following IRASA. Hierarchical clustering was used to classify the electrodes into two groups based on frequency.

- Event Detection:** For SO detection, we filtered EEG (0.16–1.25 Hz), extracted 0.8–2 s half-waves, selected events with top 30% troughs and peak-to-peak amplitudes. For SP detection, we used Convolutional Neural Networks (Mofrad et al., 2022) to improve the detection of co-occurring events across electrodes.

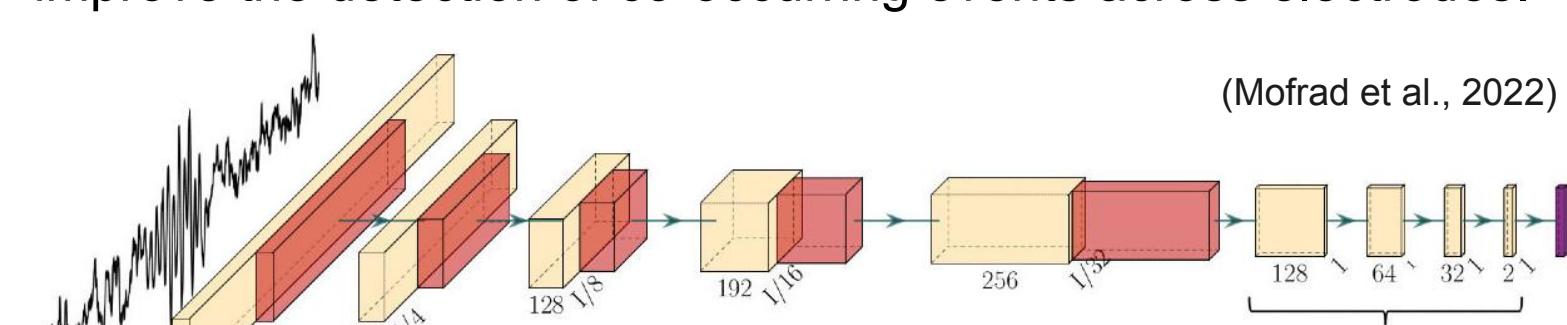


Fig. 3. The detection of spatially clustered sleep spindles using Convolutional Neural Networks (CNN).

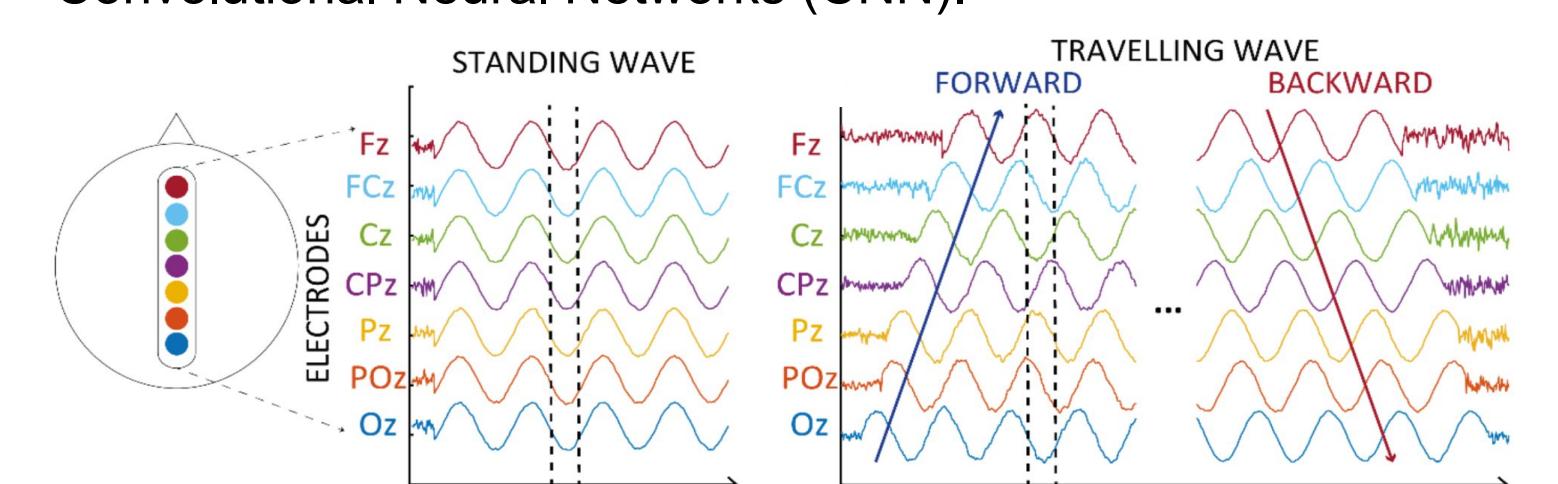


Fig. 4. Visualization of standing waves and two common types of planar traveling waves (TWs).

- Cortical Connectivity:** Cross-correlation was used to calculate the spatial correlation between each pair of electrodes within $\pm 1.5s$ of the oscillation center (SP peak, SO trough), where the maximum correlation within $\pm 0.2s$ time lag was extracted. 2000 pairs of events and non-event epochs were selected for analysis.
- Traveling Waves (TWs):** We modeled the propagation of SOs and SPs by extracting the instantaneous phase of each oscillation at each time point. The local traveling direction at each electrode was estimated using the spatial derivative of phase across neighboring electrodes, while the traveling speed was estimated by its temporal derivative. The consistency of wave propagation across electrodes was quantified using Phase Gradient Directionality (PGD), while the consistency of direction across trials was quantified by the axial mean vector length (MVL), defined as modulus of the second trigonometric moment.

- Spindle Trains:** Each SP cluster was defined as a sequence of successive SP events with peak times separated by less than 6 seconds.

RESULTS:

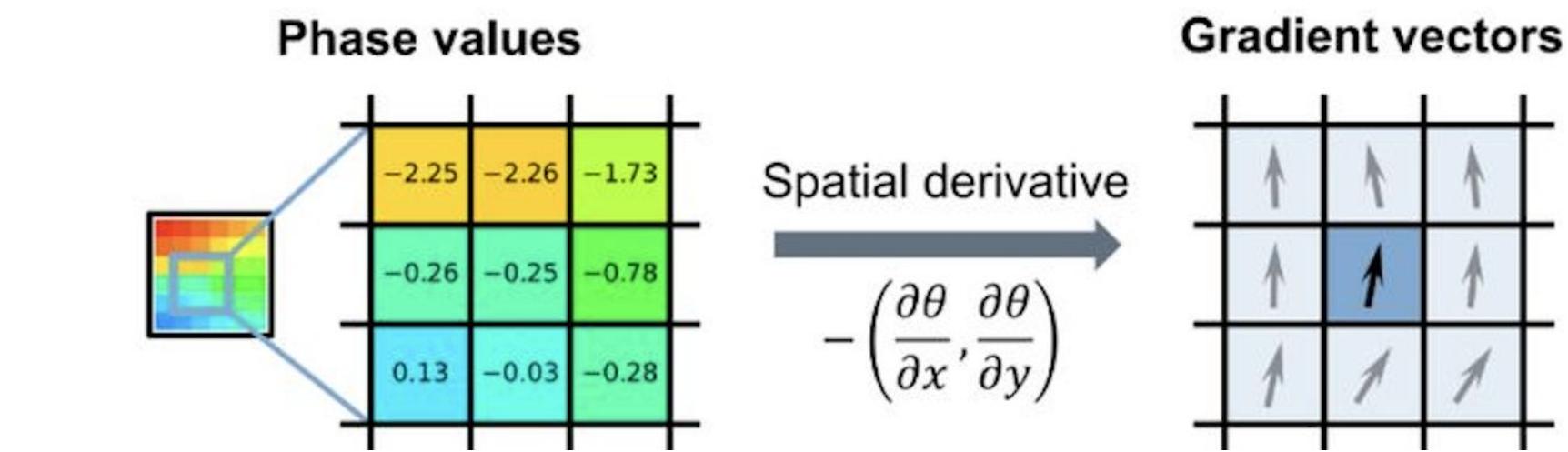


Fig. 5. The detection of traveling waves using phase gradients.

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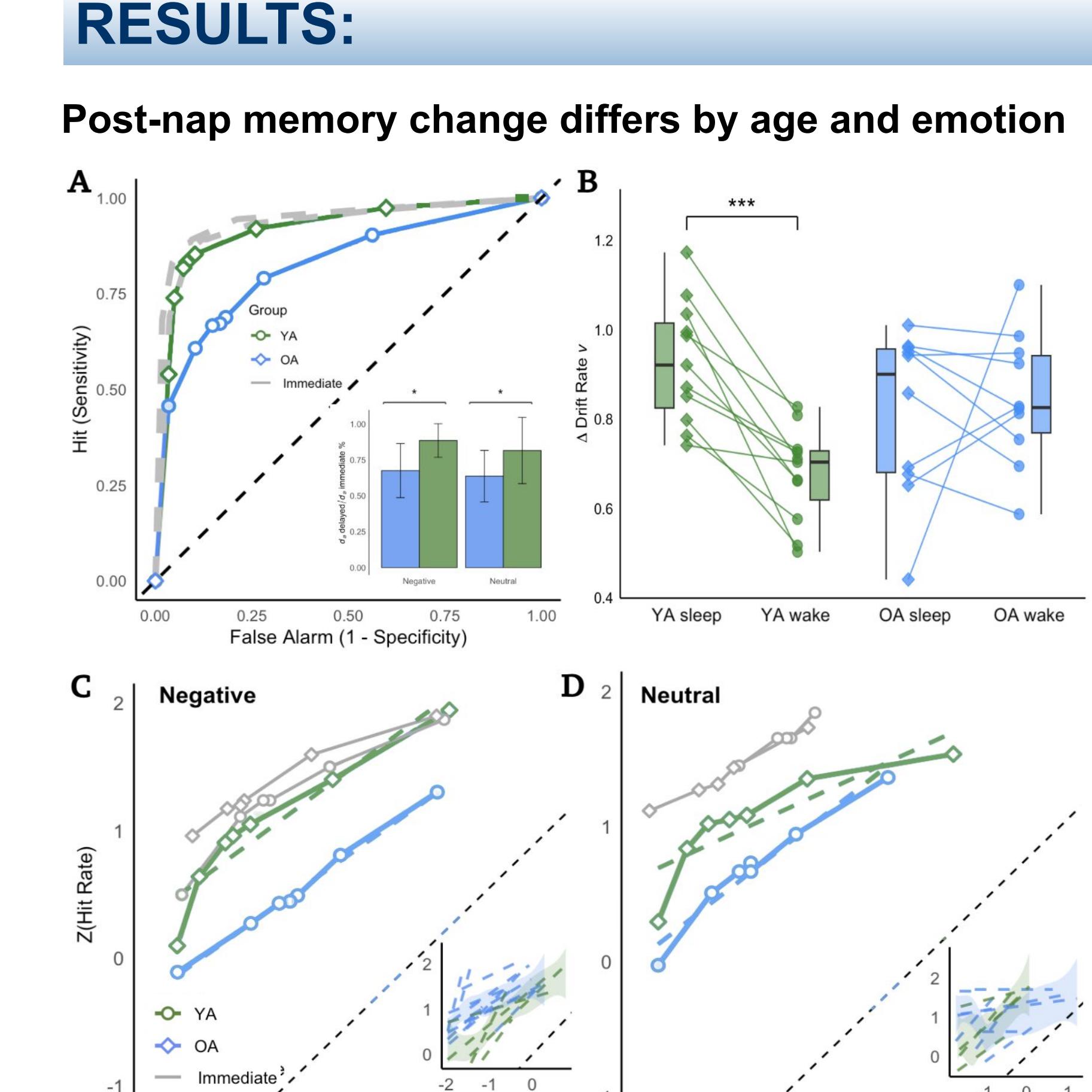


Fig. 2. Electrode rotational map in normalized polar coordinates.

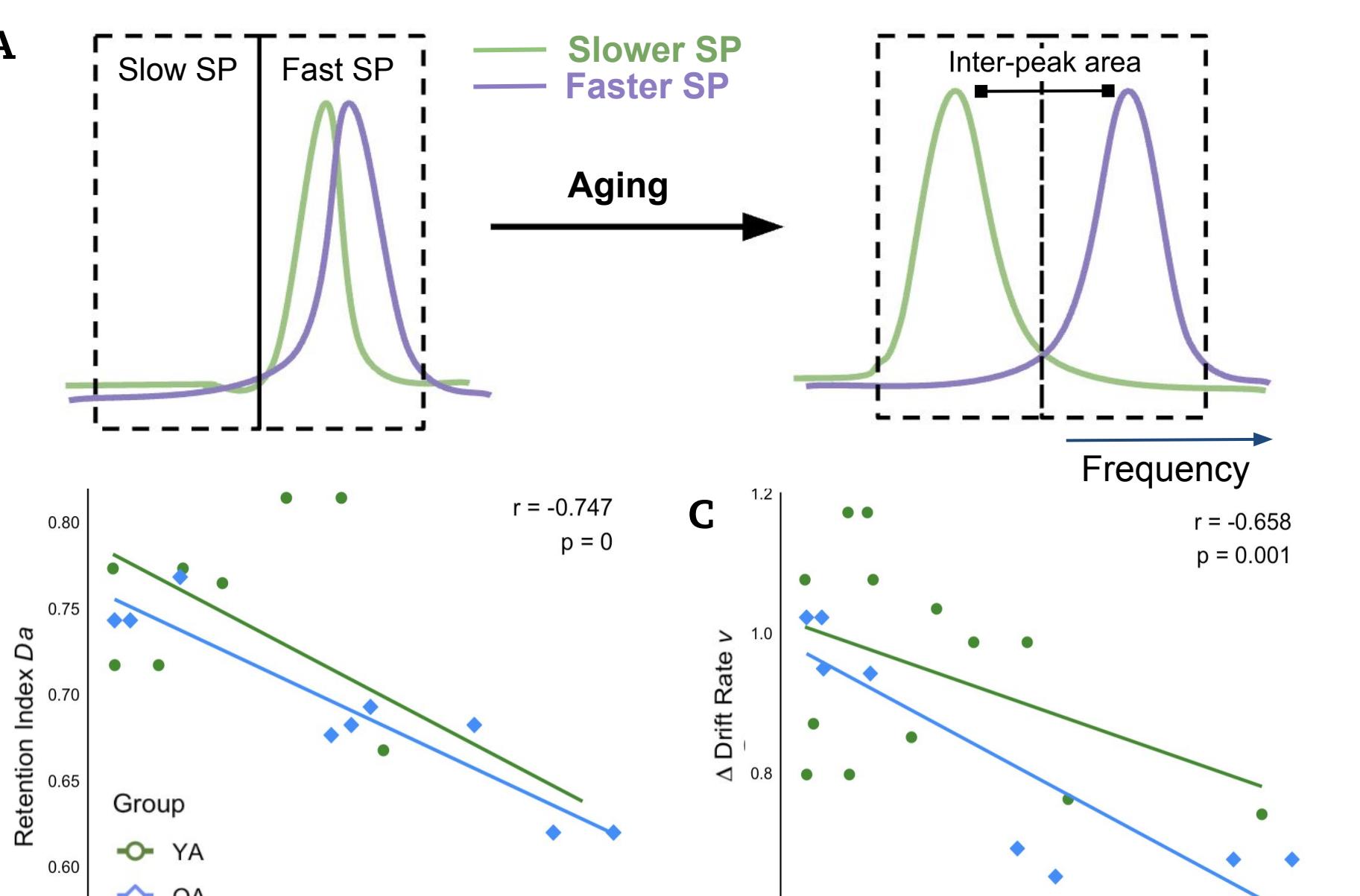
- Post-nap memory change differs by age and emotion:**
 - Panel A: ROC curves for YA and OA showing better performance for YA.
 - Panel B: Bar chart of retention index D_A for negative and neutral conditions.
 - Panel C: Scatter plot of retention index D_A vs inter-peaks area.
 - Panel D: Scatter plot of retention index D_A vs inter-peaks area for negative and neutral conditions.

- SO & SP Frequency Gaps Predict Memory Performance:**
 - Panel A: Comparison of slow and fast SPs over time.
 - Panel B: Scatter plot of retention index D_A vs inter-peaks area.
 - Panel C: Scatter plot of retention index D_A vs inter-peaks area.

- Cortical connectivity increases during oscillation events:**
 - Panel A: ROC curves for Non-SO and SO.
 - Panel B: ROC curves for Non-spindle and Spindle.
- Repeated propagation of SPs as clusters of 'trains':**
 - Panel A: Waveform and schematic of spindle train.
 - Panel B: Waveform and schematic of isolated spindle.
- SP peak frequency changes across the cortex:**
 - Panel A: Heatmap of spectral peak frequency across electrode distance.
 - Panel B: Scatter plot of average time lag vs electrode distance.
- SO-SP Coupling Meta-anal:**
 - Panel A: Heatmaps of mean count and train length difference.

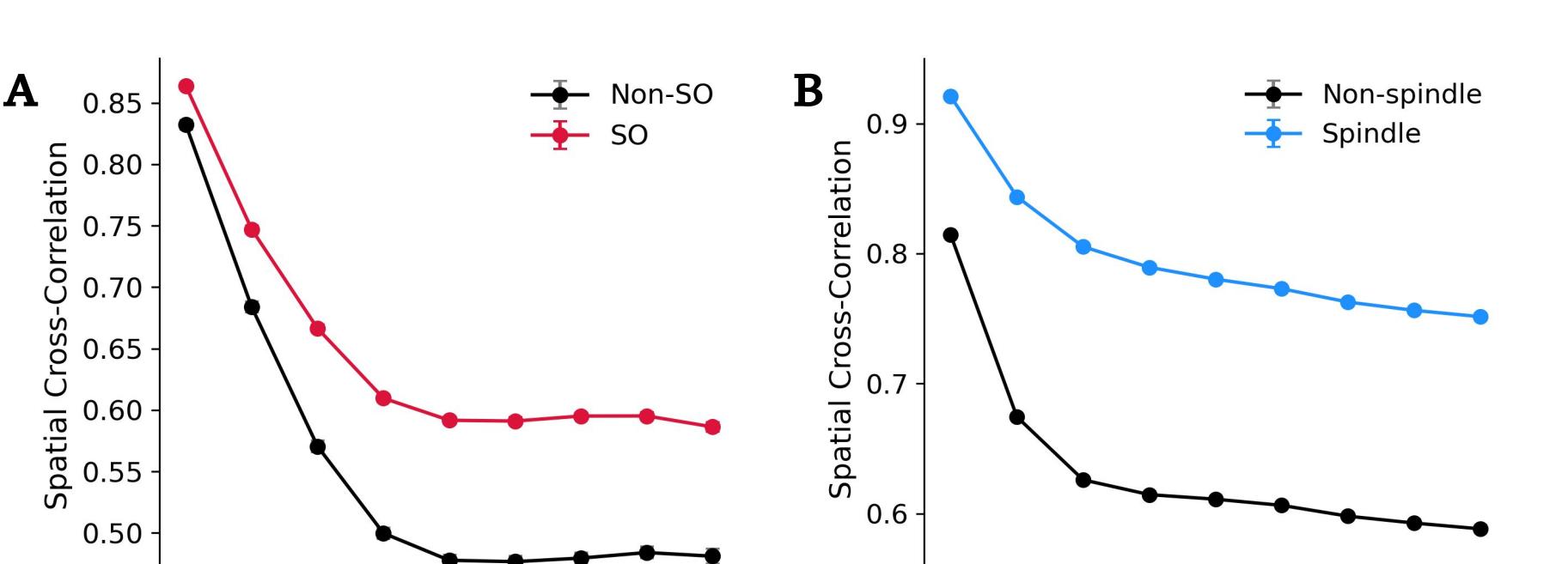
- The frequency of SOs and SPs changes smoothly across the cortex along electrode cycles in YA, rather than localized activity.
- OA exhibit a discontinuity in SP peak frequency, represented as a 'cliff' between frontal-temporal and centroparietal electrodes.
- This discontinuity may be associated with disrupted long-range communication and increased regional isolation.
- The traditional 'fast' vs 'slow' spindle classification may be subjective, as SP frequency varies continuously with age and cortical location, reflecting spatial and developmental gradients rather than distinct subtypes.

SP & SO Frequency Gaps Predict Memory Performance



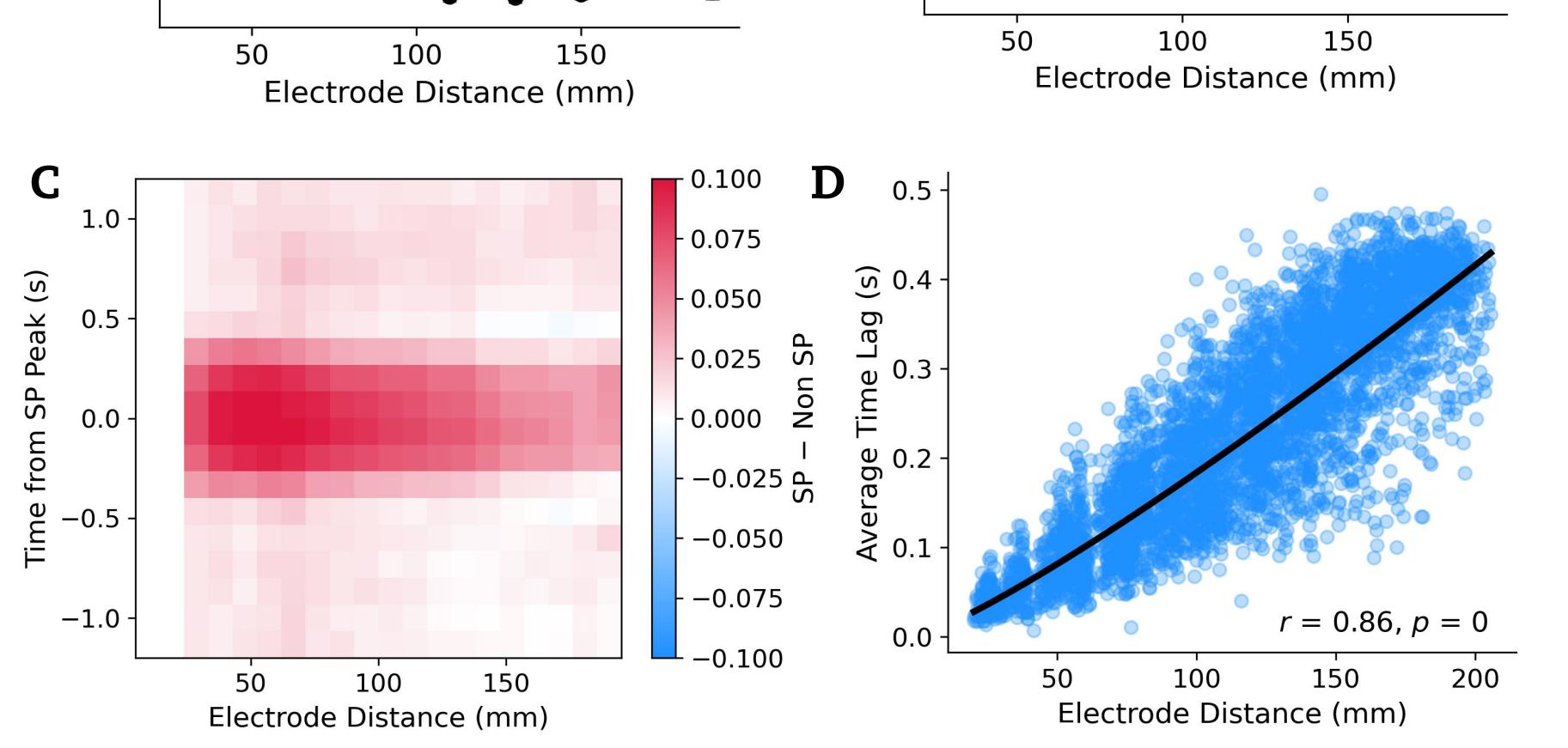
- An increased frequency gap between 'slower' frontal-temporal and 'faster' centroparietal SPs predicts poorer memory performance in both YA and OA.
- Similar associations are found between SO frequency gradients and post-nap memory performance.
- Q: What does the consistency of SO and SP frequency gradients imply about the importance of connectivity across brain regions?

Cortical connectivity increases during oscillation events



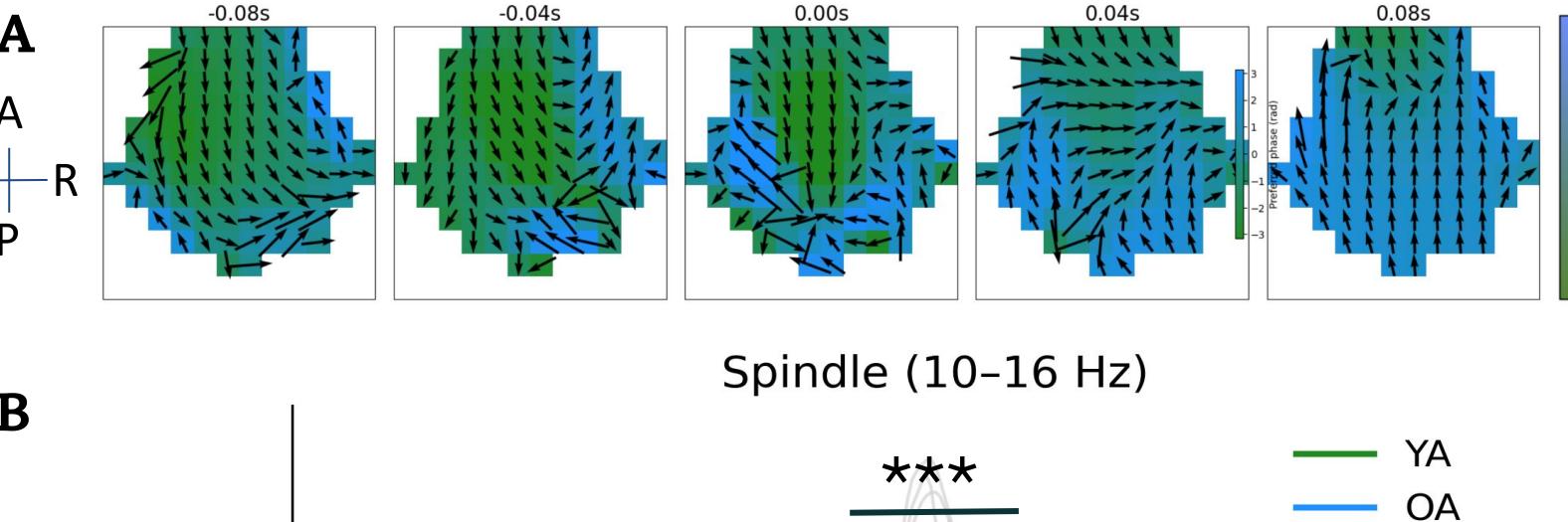
- Unidirectional connectivity of SP signals peaks at the SP peak, whereas that of SOs remains elevated throughout the entire up-state.
- The directionality of SPs is modulated by the directionality of SOs.
- Directionality decreases as the spatial extent of a TW increases.

Repeated propagation of SPs as clusters of 'trains'



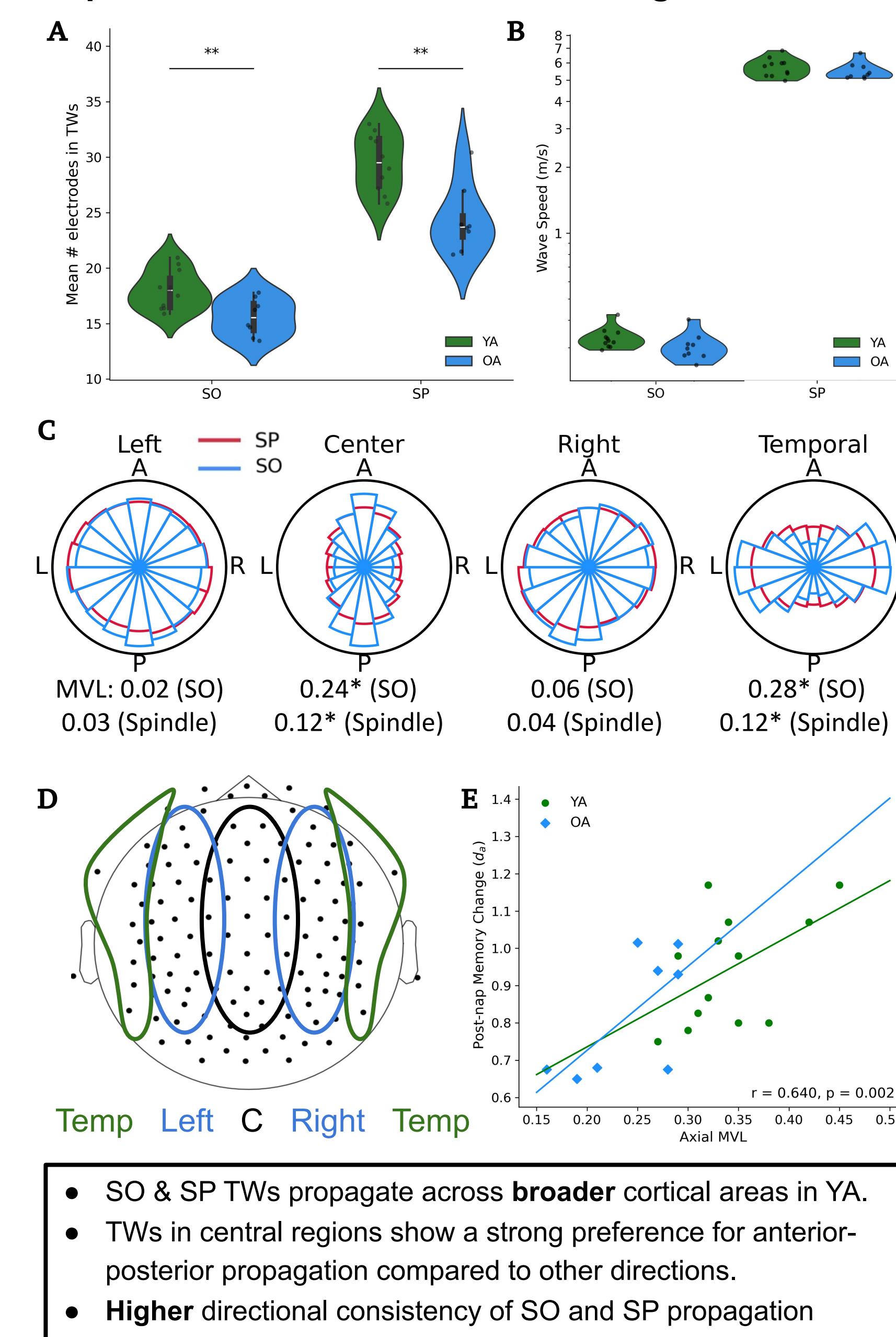
- Cortical connectivity significantly increases during SO & SP events compared to the baseline epochs during nREM sleep.
- This increase in connectivity is concentrated at the peak of SPs and the up-state of SOs.
- Q: Which type(s) of connectivity are characteristic of SOs & SPs?
 - Simultaneous connectivity
 - Unidirectional propagation
 - PAC
- The time lag of SO and SP signals between electrodes increases with inter-electrode distance, following a power law distribution.

The directionality of SOs & SPs as traveling waves



- As SP train length increases, the amplitude, duration, and frequency of SPs consistently increase, while trains occur more frequently in the frontal-central region of YAs than in OAs.
- Prior studies link increases in these metrics to improved memory.
- YA benefit more from having multiple SP events repeatedly propagating within a short timeframe, leading to stronger waves.

Properties of SOs and SPs as traveling waves



- SO and SP TWs propagate across broader cortical areas in YA.
- TWs in central regions show a strong preference for anterior-posterior propagation compared to other directions.
- Higher directional consistency of SO and SP propagation predicts better memory performance in YA and OA.

CONCLUSIONS:

- The repeated temporal coupling between the peak of SP amplitude and the SO up-state across the cortex is critical:
 - It enables maximal coordinated, unidirectional propagation of SOs and SPs, supporting long-range information transfer.
 - It facilitates cross-frequency modulation from SOs to SPs, potentially enhancing information integration.
- Disruptions in propagation gradients, consistency, and cortical involvement are related to impaired memory performance.
- Traditional definitions of 'fast' and 'slow' SPs are often subjective. SP frequency varies by age and cortical region.
- Precise spatiotemporal coordination along anterior-posterior axis during the propagation of sleep oscillations is crucial for effective memory consolidation, highlighting the functional importance of large-scale neural coordination during sleep.
- Future sleep-memory studies should include spatiotemporal structures in their analysis.

REFERENCES:

