

High-Frequency Activity in Scalp EEG Validated by Concurrent Intracranial EEG During Working Memory

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Abstract

Background

Reliable neural markers of cognitive processing support objective cognitive assessment and rehabilitation. High-frequency (HF) activity recorded with intracranial EEG (iEEG) is a well-established marker of local cortical processing, yet whether HF signals measured non-invasively from scalp EEG reflect underlying neural activity remains controversial.

Methods

We examined the physiological validity of scalp HF activity using simultaneous scalp EEG and iEEG from nine subjects performing a verbal working memory (WM) task. Using spatial-spectral and connectivity analyses, we characterized scalp HF responses (60–120 Hz) and quantified their crossmodal correspondence with intracranial HF broadband activity across WM phases and memory loads. We further extracted iEEG-informed features using scalp EEG and implemented a knowledge distillation framework in which intracranial signals guided non-invasive EEG WM decoding.

Results

Scalp HF activity exhibited robust task-dependent modulation and significant concordance with intracranial HF dynamics, particularly during WM retrieval over frontal, temporal, and parieto-occipital regions. Additionally, scalp HF activity increased with task difficulty across multiple EEG electrodes within these regions. Cross-modal coherence analyses revealed phase- and region-specific synchronization between EEG and iEEG signals, with the strongest coherence observed between frontal scalp electrodes and entorhinal cortex, as well as between temporal–parietal scalp electrodes and hippocampal regions during retrieval. Scalp EEG exhibited distinct alpha–HF coupling patterns, with enhanced parietal coupling during maintenance and frontal coupling during retrieval. WM decoding achieved a LOSO accuracy of $90 \pm 10\%$ (AUC = 0.93) using iEEG, and $74 \pm 13\%$ (AUC = 0.79) using scalp EEG, with HF-related features contributing most strongly in both modalities. Importantly, incorporating intracranial representations through a knowledge distillation framework improved EEG-based decoding performance to $80.1 \pm 7.6\%$ (AUC = 0.88), highlighting the feasibility of the proposed iEEG-guided cross-modal learning framework.

Conclusion

Our findings provide direct physiological evidence that task-related scalp HF activity reflects underlying cortical processing. This work establishes a cross-modal framework for validating non-invasive HF biomarkers using intracranial ground truth, highlights the importance of investigating higher-frequency

EEG signals beyond conventional frequency bands, and demonstrates the potential of iEEG-guided learning to improve interpretable EEG-based cognitive decoding, with potential applications in cognitive and broader neurorehabilitation.

Introduction

Non-invasive electroencephalography (EEG) remains one of the most widely used tools for studying human brain function due to its accessibility and high temporal resolution. These advantages have also supported its use in neurorehabilitation, where EEG can provide objective measures of neural function for assessing cognitive and motor processes and developing brain–computer interface (BCI)-based applications(1). However, its limited spatial specificity and susceptibility to volume conduction have historically constrained its ability to capture fine-grained neural dynamics, particularly in the higher-frequency range over 60 Hz(2–4). In contrast, intracranial EEG (iEEG, including SEEG and subdural grids) provides direct measurements of cortical activity with superior spatial resolution and signal fidelity, enabling robust characterization of high-frequency (HF) broadband (typically 70–180 Hz; also referred to as HFB) activity associated with local neuronal population firing and functional activation(5, 6), exhibiting greater spatial specificity and sensitivity to higher-order cortical engagement than lower-frequency event-related desynchronization measures(7, 8).

A central challenge in translating EEG measures to clinical applications is establishing a reliable correspondence between scalp EEG signals, particularly in the HF range, and their underlying neural sources. This is especially critical for neurorehabilitation, where repeated assessment and training demand physiologically valid, non-invasive, affordable, and stable neural measures suitable for longitudinal and potentially day-to-day use beyond clinical settings(9). While recent studies have shown evidence that under certain circumstances scalp HF signals (for example, high-frequency oscillations in epilepsy patients, also known as HFOs) are detectable (10–14), these scalp-detected events have not been validated or correlated with their cortical sources. Such cross-modal validation is critical for advancing EEG-based biomarkers and enabling reliable non-invasive neural decoding for applications including localization of epileptogenic zones for surgical planning, identification of eloquent cortex, BCIs, fine motor decoding, and neurorehabilitation.

Emerging evidence suggests that functional task engagement, such as motor execution and cognitive processing, induces localized increases in high-gamma and HF broadband power and modulates large-scale neural synchronization(7, 15–17). By eliciting robust and spatially specific HF responses, task paradigms may improve the detectability and interpretability of HF neural activity, providing a unique opportunity to investigate its cross-modal correspondence across scalp EEG and intracranial recordings. However, whether and to what extent task-induced HF activity measured by scalp EEG reflects underlying intracranial dynamics remains an open question. While a few recent studies have demonstrated correlations between EEG and iEEG in lower-frequency bands (e.g., alpha, beta rhythms)(18–20), the relationship in the HF range remains poorly understood due to signal attenuation, spatial smearing, and contamination from non-neural sources.

In this study, we investigate the hypothesis that functional tasks induce measurable HF correspondence between scalp EEG and intracranial EEG, enabling cross-modal validation of non-invasive neural signatures. To keep consistency, we use the term HF response or activity for both iEEG and scalp EEG modalities. Using simultaneous EEG–iEEG recordings in subjects undergoing clinical monitoring, we systematically quantify task-related HF activity and assess cross-modal relationships through spectral, spatial, and connectivity-based analyses. Specifically, we examine (1) cross-modal correspondence of HF power between scalp EEG and concurrent iEEG, (2) EEG–iEEG coherence, (3) phase- and amplitude-based coupling of HF activity in both modalities, and (4) working memory (WM) decoding using temporal, spectral, and connectivity features extracted from full-band and HF activity. Finally, we implemented a teacher–student knowledge distillation (KD) framework in which iEEG-derived representations guided EEG-based decoding to determine whether invasive neural signals can improve non-invasive decoding performance.

By systematically characterizing task-induced cross-modal relationships, this work aims to bridge the gap between invasive and non-invasive electrophysiology and provide a multimodal framework for physiologically validating HF EEG-based cognitive signatures. Our findings demonstrate the potential utility of HF EEG for non-invasive cognitive assessment and decoding, providing a foundation for future applications in cognitive rehabilitation and broader neurorehabilitation.

Materials and Methods

Dataset and Participants

This study utilized a publicly dataset available at [https://doi.org/10.6084/m9.figshare.11500485.v2\(21\)](https://doi.org/10.6084/m9.figshare.11500485.v2(21)). The dataset includes simultaneous scalp EEG and iEEG recordings from nine human subjects undergoing clinical monitoring for drug-resistant epilepsy. Intracranial EEG signals were acquired at 4 kHz from depth electrodes implanted primarily in medial temporal lobe (MTL) structures as part of clinical evaluation, while concurrent scalp EEG was recorded at 256 Hz using standard clinical electrode configurations following the international 10–20 system. The present study involved secondary analysis of de-identified data.

Participants performed a modified verbal WM task consisting of fixation, encoding, maintenance, and retrieval phases. During each trial, after a 1 s of fixation period, subjects were presented with a sequence of 4, 6, or 8 letters to memorize (encoding, 2 s), followed by a delay period (maintenance, 3 s), and subsequently probed to determine whether a test letter belonged to the previously presented set (retrieval, 2 s). Task paradigm, intracranial electrode locations, and study design are summarized in Fig. 1.

Signal Preprocessing

All preprocessing was performed using MATLAB platform. Intracranial EEG data were bandpass filtered between 1–500 Hz to preserve high-frequency content in the high-frequency broadband range (HFB; 70–180 Hz). Line noise was removed using notch filtering at 50 Hz and its harmonics. Signals were re-referenced using common average reference (CAR) method. Scalp EEG data were preprocessed using standard procedures. Specifically, signals were notch filtered at 50 Hz and its harmonics and then were re-referenced to CAR. Independent component analysis (ICA) was applied to identify and remove components associated with ocular, cardiac, and line noise artifacts; ICA was implemented conservatively to minimize attenuation of high-frequency signals. Channels exhibiting excessive noise or flat signals were excluded based on human inspection of the raw data.

To minimize contamination from pathological activity, epileptogenic channels and events were identified using a validated in-house automated pipeline for HFO detection and SOZ localization(22–24). Briefly, iEEG signals were temporally converted to bipolar montage and processed using an RMS-based detector to identify candidate high-frequency events. Events exhibiting isolated high-energy “bulb-like” signatures relative to background activity seen from the time-frequency (T-F) map and meeting standard HFO criteria (defined as oscillatory waveforms with at least four consecutive cycles and durations of 20–100 ms following > 80 Hz filtering) were automatically detected and marked. Automated detections were further processed using a DBSCAN-based clustering approach to evaluate morphological similarity and ensure that the identified HFOs were associated with epileptic spikes or sharp waves. The resulting detections were subsequently cross validated against clinically annotated SOZ information. Electrodes with frequent interictal spikes or HFOs that overlapped with the clinically defined SOZ were excluded from further analysis.

Evaluation of Task-induced Intracranial and Scalp Response

For both scalp EEG and iEEG, task-induced power change was evaluated in HF band (60–120 range were inspected for scalp EEG, referred to as scalp HF response in this study; 70–180 Hz HFB range for iEEG) using signal recorded from all channels during the four WM phases in each subject. For iEEG HF response calculation, the data were filtered using 10 Hz non-overlapping windows (two-way, zero-lag, 64th-order FIR filters), and the instantaneous amplitude was derived by computing the signal modulus after applying the Hilbert transform. We took the z-score of the signal in each 10-Hz band and divided these power-time series by the signal within the same frequency band during the 200 ms pre- stimulus period to evaluate the task-induced power augmentation relative to baseline. The standardized amplitude-time series were averaged together to obtain an overall estimation of the power change in the HF broadband and to avoid the power-law decay in the high band. This evaluation was performed across all four WM phases and memory loads (4, 6, and 8 items) for both EEG and iEEG modalities.

EEG and iEEG Cross-Modal Correspondence Analysis

To evaluate both iEEG–EEG synchronization and cross-frequency interactions, several connectivity metrics were computed. Cross-modal spectral coherence was quantified using multitaper magnitude-squared coherence across the theta, alpha, beta, gamma, and HF bands to assess frequency-specific synchronization between scalp and intracranial signals. For signals $x(t)$ and $y(t)$, coherence at frequency f was defined as:

$$C_{xy}(f) = \frac{|S_{xy}(f)|^2}{S_{xx}(f) S_{yy}(f)}$$

1

,

where $S_{xy}(f)$ is the cross-spectral density and $S_{xx}(f)$, $S_{yy}(f)$ are the corresponding auto-spectral densities. Coherence values range from 0 to 1 and reflect the consistency of phase and amplitude relationships across time.

T-F coherence analyses were performed using sliding-window spectral decomposition:

$$C_{xy}(t, f) = \frac{|S_{xy}(t, f)|^2}{S_{xx}(t, f) S_{yy}(t, f)}$$

2

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T-F coherence enabled identification of temporally localized synchronization patterns associated with different WM stages and cognitive demands.

Phase–amplitude coupling (PAC) was used to evaluate cross-frequency interactions between low-frequency oscillatory phase and high-frequency activity within each modality. Low-frequency components were extracted using bandpass filtering followed by Hilbert transformation to obtain instantaneous phase, while HF activity was transformed into amplitude envelopes.

Feature extraction

To examine the temporal-spectral features from scalp HF EEG signals, we extracted both classical descriptors and specialized HF-focused features informed by the characteristics of iEEG HF broadband activity and empirical data inspection. Feature Group 1 are classical EEG descriptors including the peak amplitude, spectral centroid, sub-band power, and statistical moments (mean, variance, skewness, kurtosis) computed from wavelet decomposition across six sub-bands. Feature Group 2 are iEEG HF-informed features(24) including (1) sub-band power ratio: the ratio of the signal power in the presumed high-band to the power in low band using the periodogram, computed as $R = \frac{P_{[60 \sim 180Hz]}}{P_{[4 \sim 30Hz]}}$; (2) high-band

ERS; (3) high-band spectral entropy defined as $H = - \sum_f f \log [s(f)]$, where $s(f)$ represents the normalized signal spectral representation derived from the denoised T-F map; (4) short-time line length: computed from the high-pass filtered signal (> 60 Hz): $D = \frac{\log_{10}(N)}{\log_{10}(\frac{d}{L}) + \log_{10}(N)}$, where L denotes the sum of distances between successive points, and d is the distance between the first point of the sequence and the point of the sequence that provides the farthest distance; (5) relative peak amplitude: defined as the ratio of local maxima to a threshold derived from the trial envelope after applying an 60 Hz high-pass filter; (6) peak-to-notch energy ratio: we identify the HF spectral peak (> 60 Hz) and the nearest spectral notch (local minimum) within 30 Hz below the peak frequency, the energy ratio E_p/E_n serves as an indicator of spectral sharpness; and (7) cross-frequency modulation quantified by PAC: for each trial, PAC is computed between α to HF pairs. This procedure yielded a total of 40 features. Feature values were compared between the retrieval and fixation phases to identify task-related modulations.

IEEG informed EEG-decoding framework

We employed a graph-based learning framework to classify WM task conditions from both EEG and iEEG by integrating spectral-temporal features with graph convolutional networks (GCNs). For each trial, EEG signals were transformed into channel-wise feature representations, each trial was represented as a feature matrix $X \in \mathbb{R}^{N \times F}$, where N is the number of channels and $F = 40$ is the number of features. Functional connectivity was defined using a HF band focused connectivity measure. Specifically, analytic signals of the HF components (60–120 Hz for EEG, 70–180 Hz for iEEG) were extracted using the Hilbert transform. Instantaneous power time series were computed as the squared magnitude of the analytic signal. The resulting adjacency matrix $A \in \mathbb{R}^{N \times N}$ was symmetrized (via absolute value), self-connections were removed, and the matrix was normalized as:

$$\tilde{A} = D^{-1/2} (A + I) D^{-1/2}$$

3

where D is the degree matrix and I is the identity matrix.

Each trial was thus modeled as a graph $G = (X, \tilde{A})$, which served as input to a two-layer GCN. The graph convolution operation at layer l is defined as:

$$H^{(l+1)} = \sigma \left(\tilde{A} H^{(l)} W^{(l)} + b^{(l)} \right)$$

4

where $H^{(l)}$ is the node representation at layer l , $W^{(l)}$ and $b^{(l)}$ are learnable parameters, and $\sigma(\cdot)$ denotes a nonlinear activation function (ReLU). The network consisted of two graph convolution layers

(with 64 and 32 hidden units, respectively), followed by global mean pooling:

$$z = \frac{1}{N} \sum_{i=1}^N H_i^{(2)}$$

5

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which aggregates node-level embeddings into a graph-level representation. The pooled representation was then passed to a fully connected classifier to produce logits for task classification.

Finally, we sought to determine whether concurrently recorded iEEG signals provide complementary physiological information that could facilitate neural decoding of the WM task. To address this question, we implemented a knowledge distillation (KD) framework in which the iEEG model served as a “teacher” to guide learning of an EEG-based “student” model(25). the teacher model was first trained using iEEG-derived neural features in the HF band. The EEG student model was subsequently optimized not only to predict task labels from scalp EEG input, but also to align with informative representations learned by the iEEG teacher. The iEEG teacher model was first trained independently to generate class probability distributions for each trial. These teacher probabilities, p_T , were aligned with the corresponding EEG trials and used as soft targets during student training. The EEG student was optimized using a combined objective consisting of conventional supervised cross-entropy loss with the ground-truth task labels and a KD loss that encouraged the student’s softened output distribution to match the teacher’s output distribution.

The hard-label cross-entropy loss was defined as:

$$\mathcal{L}_{CE} = -\frac{1}{N} \sum_{i=1}^N \sum_{c=1}^C y_{i,c} \log p_{S,i,c},$$

6

where N is the batch size, C is the number of task classes, $y_{i,c}$ is the one-hot class label, and $p_{S,i,c}$ is the student-predicted probability for class c .

For KD, teacher probabilities were softened using a temperature parameter τ :

$$q_{T,i,c} = \frac{p_{T,i,c}^{1/\tau}}{\sum_{k=1}^C p_{T,i,k}^{1/\tau}},$$

7

and student logits z_S were similarly softened:

$$q_{S,i,c} = \frac{\exp(z_{S,i,c}/\tau)}{\sum_{k=1}^C \exp(z_{S,i,k}/\tau)}.$$

8

The distillation loss was computed as the Kullback–Leibler divergence between the softened teacher and student distributions:

$$\mathcal{L}_{KD} = \frac{1}{N} \sum_{i=1}^N \sum_{c=1}^C q_{T,i,c} \log \frac{q_{T,i,c}}{q_{S,i,c}}.$$

9

The final training objective was:

$$\mathcal{L} = (1 - \alpha) \mathcal{L}_{CE} + \alpha \tau^2 \mathcal{L}_{KD},$$

10

where α controls the relative contribution of teacher guidance and τ controls the softness of the probability distributions. In this study, we used $\alpha = 0.6$ and $\tau = 3$.

Training was performed in a LOSO framework. For each fold, trials from all non-held-out subjects were used for KD pretraining of the EEG student with iEEG teacher supervision. For the held-out subject, a small subset of trials was used for EEG-only fine-tuning, and the remaining trials were reserved for testing. The student model was first trained for 100 epochs using the combined KD objective and then fine-tuned for 30 epochs using only the supervised cross-entropy loss. This two-stage procedure allowed the EEG model to learn physiologically informed representations from the iEEG teacher.

Ablation Analysis

To quantify the relative contribution of individual features to decoding performance, a feature ablation analysis was performed separately for EEG and iEEG models. Starting from the full feature set, each feature was removed individually and the resulting change in decoding accuracy under LOSO cross-validation was measured. Feature importance was defined as the decrease in model performance following feature removal, with larger reductions indicating greater contributions to decoding. The relative contribution of each feature was subsequently normalized to percentage values.

Statistical Analysis

Connectivity and coupling measures were computed separately for each trial and task phase. Task-wise statistical comparisons were subsequently performed across task phases. A pairwise Wilcoxon sign rank test was performed between each pair of conditions. Workload-dependent modulation was

assessed by correlating scalp HF responses with WM load (set sizes 4, 6, and 8) using a Pearson correlation test. In addition, HF power differences between workload conditions were also assessed using a nonparametric permutation test with 5,000 random permutations. Statistical significance was determined at each time point, and consecutive significant time points were grouped into temporal clusters. Cluster duration and the minimum permutation-derived p value for each cluster are reported.

For coherence estimated using the multitaper method, significance at each frequency bin was determined using the theoretical 95% confidence limit. For wPLI, PAC analyses, nonparametric permutation testing was performed. Surrogate null distributions were generated by randomly shuffling trial labels or temporal relationships, and empirical p -values were estimated by comparing observed measures against permutation-derived null distributions. Same test were also applied to HF power-time course analyses to identify significant task-related power modulations over time. Significance of T-F coherence was assessed using a time-shift surrogate procedure, in which one signal was circularly shifted relative to the other to generate a null distribution while preserving the temporal and spectral structure of each channel. Coherence values exceeding the surrogate distribution threshold ($p < 0.01$) were considered significant.

For classification analyses, decoding performance metrics including accuracy, F1 score, and AUC were computed separately for each subject. Statistical comparisons between decoding approaches were performed using paired Wilcoxon signed-rank tests across subjects.

Results

Electrode Localization

Patient demographic data and clinical characteristics are presented in Supplementary Tabel S1. As it is shown in Fig. 1, intracranial electrode contacts ($n = 502$) were assigned to regions of interest (ROIs) based on electrode Montreal Neurological Institute (MNI) coordinates and the Automated Anatomical Labeling (AAL) atlas(26). Electrode coverage was concentrated primarily within medial and lateral temporal lobe structures, including the hippocampus ($n = 110$), amygdala ($n = 36$), para-hippocampal cortex ($n = 24$), fusiform ($n = 24$), and lateral temporal regions, including middle temporal gyrus ($n = 211$), inferior temporal gyrus ($n = 36$), superior temporal gyrus ($n = 21$), and temporal pole ($n = 37$). Unlabeled electrodes and ROIs with limited electrode coverage were excluded from subsequent ROI-level analyses to improve robustness of regional estimates.

Epileptic HFOs were detected using an in-house detector(22–24), and channels exhibiting elevated HFO activity were defined as those with HFO rates exceeding two standard deviations above the mean across channels. Using this criterion, epileptic HFOs were identified in approximately 4% of all channels, of which 16 electrodes were located within clinician-defined SOZ. These contacts were excluded from all subsequent analyses.

WM task introduced HF response in both intracranial and scalp EEG

The verbal WM task elicited robust and consistent HF responses in both iEEG and scalp EEG recordings. In Fig. 2 we provide the ROI-based iEEG spatial map and EEG topological map showing the HF activation across the four task phases (i.e., fixation, encoding, maintenance, and retrieval).

For iEEG, the results were aggregated across all electrodes and mapped to anatomical ROIs. HF response exhibits condition- and workload-dependent modulation (Fig. 2A and Supplementary Fig. S1), with encoding and maintenance characterized by stronger left-lateralized activation in temporal and medial temporal regions. During retrieval, activation became more spatially distributed and bilateral, with increased HF responses in right medial temporal structures relative to earlier task stages. Significant workload modulated changes were observed in most of subjects (Supplementary Table S2). Maintenance-related HF workload modulation primarily involved hippocampal and entorhinal contacts. Retrieval-related modulation engaged amygdala contacts in addition to the hippocampus.

In scalp EEG, HF activity was also detectable, albeit with reduced amplitude and power. Overall, scalp HF response patterns demonstrated clear task- and workload-dependent modulation across WM phases. The temporal and spatial profile of scalp HF activity mirrored those observed in iEEG, with transient increases during encoding and retrieval and more sustained activity during maintenance. As shown in Fig. 2B, task-related HF response evolved from relatively local left temporal-occipital activation at baseline to more widespread bilateral central-parieto-occipital activation during retrieval, including C3/C4/Cz, O1/O2, and moderate F3 and Pz electrodes. This pronounced frontal, central and midline-to-posterior activation potentially reflects the increased neural demands associated with memory recall, memory-guided decision making, and motor preparation for behavioral response.

Figure 2C illustrates workload-dependent scalp EEG HF responses in a representative subject (S1) and the group-averaged results at electrode F3 during retrieval phase. The highest workload condition (set size 8) elicited the most pronounced HF activation compared with set sizes 4 and 6. Similar workload-dependent effects were observed bilaterally across frontal, parietal, and occipital electrodes. In Fig. 2D, we present group-level scalp HF magnitudes for four electrodes (F3, F4, P4, O1) that showed significant or near-significant correlations between scalp HF power and WM load. Results for each individual subject is presented in Supplementary Table S3. On individual level, significant scalp HF workload modulation (permutation test, all $p < 0.05$) was observed in 3 participants during maintenance and 4 during retrieval. Maintenance-related effects were primarily localized to frontal electrodes, whereas retrieval-related modulation showed a broader spatial distribution involving frontal, parietal, and occipital electrodes. These findings demonstrate that working memory-related HF activity is not confined to intracranial recordings but can also be detected non-invasively at the scalp level.

Task-induced HF response in scalp and intracranial EEG showed correspondence

We asked whether the scalp detect HF response show spatial-spectral correspondence with the iEEG HF activities during WM processing. Figure 3 demonstrates the HF response in iEEG and scalp EEG, their spatial correlation, and T-F coupling in a representative subject (S1). Spatial mapping of intracranial HF response during retrieval revealed prominent activation within the left temporal pole, right mesial temporal structures, and lateral temporal regions bilaterally. Concurrent scalp EEG demonstrated strong HF modulation over C3, T3, P4, and T6 electrodes (Fig. 3A). In this subject, time-resolved HF broadband power analysis demonstrated temporally aligned task-related modulation between entorhinal electrodes mECL5, mECL6 and scalp C3, T3 (Fig. 3B). Cross-modal T-F coherence analysis revealed time-locked, frequency-specific and spatially selective coupling between intracranial and scalp EEG on a single trial level (Fig. 3C). In this subject significant coherence patterns were observed between mECL6 and temporally proximal scalp electrodes such as C3 and T3 (time-shifted permutation test, FDR-corrected $p < 0.01$).

Figure 4 depicts EEG-iEEG coherence within the HF range (60–120 Hz), averaged across all subjects during fixation and retrieval. In Fig. 4A, each circular plot represents a scalp EEG electrode, with the surrounding nodes correspond to intracranial electrodes arranged according to their anatomical locations. Compared with fixation, the retrieval phase demonstrated increased coherence magnitude and a higher density of cross-modal connections involving F7-left entorhinal, T3-left hippocampal/entorhinal, T4-right hippocampal/entorhinal, T6-right hippocampal, and P4/Pz-right hippocampal. These findings indicate enhanced spatially aligned coupling between scalp-recorded HF activity and intracranial hippocampal and entorhinal sources during WM retrieval. Averaged across scalp–intracranial electrode pairs, HF coherence was significantly increased during retrieval (Wilcoxon paired test $p < 0.01$), indicating stronger cross-modal coupling between intracranial activity and scalp-recorded signals, and that retrieval-related HF activity is more consistently detectable at the scalp level (Fig. 4B).

In Fig. 4C we show the change in EEG-iEEG coherence during memory maintenance and retrieval relative to fixation, averaged across 9 subjects, for both alpha and HF bands. Compared to baseline, WM maintenance produced increased cross modal coherence in alpha over bilateral posterior-temporal and parietal scalp regions, whereas retrieval elicited stronger alpha coherence over frontal and temporal regions. On the other hand, during maintenance, HF coherence changes were generally weak and predominantly negative across the scalp. During retrieval, HF coherence increase was observed over frontal, central and parieto-occipital regions.

We further examined task-related changes in cross-modal phase synchronization between scalp EEG and iEEG using wPLI across theta, alpha, beta, gamma, and HF bands. For each iEEG–EEG channel pair, connections exhibiting significant phase locking (Rayleigh test, $p < 0.01$) were retained. Group-level wPLI differences $\Delta wPLI$ (Retrieval – Fixation) were then computed, results are provided in Fig. 4D. Consistent to coherence results, higher-frequency bands demonstrated pronounced increases in scalp frontal-MTL

coupling, particularly involving frontal F3/F4 and amygdalohippocampal/entorhinal regions (AR, AHR, PHR, ECR), as well as midline–hippocampal coupling (e.g., Cz–PHR). These findings may reflect enhanced prefrontal–hippocampal coordination during memory-guided task execution.

Alpha-HF phase-amplitude coupling during WM

Phase–amplitude coupling (PAC) reflects the coordination between slow oscillatory rhythms and local high-frequency activity, providing a mechanism through which large-scale network dynamics may regulate neuronal processing(27). Given the established role of alpha oscillations in WM(28), we specifically examined alpha–HF PAC using the modulation index (MI) in both scalp EEG and iEEG modalities. For iEEG, PAC values were computed by aggregating posterior hippocampal electrodes (mPHL and mPHR); for scalp EEG, PAC was calculated separately for each electrode. Results are shown in Fig. 5.

Overall, alpha–HF PAC exhibited distinct temporo-spatial patterns across WM phases in both intracranial and scalp recordings. In the posterior hippocampus, PAC strength was greatest during maintenance and decreased during retrieval. At the scalp level, significant phase-dependent modulation of PAC was observed primarily over frontal and parietal regions. Specifically, F7 demonstrated increased coupling during retrieval, whereas Pz exhibited stronger coupling during maintenance (Fig. 5A). Analysis of preferred coupling phase further revealed a pronounced phase preference in posterior hippocampal electrodes during maintenance, while phase locking became less distinct during retrieval (Fig. 5B). Similarly, scalp recordings exhibited stronger phase-specific alpha–HF coupling over frontal electrodes during retrieval and over parietal electrodes during maintenance (Fig. 5C). These findings are consistent with previous studies suggesting that alpha–gamma coupling supports WM maintenance by temporally organizing local high-frequency activity through slower oscillatory gating mechanisms. The enhanced scalp frontal coupling during retrieval may reflect the increased coordination between long-range control processes and local neuronal activation during WM retrieval.

Scalp HF features help WM task decoding

As shown in Fig. 6A, most HF-related features exhibited significant differences during WM retrieval relative to the fixation baseline (paired Wilcoxon signed-rank test, $p < 0.05$), including both conventional features (Group 1) and iEEG-inspired features (Group 2). Using the EEG-based decoding framework, WM states were classified with an accuracy of $74.1 \pm 13\%$ (95% CI: 63.7–84.4%; AUC = 0.79 ± 0.21 ; F1 = 0.75). Notably, removal of all HF-related features reduced EEG decoding accuracy to $56.0 \pm 6\%$. As anticipated, substantially higher performance was achieved using iEEG recordings within the same framework, yielding an accuracy of $90.0 \pm 10\%$ (95% CI: 81.8–98.0%; AUC = 0.93 ± 0.1 ; F1 = 0.89). Feature ablation analyses further revealed that HF-related features, particularly relative peak amplitude, contributed most strongly to decoding performance, with four of the five most informative features in both iEEG and scalp EEG being HF-related (Fig. 6B). These findings indicate that task-related HF activity encodes physiologically meaningful information underlying working memory processing.

Finally, we implemented a knowledge distillation (KD)(25) framework to transfer the rich information from invasive to non-invasive recordings. The KD-enhanced EEG decoder achieved an improved classification accuracy of $80.1 \pm 7.6\%$ (95% CI: 74.2–86.0%; AUC = 0.88 ± 0.07 ; F1 = 0.81), corresponding to a mean accuracy improvement of 6.1% over the EEG-only model. Performance improved in 7 of 9 subjects, with individual gains ranging from 1% to 36%. In addition, the KD-EEG demonstrated more stable cross-subject generalization, as reflected by reduced inter-subject variability and smaller performance standard deviation across LOSO folds (Fig. 6C). These findings suggest that physiologically informed cross-modal learning may improve the performance and robustness of non-invasive HF EEG decoding frameworks.

Discussion

In this study, we demonstrated that task-related high-frequency neural activity recorded with iEEG exhibits measurable correspondence with concurrent scalp EEG during verbal working memory processing, a cognitive domain commonly assessed and targeted in cognitive rehabilitation. Cross-modal analyses revealed task- and workload-dependent, temporally and spatially structured coherence and phase coupling patterns, particularly involving frontal, parietal, hippocampal and limbic regions, suggesting that scalp EEG can capture physiologically meaningful signatures of underlying neural dynamics within the HF range. Furthermore, HF-informed feature representations supported successful non-invasive task decoding. These findings provide evidence that carefully characterized scalp EEG signatures preserve physiologically relevant information from underlying cortical dynamics and may serve as viable biomarkers for non-invasive neural decoding and objective assessment of neural function.

Concurrent EEG-iEEG Recording

Simultaneous scalp EEG and intracranial recordings during cognitive tasks provide a unique opportunity to directly examine the extent to which non-invasive signals reflect underlying cortical activation, thereby enabling the validation of non-invasive biomarkers and the development of improved analytical methods(29). While the original dataset established the feasibility of simultaneous multimodal recordings and validated the relationship between neuronal spiking activity and local field potential dynamics below 30 Hz(21), the present study addresses a distinct translational question regarding the physiological validity of non-invasive scalp-recorded activity, particularly in the underexplored higher-frequency range. Several limitations of this approach should be acknowledged. Intracranial electrode implantation is clinically determined, resulting in incomplete and heterogeneous sampling of cortical regions, and the absence of correspondence between scalp EEG and a given iEEG contact should not be interpreted as evidence that scalp activity lacks a cortical origin. In addition, the relationship between scalp and intracranial recordings is influenced by multiple biophysical factors, including source depth, cortical geometry, spatial extent, synchronization, and volume conduction. Intracranial implantation may itself alter signal transmission through potential breach effects associated with burr holes and lead trajectories, further complicating the interpretation of direct correspondence between the two

modalities. Nevertheless, simultaneous scalp EEG and intracranial recordings provide the closest available physiological ground truth for understanding how cortical activity is represented at the scalp. By integrating multiple complementary analyses and demonstrating consistency across these independent measures, we provide converging evidence supporting the physiological relevance of scalp-recorded HF activity during WM. Future studies with larger cohorts, broader cortical sampling, and subject-specific forward modeling will further refine the quantitative relationship between intracranial and scalp HFB signals and improve the generalizability of these findings.

Task-induced HF activity in EEG

HF activity above the conventional gamma range (> 60 Hz) in scalp EEG has historically received limited attention because of concerns regarding contamination from cranial muscle activity, ocular artifacts, and volume conduction effects, as well as uncertainty regarding whether HF neural signals can be reliably detected through the skull(4, 30, 31). In contrast, intracranial studies have consistently demonstrated that HF broadband activity closely reflects local cortical processing, neuronal firing, and cognitive functions including WM(32–36). Studies investigating functional scalp high-band activity, however, have reported conflicting findings. While a few reports have identified task-related gamma or high-gamma responses associated with sensory, motor, and cognitive processing(37, 38), others have argued that much of the observed scalp HF activity may originate from non-neural sources such as microsaccades or muscle artifacts(4, 39). These discrepancies likely arise from the inherently low amplitude of task-related HF signals, their broad spatial distribution across functional networks, and importantly, the lack of direct physiological validation. Compared with scalp HFOs reported in epilepsy, functional HF activity is generally weaker and less spatially focal, making its detection substantially more challenging.

By combining simultaneous scalp EEG and intracranial recordings, the present study provides direct cross-modal evidence that cognitively relevant scalp HF activity reflects underlying cortical dynamics. The observed spectral, spatial, and functional correspondence above 60 Hz suggests that at least a subset of scalp HF signals has a physiological origin, supporting their inclusion in future studies of cognition and brain function rather than their routine exclusion as noise. Importantly, cross-modal coherence and phase-amplitude coupling were strongest during retrieval, particularly between frontotemporal-entorhinal and temporoparietal-hippocampal EEG-iEEG pairs, suggesting that retrieval engages coordinated interactions between distributed cortical and MTL memory networks which are reflected across both intracranial and scalp recordings. These observations are consistent with intracranial studies demonstrating encoding- and retrieval-related HF broadband increases within distributed frontotemporal and medial temporal networks(40–42), as well as EEG studies reporting task-dependent posterior gamma modulation during memory processing(43, 44). Moreover, the observed EEG–iEEG correspondence was both spatially and frequency specific, with the strongest relationships involving frontotemporal-parietal regions implicated in verbal WM, arguing against a purely nonspecific or artifactual origin of the observed HF activity.

HF in relation with alpha during WM

HF activity is widely regarded as an index of local cortical activation and information processing. Consistent with this framework, we observed significantly stronger HF activation during retrieval than during maintenance, suggesting that retrieval engages broader cortical recruitment and stronger cross-modal coupling between intracranial and scalp recordings. These findings further suggest that cognitively demanding task states may provide a more effective paradigm for validating scalp HF biomarkers than resting-state recordings by enhancing the detectability of physiologically relevant cortical activity. This retrieval-dominant HF response contrasts with the well-established role of alpha oscillations during WM, which typically increase during the maintenance period and are thought to reflect functional inhibition and suppression of task-irrelevant information(28, 45, 46). In contrast, HFB activity has consistently been linked to active information processing, attentional engagement, and task execution. Our observation of workload-dependent scalp HF activity extends this framework, suggesting that HF activity indexes the recruitment and strength of cortical representations as mnemonic demand increases. Collectively, these findings support the growing view that low-frequency oscillations coordinate large-scale network interactions, whereas HF activity reflects local cortical computations during WM(27, 47, 48). The observed HF–alpha coupling provides further support for this hierarchical organization. Previous MEG and intracranial studies have shown that alpha phase modulates the amplitude of higher-frequencies, enabling both local cortical computation and long-range communication across frontal, temporal, and occipital regions(49, 50). Our findings are consistent with this model and suggest that alpha-band synchronization may regulate the timing of local HF activation during verbal WM. Such dynamic cross-frequency interactions may facilitate flexible transitions between sensory disengagement, memory stabilization, and retrieval, consistent with recent evidence that alpha oscillations adapt to task structure, encoding demands, and memory stage(45, 46, 51, 52).

Scalp HF features and neural decoding

The importance of HF-related spatial–spectral features for cognitive state decoding was also demonstrated through both feature ablation analyses and a novel iEEG-guided KD framework. KD approaches have been increasingly adopted in neurophysiological applications, including EEG-based emotion recognition(53), sleep staging(54), and depression detection(55) where knowledge from richer or multimodal representations is transferred to a more practical unimodal model to improve performance and generalizability. Existing KD frameworks largely focus on transferring information between behavioral or non-invasive physiological measures that offer complementary information. In contrast, our framework employs intracranial recordings as the teacher model, providing a unique source of physiologically grounded supervision. Because iEEG provides a more direct and spatially specific measure of cortical activity than scalp EEG, the transferred knowledge enables the EEG model to learn task-relevant neural signatures that better reflect the underlying cortical dynamics. The observed improvement in decoding performance suggests that intracranial activity contains latent task-relevant information that is only partially accessible from scalp recordings, and that KD can help bridge this gap. We recognize that the clinical use of iEEG is inherently limited to specific patient populations, restricting

the access to very large-scale datasets. Nevertheless, the framework proposed here demonstrates how invasive recordings can be leveraged to improve non-invasive neural decoding and may serve as a foundation for future studies employing larger concurrent EEG–iEEG datasets with standardized acquisition protocols. Such efforts could facilitate the development of more generalizable and interpretable EEG-based biomarkers and decoding frameworks that can be applied beyond clinical populations.

Potential influence of epilepsy pathology

We are mindful that the potential influence of epilepsy pathology on the observed HFB responses should be considered. In the current study, electrodes exhibiting frequent interictal spikes and/or pathological HFOs within the SOZ were excluded from the primary analyses. Consequently, the reported HF activity was derived primarily from non-pathological recordings and is more likely to reflect physiological task-related responses. Nevertheless, epilepsy-related functional reorganization cannot be completely excluded. In particular, altered recruitment of medial temporal structures has been reported in patients with mesial temporal epilepsy, especially in the presence of hippocampal dysfunction(56). Such reorganization could potentially contribute to the right-lateralized HF responses observed during retrieval. However, this explanation is unlikely to fully account for the present findings because the cohort was predominantly composed of patients with right mesial temporal epilepsy (6 right vs. 3 left). Consequently, a strong group-level rightward shift would not be expected if left-sided pathology and functional re-organization were the primary driver. Therefore, while epilepsy-related reorganization may have contributed to the observed activation patterns in individual patients, it is unlikely to fully explain the group-level lateralization. Future studies in larger cohorts with balanced seizure lateralization and comprehensive language and memory mapping will be needed to better characterize the contributions of epilepsy-related cortical reorganization.

Study limitations

Several limitations should be considered when interpreting the present findings. First, the current analyses were restricted to the 60–120 Hz range due to the sampling frequency of the dataset. As a result, higher-frequency activity such as broader HFB responses commonly examined in intracranial studies, was not assessed. Future investigations of scalp HF activity would benefit from substantially higher sampling rates (preferably ≥ 1 kHz rather than the conventional ~ 200 Hz commonly used in scalp EEG recordings) to improve characterization of scalp HF signatures and facilitate more comprehensive cross-modal analyses. Second, the relatively sparse scalp electrode coverage limited the spatial resolution of the scalp EEG and may have reduced sensitivity to localized cortical activity. Future studies using high-density EEG systems, such as 10–10 or 10–5 systems, together with electrode digitization and individualized head models, should provide more accurate characterization of the spatial correspondence between scalp and intracranial activity. Finally, the current study did not explicitly investigate potential breach effects associated with burr holes and iEEG lead trajectories. Although fixation-baseline normalization was applied in the coherence analysis and may partially reduce stable, task-independent alterations in signal transmission, it cannot fully account for potential changes in

volume conduction introduced by skull defects. Future studies incorporating rigorous forward modeling will be needed to directly characterize and account for these effects.

Declarations

Ethics approval and consent to participate

The present study involved secondary analysis of de-identified data from a previously published dataset. The original data collection was approved by the Institutional Review Board (Kantonale Ethikkommission Zürich, PB-2016-02055), and all participants provided written informed consent. The de-identified dataset is publicly available through <https://doi.org/10.6084/m9.figshare.11500485.v2>.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author Contribution

S.L. and Y.Z. conceived and designed the study. S.L. performed the data analysis and drafted the manuscript. S.L., N.L., and Y.Z. contributed to data interpretation and critically revised the manuscript. All authors reviewed, edited, and approved the final manuscript.

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Data Availability

The present study involved secondary analysis of de-identified data from a previously published dataset. The original data collection was approved by the Institutional Review Board (Kantonale Ethikkommission Zürich, PB-2016-02055), and all participants provided written informed consent. The de-identified dataset is publicly available through <https://doi.org/10.6084/m9.figshare.11500485.v2>. The data used

and/or analysed during the current study are available from the corresponding author on reasonable request.

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Figures

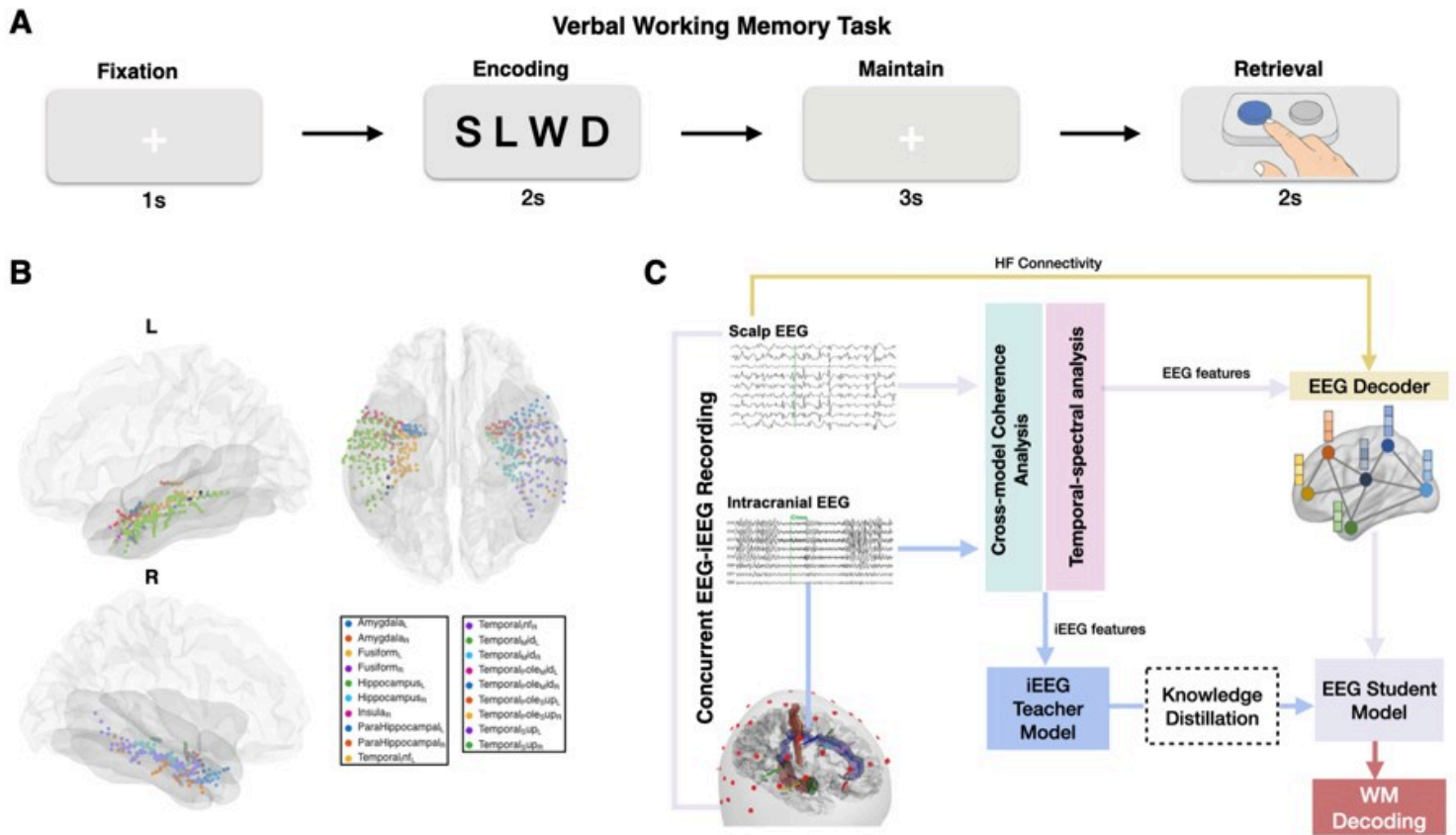


Figure 1

(A) Verbal working memory (WM) task paradigm. In the original study, concurrent neuronal spike-iEEG-scalp EEG recordings were acquired while subjects performed a modified Sternberg task (ref). Each trial began with a 1-s fixation phase, followed by an encoding phase in which 4, 6, or 8 letters were presented for 2 s. This was followed by a 3-s maintenance period. After the presentation of a probe cue, subjects were shown a test letter and had 2 s to determine whether it belonged to the previously presented memory set, corresponding to the retrieval phase. **(B)** Intracranial electrode locations for all nine subjects (n = 509 contacts). Electrodes are colored according to their assigned anatomical regions of interest based on the Automated Anatomical Labeling (AAL) atlas. **(C)** Overview of the current study. Scalp HF activity was validated against concurrent intracranial HF broadband signals using cross-modal coherence analyses and temporal-spectral feature comparisons. Features extracted from both the conventional lower frequency range and the HF band were used as inputs to a graph convolutional network framework for WM decoding. Finally, a knowledge distillation approach was employed to transfer information from iEEG to EEG, allowing intracranial signals to guide non-invasive decoding of working memory states (retrieval vs. encoding).

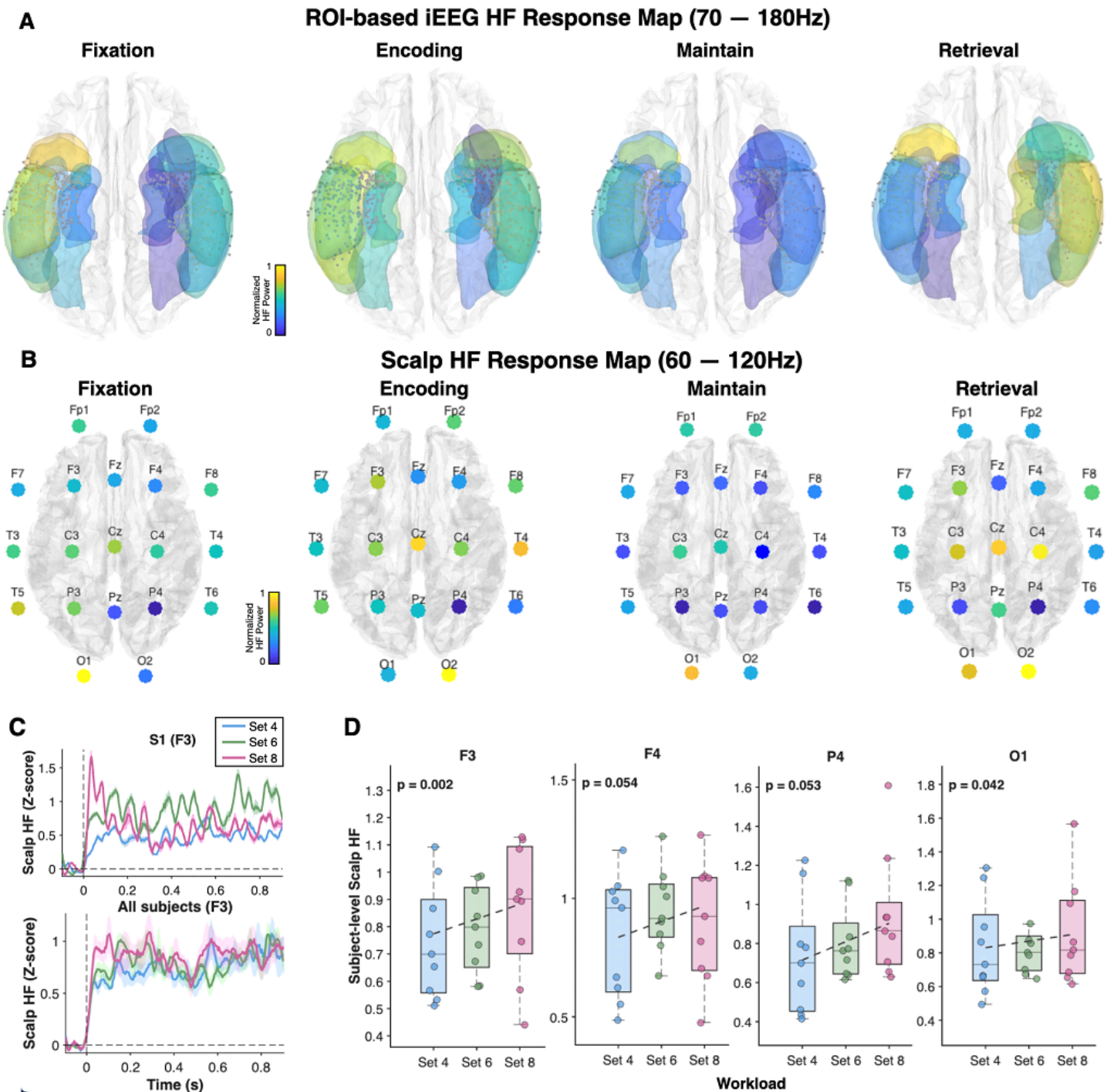


Figure 2

Concurrent EEG-iEEG captured task phase and workload modulated HF response. (A)ROI-based intracranial HF broadband activity across task phases of the verbal working memory task: fixation, encoding, maintenance, and retrieval. Activity is aggregated across 502 electrodes and mapped to anatomical ROIs. **(B)** HF response in scalp EEG across task phases. Values represent subject-averaged HF power at each electrode location. Results for each individual subject is presented in Supplementary Fig. S2. **(C)** Workload-dependent scalp HF responses in a representative subject (S1) and across all subjects, measured at electrode F3 during the retrieval phase. The highest memory load condition (set size 8) elicited the strongest HF response, compared with set sizes 4 and 6. **(D)**Correlation between

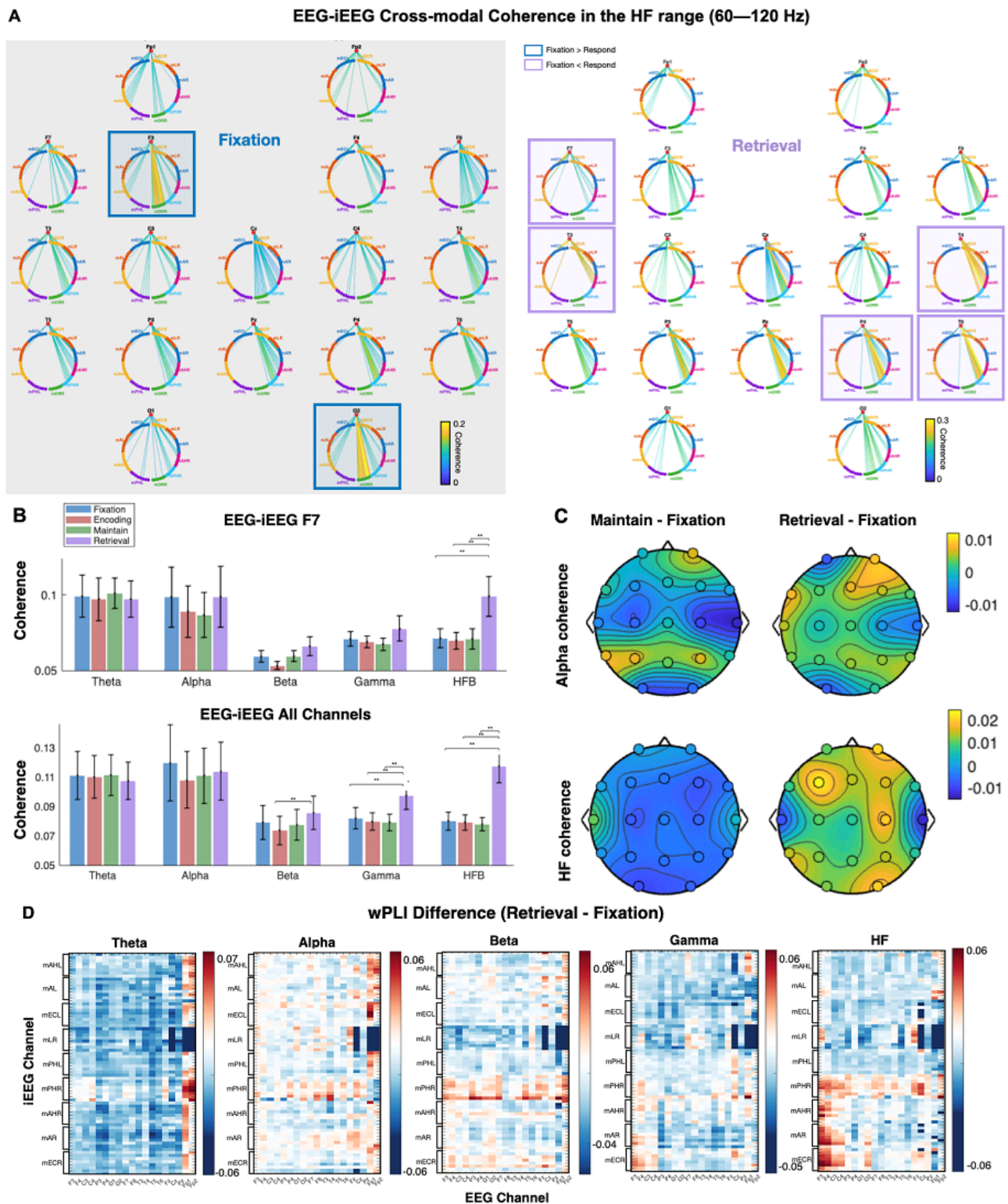


Figure 4

Cross-modal HF coherence analysis in nine subjects. (A) Group-averaged cross-modal HF coherence (60–120 Hz) between scalp EEG and iEEG during fixation and retrieval. Each circular plot represents a scalp EEG electrode, with surrounding nodes indicating intracranial electrodes arranged by anatomical location. Retrieval showed increased coherence involving F7–left entorhinal, T3–left hippocampal/entorhinal, T4–right hippocampal/entorhinal, P4/T6–right hippocampal-parietal regions.

(B) Group-averaged HF coherence across all EEG-iEEG electrode pairs during fixation and retrieval. Retrieval exhibited significantly greater HF coherence than fixation (paired Wilcoxon signed-rank test, $p < 0.01$). **(C)** Topographic maps of changes in EEG-iEEG coherence during maintenance and retrieval relative to fixation for the alpha and HF bands. Maintenance and retrieval exhibited distinct spatial patterns of alpha and HF coherence modulation. **(D)** Group-level changes in cross-modal phase synchronization ($\Delta wPLI = \text{Retrieval} - \text{Fixation}$) across theta, alpha, beta, gamma, and HF bands. Increased $\Delta wPLI$ was mostly observed for frontal and midline scalp electrodes coupled with entorhinal-hippocampal structures.

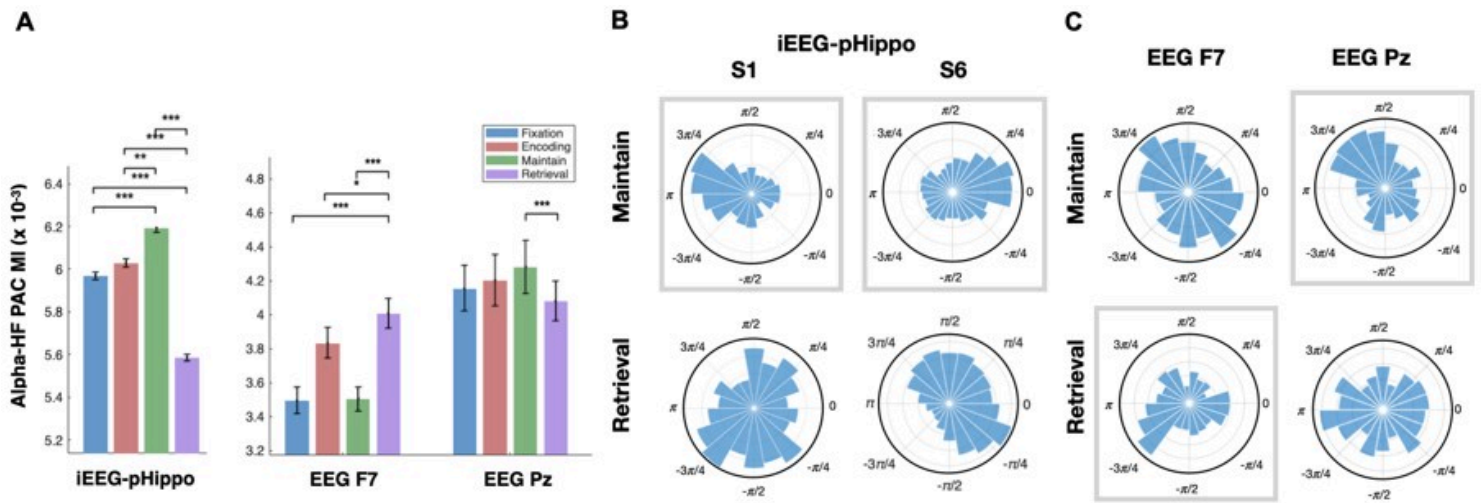


Figure 5

Within-modal alpha-HF PAC analysis during WM maintenance and retrieval. **(A)** Magnitude of alpha-HF phase-amplitude coupling (PAC), quantified using the modulation index (MI), for both iEEG and scalp EEG. For iEEG, MI values were calculated by aggregating posterior hippocampal electrodes (mPHL and mPHR) across all subjects. The strongest coupling was observed during the working memory maintenance phase, whereas coupling was reduced during retrieval over the posterior hippocampus. For scalp EEG, significant differences in coupling strength across task phases were observed over frontal and parietal electrodes. F7 exhibited the strongest coupling during retrieval, while Pz showed maximal coupling during maintenance. **(B)** Preferred phase of intracranial alpha-HF coupling over mPHL in two subjects (S1 and S6). Compared to retrieval, mPHL exhibited a more pronounced phase preference during maintenance (boxed). **(C)** Preferred phase of scalp alpha-HF coupling over F7 and Pz across all subjects. F7 demonstrated stronger phase-specific coupling during retrieval, whereas Pz showed stronger coupling during maintenance (boxed).

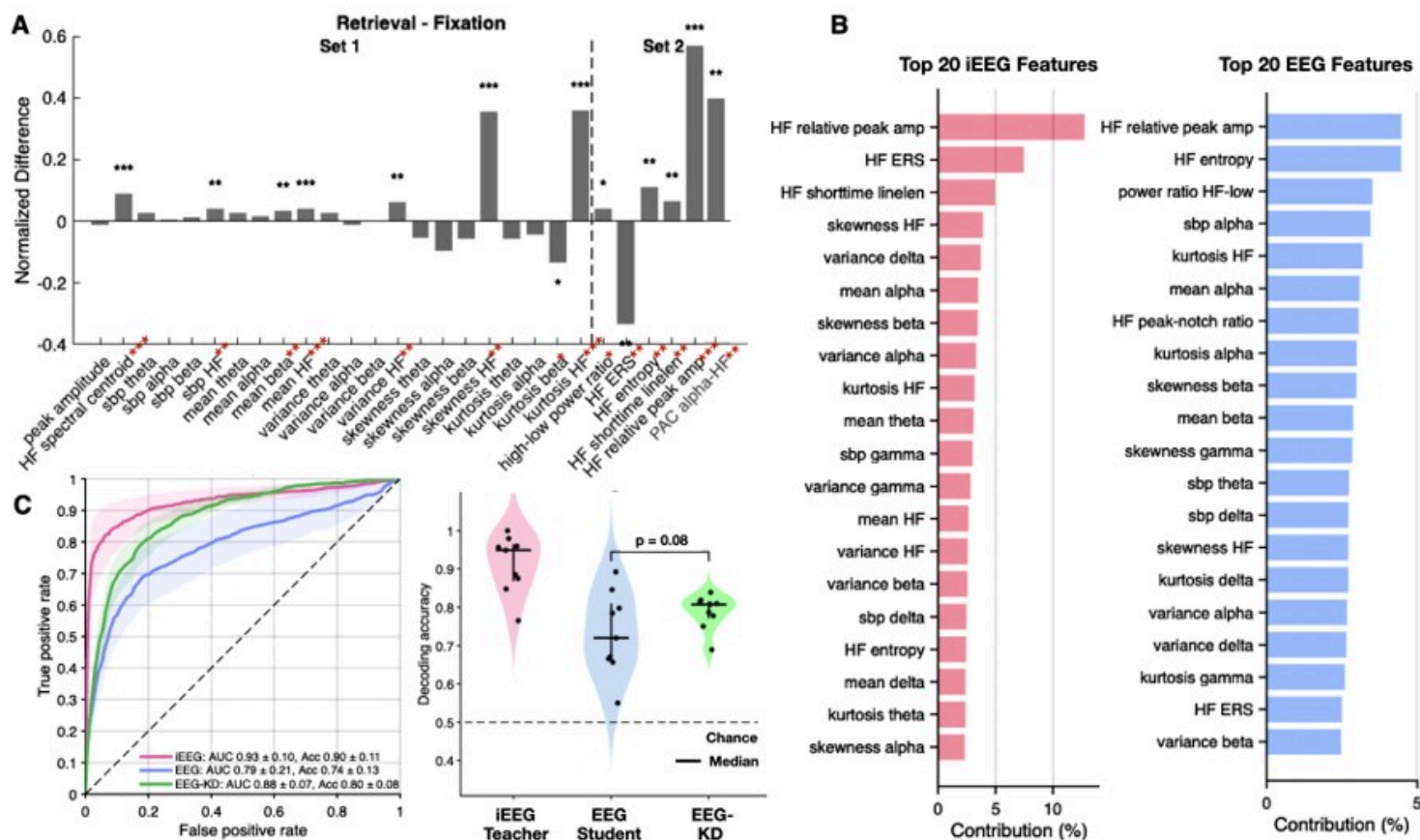


Figure 6

Scalp and intracranial HF features in WM decoding. (A) Feature comparison between retrieval and fixation in scalp EEG. Only a subset of features is shown for a clear presentation. Compared with fixation baseline, retrieval induced marked changes in multiple features, particularly those related to HF activity. **(B)** Feature importance derived from ablation analysis for iEEG- and EEG-based WM decoding. HF-related features contributed most strongly to decoding performance in both modalities. In particular, the HF relative peak amplitude was the most informative feature, and four of the top five features were HF-related. **(C)** Decoding performance of the iEEG-, EEG-, and iEEG-guided EEG knowledge distillation (EEG-KD) frameworks under LOSO cross-validation. Knowledge distillation improved EEG decoding performance in 7 of 9 subjects, resulting in a mean accuracy increase of 6.1%.

Supplementary Files

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