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Stage-dependent directed connectivity in a PFC–thalamus–hippocampus circuit during sleep fMRI with cues for memory consolidation

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Abstract

Sleep is a dynamic neurophysiological process characterized by continuous transitions between wakefulness, non-rapid eye movement (NREM) sleep, and rapid eye movement (REM) sleep throughout the night. The cortical regulation-thalamic gating-hippocampal processing circuit, comprising the prefrontal cortex (PFC), thalamus (THAL), and bilateral hippocampus (HIP-L/HIP-R), may participate in information processing mode switching and be associated with memory consolidation. This study, based on overnight sleep fMRI, integrates data-driven staging evidence with directional modeling to quantify stage-dependent modulation across five stages within a four-node framework. Results indicate that connectivity undergoes systematic reorganization during sleep: cortical outbound regulation dominates during wakefulness and sleep onset, shifts toward enhanced thalamic-hippocampal axis activity during stable sleep, and declines overall during REM sleep while preserving hippocampal-related connections. This information flow migration aligns with thalamic gating and hippocampal-cortical interaction mechanisms required for sleep-related memory consolidation, providing insights for inferring memory-related mechanisms and clinical assessment.

Keywords: Sleep; Prefrontal Cortex(PFC); Thalamus (THAL); Hippocampus(HIP); memory consolidation; Data-driven; directional modeling;

Introduction

Sleep dynamically transitions throughout the night between wakefulness (W), non-rapid eye movement (NREM) light sleep stages (N1/N2), deep sleep stage (N3), and rapid eye movement (REM) sleep (American Academy of Sleep Medicine., 2012). This process is accompanied by stage-specific differences in electroencephalographic rhythms, arousal levels, and autonomic activity, as well as the repeatable reorganization and progressive migration of large-scale brain network configurations (Daneault et al., 2021; Setzer et al., 2022). Sleep disorders are highly prevalent and prone to recurrence, correlating with outcomes such as mood disorders, cognitive decline, and cardiovascular/cerebrovascular risks, thereby continuously increasing healthcare and societal burdens (Khaing et al., 2025; Carvalho et al., 2025). Given the strong heterogeneity and broad disease course of sleep disorders, static descriptions at a single time point often fail to reveal how directional interactions between key hubs are systematically remodeled during phase transitions. Therefore, it is necessary to focus on core circuits closely related to rhythm generation, information gating, and memory processing to establish comparable, quantifiable network-level mechanism

representations.

Against this backdrop, we focus on the thalamic-prefrontal-hippocampal pathway, which is closely associated with rhythm generation, information gating, and memory processing. The thalamus (THAL) serves as a crucial hub for initiating and coordinating rhythmic activities such as sleep spindles, while also playing a gating role in suppressing sensory input and maintaining sleep (Fernandez and Luthi, 2020; Dickey et al., 2024). The hippocampus (HIP) underpins representations related to episodic and spatial memory. Cross-structural synchronization and information replay during sleep, particularly in non-rapid eye movement (NREM) stages, are considered closely linked to memory consolidation processes. Recent studies further suggest that coupling between the hippocampus and the thalamus and cortex is critical for sleep-related memory support (Geva-Sagiv et al., 2023). The prefrontal cortex (PFC), associated with higher-order executive control, exhibits state-dependent activity during slow-wave sleep and whole-brain synchronization processes linked to sleep homeostasis regulation and changes in arousal thresholds (Zou et al., 2025; Marsh et al., 2023). Consequently, THAL–PFC–HIP interactions may represent a critical pathway for integrating rhythmicity generation, information gating, and memory processing during sleep stage transitions. Recent human closed-loop stimulation and intracranial recording studies further indicate that enhancing prefrontal-medial temporal lobe synchronization during sleep and strengthening the coupling between hippocampal ripples and thalamocortical spindle activity improves overnight memory performance, suggesting that synergistic information flow within this pathway may participate in memory consolidation (Geva-Sagiv et al., 2023).

Methodologically, resting-state functional magnetic resonance imaging (rs-fMRI) reveals systematic alterations in network connectivity during sleep onset, suggesting a gradual transition from wakefulness to sleep rather than discrete segmentation (Damaraju et al., 2020; Song et al., 2022). Meanwhile, machine learning and deep learning have advanced automated staging and sleep event detection, yet most studies remain focused on staging performance or unidirectional connectivity strength, failing to directly address the mechanism of directional regulation and pathway differences during stage transitions (Zhang et al., 2024). To obtain interpretable directional results while preserving continuous transition information, a natural approach involves decomposing con-

tinuous data into states using models that capture implicit dynamic states and their transitions, then integrating state information into interpretable causal modeling frameworks. State-space methods, exemplified by Hidden Markov Models (HMM) and their autoregressive extensions (AR-HMM),

provide soft state representations for whole-night sleep and characterize state transition structures. Recent whole-night fMRI studies have demonstrated that such methods yield stable, interpretable state dynamics patterns during sleep (Yang et al., 2024). On the other hand, Dynamic Causal Modeling

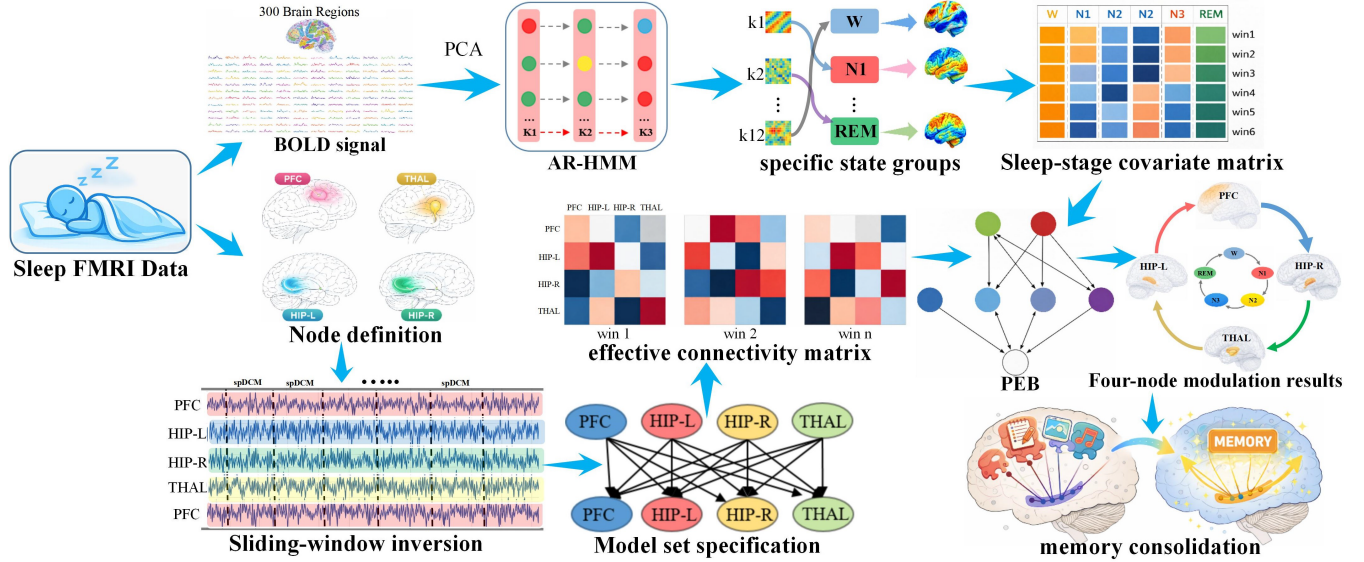


Figure 1: Modeling and Analysis Framework

(DCM), proposed by Friston et al., employs spectral dynamic causal modeling (spDCM) for resting-state data. This approach robustly estimates directional coupling within networks through frequency-domain features and mutual spectral density fitting (Friston et al., 2014; Novelli et al., 2024). At the population level, parametric empirical Bayesian (PEB) methods are employed to test individual-level modulation effects and quantify uncertainty (Friston et al., 2016). Building upon this, Park et al. decomposed state-dependent effective connectivity within PEB by treating state sequences as regression targets (Park et al., 2021). However, state estimation remains relatively decoupled from DCM inversion and may not adequately accommodate sleep processes characterized by discrete staging, frequent transitions, and mixed states.

Inspired by this and to address the limitations of existing studies in characterizing stage-related directional regulation, this research treats the HIP, PFC, and THAL as network nodes. To mitigate confounding effects from lateralization, the HIP is further subdivided into left and right hippocampi (HIP-L/HIP-R), constructing a four-node network. Coupling phasing soft-state evidence with windowed spDCM, and quantifying phasing-specific modulation of connection parameters within a hierarchical Bayesian framework, we obtained interpretable phasing-specific directional regulation results and elucidated loop remodeling mechanisms based on these findings. Specific contributions include:

1) Proposing an adaptive state modeling strategy—specifically state number selection and stage-specific state group screening—enables the construction of a more robust staging

covariate design matrix while reducing state uncertainty bias. This provides reliable stage-specific evidence for subsequent discussions on memory-related information flow changes.

2) Extend existing state-dependent effective connectivity pathways to encompass the overnight sleep paradigm, enabling unified modeling of phased stages and directional effective connectivity inference.

3) Using a four-node loop as the target, we provide comparable stage-specific connectivity and directional modulation metrics. This offers empirical support for interpreting the re-modeling of HIP, PFC, and THAL pathways during stage transitions and proposes testable hypotheses regarding their role in memory consolidation.

Method

To uniformly characterize the correspondence between evidence of sleep staging throughout the night and directionally effective connectivity, we constructed a staging-specific effective connectivity analysis workflow based on AR-HMM latent state decomposition and windowed spDCM-PEB hierarchical inference, as shown in Figure 1. First, AR-HMM is applied to decompose the overnight BOLD time series into latent states. Based on the predominant occurrence phase of each latent state within the manually labeled stages, these states are consolidated into a set of stage-specific states corresponding to five sleep stages. Subsequently, four node time series are extracted and divided into sliding windows. SpDCM is fitted to each window to obtain window-level effective connectivity parameters. Next, the proportion of

phase-specific state sets within each window is aggregated to derive window-level soft phase evidence. This evidence is used to construct a PEB secondary design matrix, establishing a mapping relationship between window-level connectivity parameters and phase evidence at the individual level. Finally, hierarchical PEB aggregation inference is performed at the group level to reveal directional effective connectivity patterns across the four-node network during the five sleep phases, along with their temporal dynamics.

AR-HMM Sleep Latent State Modeling

We perform latent state decomposition on the entire night's ROI-level BOLD sequence using AR-HMM, and characterize the state proportion at each time point with posterior soft assignment weights. Denote the latent state as $Z_t \in \{1, \dots, K\}$. The posterior assignment weight is defined as:

$$\Gamma_{t,k} = p(Z_t = k | \tilde{\mathcal{Y}}_{1:T}) \quad (1)$$

Here, $\tilde{\mathcal{Y}}_{1:T}$ denotes the preprocessed observation sequence used for modeling, where $t=1, \dots, T$ and $k=1, \dots, K$. To determine the number of latent states K , we train the model on each candidate set and compute the log-likelihood and maximized entropy for the full-night sequence. Let:

$$\mathcal{L}(K) = \log p(\tilde{\mathcal{Y}}_{1:T}; K) \quad (2)$$

$$\mathcal{H}(K) = -\frac{1}{T} \sum_{t=1}^T \sum_{k=1}^K \Gamma_{t,k} \log \Gamma_{t,k} \quad (3)$$

Here, $\mathcal{L}(K)$ measures the goodness-of-fit, while $\mathcal{H}(K)$ quantifies the uncertainty in state assignments and the degree of soft assignment. We select K for subsequent analysis based on a compromise between likelihood fit and posterior entropy (combined with changes in information criteria). To align data-driven latent states with manually assigned stages, we calculate the stage proportion of each latent state k over true stage labels $s \in \{1, \dots, 5\}$ (corresponding to W, N1, N2, N3, REM, respectively) and define stage specificity:

$$P(s|k) = \frac{\sum_{t=1}^T \Gamma_{t,k} \mathbb{I}(g_t = s)}{\sum_{t=1}^T \Gamma_{t,k}} \quad (4)$$

Where $\mathbb{I}(\cdot)$ denotes the indicator function. To avoid inconsistencies in phase interpretations caused by state numbering permutations across subjects and to ensure each phase possesses at least one stable representative latent state at the group level, we employ a purity-anchoring strategy to construct phase-specific state groups:

$$K_s = \{k \in \{1, \dots, K\} : \arg\max_{s \in \{1, \dots, 5\}} P(s|k) = s\} \quad (5)$$

Furthermore, we aggregate the continuous latent state weights into window-level soft evidence for classification. After partitioning the entire sequence into windows ω ($\omega = 1, \dots, W$), the soft evidence for classification s in window ω is defined as follows:

$$x_\omega(s) = \frac{1}{|\omega|} \sum_{t \in \omega} \sum_{k \in K_s} \Gamma_{t,k} \quad (6)$$

where $|\omega|$ denotes the number of time points within the window. This yields the phased soft evidence vector $x_\omega = [x_\omega(1), \dots, x_\omega(5)]$ for each window, which is used for subsequent construction of the PEB secondary covariates.

spDCM effective connectivity estimation

We partition the four-node ROI time series into overlapping sliding windows and use spDCM to fit the cross-spectral density in the frequency domain for each window to estimate directional effective connectivity (Razi et al., 2015). Each window outputs a window-level effective connectivity matrix $A_\omega \in \mathbb{R}^{4 \times 4}$ which serves as the dependent variable input for subsequent PEB analysis.

PEB Hierarchy Inference

At the individual level, we treat the effective connectivity parameter of each window (quantified by A_ω) as an observation variable and use the window-level soft phasing evidence x_ω as a regression covariate. Within the PEB framework, we establish a linear model for window-level connectivity parameters:

$$\theta_\omega = X_\omega \beta + \varepsilon_\omega \quad (7)$$

Here, θ_ω denotes the connectivity parameter vector for window ω , X_ω represents the design matrix row constructed from x_ω (including the constant term and phase-specific covariates), β corresponds to the regression coefficients, and ε_ω is the residual term. Subsequently, hierarchical PEB aggregation inference is performed at the group level to obtain phase-specific connectivity modulation effects.

Sliding Window Filtering

To select the window length and stride, we construct model M_1 incorporating periodic covariates and baseline model M_0 containing only constant terms on the candidate combinations. The evidence gain is measured by the difference in variational free energy between the two models:

$$\Delta F = F(M_1) - F(M_0) \quad (8)$$

Select the parameter combination with the maximum ΔF as the final window setting, where $F(\cdot)$ denotes the variational free energy approximation for the corresponding model. This criterion is equivalent to comparing the log-evidence gain of the dynamic state model relative to the static model and has been applied in PEB-based window parameter selection and state-dependent effective connectivity analysis (Zarghami & Friston, 2020).

Experiment

Dataset

The data for this study were obtained from a synchronously recorded EEG-fMRI sleep experiment. Forty-eight participants completed approximately 2 hours of recording during the night (approximately 1:00–3:30 a.m.) after providing informed consent. EEG data were manually staged and annotated by a specialist physician in 30-second epochs.

Data Processing

Resting-state fMRI underwent standardized preprocessing using DPABI (Yan et al., 2016), with confound control and quality screening performed according to recent recommendations regarding the impact of head motion and confound

regression on functional connectivity estimation (Lu & Yan, 2023; Wang et al., 2024). This included temporal correction, head motion correction, spatial normalization, smoothing, and confounder covariate removal. After excluding subjects with excessive head motion, missing data, or poor-quality scans, 34 participants were ultimately included in subsequent analyses. Following preprocessing, we employed the 300-region brain partition proposed by Schaefer et al. (2018) as the fundamental unit of analysis. Functional magnetic resonance imaging blood oxygen level-dependent (BOLD) signals were spatially aggregated within each region to generate regional-level time series. These were further processed through PCA dimensionality reduction and normalization to obtain input features for AR-HMM latent state modeling. Concurrently, for directional effective connectivity analysis, we extracted BOLD time series from four nodes—PFC, HIP-L, HIP-R, and THAL—within individual spaces based on predefined ROI masks. Using the VOI (volume of interest) workflow from the SPM12 toolbox (Statistical Parametric Mapping), we obtained representative signals for each ROI, which served as input feature vectors for spDCM.

Experimental Paradigm

This experiment employed the ssm toolkit from the Linderman laboratory to train the AR-HMM model, setting the AR order to 3. It referenced recent assessments of AR-HMM robustness and practical recommendations for brain state recognition and state transition modeling (Ezaki et al., 2021; Pieramico et al., 2025). The optimal number of latent states was selected by scanning candidate K values and combining likelihood fit with the posterior entropy criterion. Sliding window size and stride were determined based on free energy difference. Both spDCM and PEB were implemented in SPM12, completing window-level spDCM inversion, hierarchical parameter aggregation, and group-level inference to ensure reliability (Novelli et al., 2024).

Evaluation Metrics

This study evaluates the model across three dimensions: model fit, model complexity, and inferential robustness. It employs the log-likelihood of the training data and information criteria (AIC/BIC) to assess the trade-off between model fit and complexity for the AR-HMM and determine the number of latent states K . Period-specificity and purity were used to assess the consistency between latent periods and manually defined periods. Additionally, posterior probability (p) and posterior mean (effect size) were employed to evaluate the interpretive strength and robustness of period-specific soft evidence in modulating effective connections.

Results and Analysis

Window Parameter Selection Results

Given that EEG manual segmentation uses 30 s as an epoch, we fixed the sliding window stride to 30 s to ensure alignment between window-level segmentation evidence and annota-

tion granularity. We then compared the variational free energy difference ΔF across candidate window lengths to determine the optimal window length. As shown in Figure 2, ΔF initially increases with window length before plateauing, reaching a peak at a window length of 120 s. Consequently, subsequent analyses employ a window configuration of 120 s window length and 30 s stride.

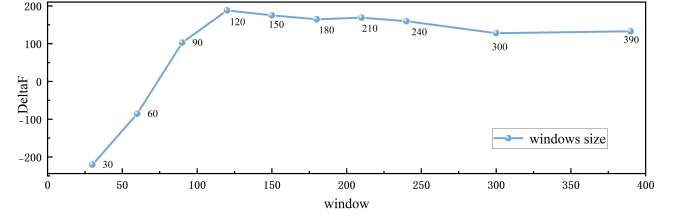


Figure 2: Window size versus relative free energy difference

AR-HMM Modeling Stage-by-Stage Results

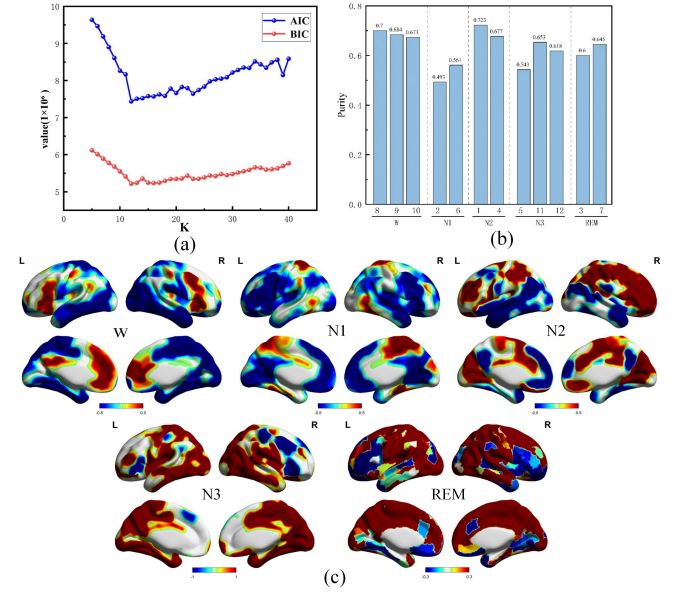


Figure 3: AR-HMM modeling results. (a) Candidate values for the number of hidden states K ; (b) State specificity and screening results; (c) Visualization of specific state groups.

To determine the number of latent states K , we computed the information criteria within the candidate range and selected K as the compromise choice where both AIC and BIC reached their minimum values simultaneously. As shown in Figure 3(a), AIC/BIC initially decreases rapidly with increasing K , then flattens before rising again: excessively small K merges distinct developmental segments, failing to capture pentaphasic differences; excessively large K tends to redundantly describe the same phase, producing low-purity states while increasing complexity and computational burden. Balancing both criteria, we ultimately selected $K=12$ for subsequent analysis. At $K=12$, we calculated the stage specificity of each latent state and grouped them into stage-specific state clusters. Figure 3(b) shows that this state organization aligns

with the five-stage structure: each stage corresponds to at least one highly specific state, while allowing multiple states within the same stage to capture subtle internal variations rather than being compressed into a single state.

To examine the spatial interpretability of the phase-specific state groups, we projected the observed means of each latent state back onto the Schaefer300 network and aggregated them within the same phase state group to obtain phase-averaged activation distributions. Visualizations highlight only the strongest components of positive and negative changes to emphasize key features. Figure 3(c) reveals distinct spatial patterns across five stages: W shows heightened differences in higher-order associative regions, with default network-related areas relatively enhanced while attention and control-related areas are relatively weakened, reflecting the relative equilibrium between internal thought and external orientation regulation during wakefulness (Daneault et al., 2021; Yang et al., 2024). N1 exhibits opposite activation patterns between primary sensory cortex and subcortical structures like thalamus and basal ganglia. N2 shows more extensive and structurally consistent distributions, highly overlapping with known fMRI patterns associated with sleep spindles, reflecting coordinated changes across multiple associative networks (Fernandez & Lüthi, 2020; Li et al., 2024). The N3 stage is characterized by overall widespread attenuation, with more pronounced reductions in regions such as the frontal and insular cortex, while retaining some localized enhancements. This aligns with the global downregulation and local retention pattern typical of slow-wave sleep stages (Houldin et al., 2021). During REM sleep, while retaining the background configuration, localized differential enhancements emerge. Changes in posterior cortical and limbic-related regions become more pronounced, indicating that REM sleep does not simply revert to wakefulness-like patterns but maintains a distinct reorganization scheme (Yang et al., 2024). In summary, this state group provides interpretable, quantifiable spatial staging representations based on temporal alignment, laying the groundwork for subsequent window-level covariate construction and stage-dependent effective connectivity analysis.

spDCM fitting results

We employed sliding window spDCM to fit each phase window in the frequency domain, yielding the autocorrelation (dashed lines) and cross-correlation (solid lines) for the four nodes, as shown in Figure 4. Nodes 1–4 correspond to PFC, HIP-L, HIP-R, and THAL, where (i,j) denotes spectral association from j to i. Overall, autocorrelation significantly exceeds cross-correlation, with energy concentrated between 0.01–0.04 Hz. Each stage exhibits low-frequency modulated sequences deepening with sleep progression: W shows a moderate low-frequency peak with gradual attenuation; N1 exhibits elevated and more dispersed peaks; N2 demonstrates the most pronounced low-frequency enhancement with clearer autocorrelation separation; N3 maintains a strong main peak with more converged high-frequency tails; REM shows overall decline, though some cross-correlations retain

low-frequency differences. This frequency-domain fitting supports subsequent PEB testing to identify stage-dependent changes in functional connectivity.

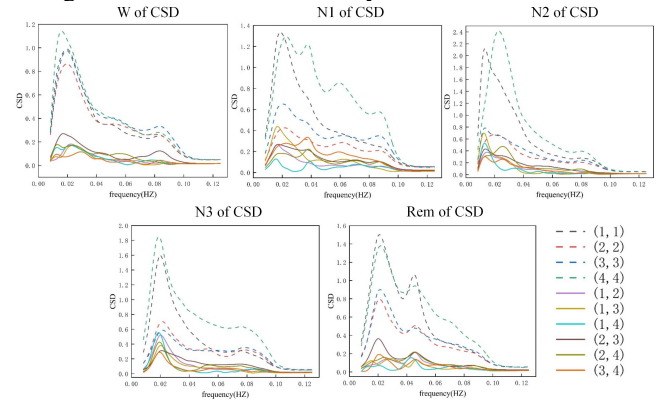


Figure 4: Five-stage mutual spectrum and self-spectrum fitting results

Modulation results inferred by PEB

Figure 4 summarizes the effective connectivity modulation results across four-node networks during five sleep stages, reporting only robust effects—positive modulation with posterior probability $P > 0.95$ and negative modulation with $P < 0.05$. Arrows indicate modulation strength in corresponding stages and directions (positive values indicate enhancement, negative values indicate attenuation). Overall, network modulation exhibits an ordered transition from cortical dominance to thalamic-hippocampal axis dominance across stages. During wakefulness (W), outward drive from the PFC is most prominent, while THAL maintains baseline coupling with HIP-L and HIP-R, reflecting more pronounced top-down regulation. During the sleep onset transition (N1), significant modulation shifts from PFC-centric to pathways associated with THAL and bilateral hippocampi, with PFC-related modulation relatively diminishing, suggesting the initiation and strengthening of gating circuits. During stable sleep (N2), bidirectional interactions between THAL and HIP-L/HIP-R further intensify, with HIP-L and HIP-R exhibiting more consistent coupling. This is accompanied by coordinated adjustments in autoconnectivity at key nodes, indicating the network enters a more stable state of gating and medial temporal lobe coordination (Staresina et al., 2023). During deep sleep (N3), modulation effects are most concentrated and pronounced, primarily affecting THAL–hippocampal pathways and hippocampal autoconnections. This points to intrinsic circuit reorganization against a slow-wave background and stronger suppression of external inputs (Staresina et al., 2023; Ngo et al., 2023). During REM sleep, robust modulation persists in a few key pathways, though overall intensity declines compared to N3. This manifests as weakened THAL gating alongside selectively enhanced hippocampal-related pathways, suggesting persistent selective interactions with medial temporal lobe processing despite reduced gating.

This information flow migration manifests as predominantly cortical-dominated processing during wakefulness and

sleep onset, significantly enhanced thalamic-hippocampal axis activity during stable sleep, and reduced thalamic gating with preserved hippocampal-related selective interactions during REM sleep. This phasic pattern aligns with the classical framework of offline information processing and memory consolidation during sleep. Stable sleep phases, often associated with spindles and slow waves, feature enhanced thalamic gating and hippocampal-cortical interactions, potentially providing neural conditions for reactivation and integration

of memory traces. During REM sleep, despite overall reduced gating, the preservation of hippocampal-dominant selective interactions may correspond to a tendency toward further reorganization and integration of existing representations. Thus, the observed stage-dependent directional reorganization of information flow may constitute indirect network-level evidence for sleep-dependent memory consolidation and support characterizing offline memory processing from an information flow perspective.

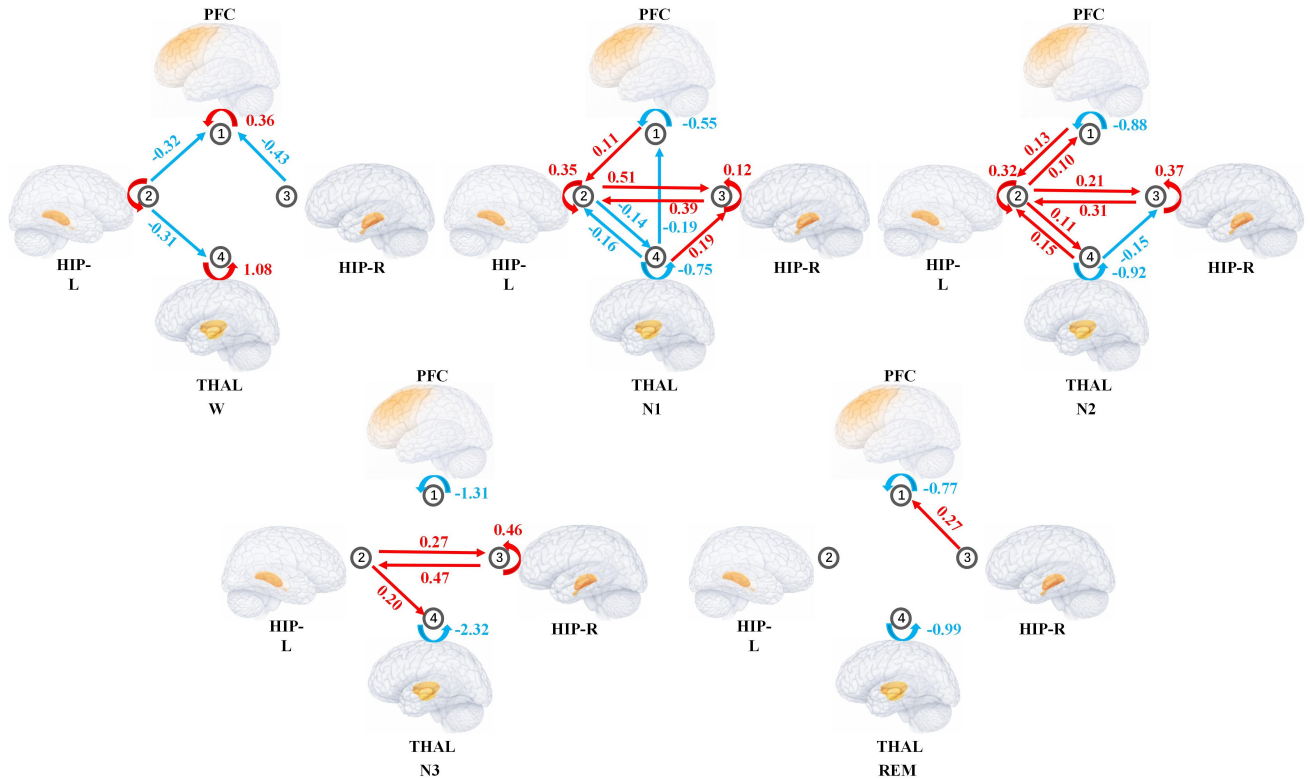


Figure 5: Modulation Results for Five-Phase Four-Node Effective Connections

Conclusion

This study focuses on the directional remodeling of key hub circuits during sleep stage transitions. We constructed a stage-dependent effective connectivity analysis framework centered on nodes including the prefrontal cortex (PFC), thalamus (THAL), and bilateral hippocampus (HIP-L/HIP-R). Under a unified model integrating data-driven stage evidence and directional networks, we characterized stage-specific modulation patterns across five sleep stages. Results indicate that effective connectivity within this circuit undergoes directional, structured dynamic reparameterization throughout sleep: during wakefulness and sleep onset, outward regulation from the PFC is more prominent; during stable sleep stages, the modulation focus shifts to the thalamus-hippocampus axis, particularly manifesting in robust enhancement and reorganization of thalamic and bilateral hippocampal-related pathways during N2/N3; during REM sleep, overall

connectivity amplitude declines but selective hippocampal-related pathways remain preserved. These findings provide a network-level quantitative characterization of the coordinated switching between thalamic gating, cortical regulation, and hippocampal processing across sleep depths. Furthermore, this stage-dependent information flow migration aligns with memory consolidation frameworks: enhanced thalamic-hippocampal coupling and bilateral hippocampal synchronization during stable sleep stages may facilitate memory trace reactivation and integration. The persistence of hippocampal-related selective interactions during REM sleep despite reduced gating may correspond to further representational reorganization. Thus, this study provides quantifiable candidate network phenotypes for sleep-dependent memory processing. Future work will validate reproducibility using larger samples and more complete overnight recordings, while integrating memory behavior and multimodal physiological features to extend findings to larger circuit scales, thereby enhancing mechanistic interpretation and potential clinical applicability.

Acknowledgments

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