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Decoding state specific connectivity during speech production and perception

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eLife Assessment

This work represents a **valuable** finding of how single-trial functional connectivity may be used to infer different cognitive states involved in speech perception and production. Although the data and analyses are overall **convincing**, the theoretical advance and novelty of the finding are less clear. With a clearer idea of the functional significance of the connectivity data, the paper would be of interest to those interested in brain networks and communication.

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Abstract

Understanding how dynamic brain networks support language perception and production is central to cognitive neuroscience. A vast network based literature has employed functional connectivity (FC), primarily using resting-state and task-based fMRI. However, methodological limitations have hindered this approach in language processing, particularly during speech production. Here, we address this gap by employing a large cohort of electrocorticographic (ECoG) patients (N=42) to investigate the networks driving speech perception and production. We acquired data while patients were engaged in a controlled battery of speech production tasks focusing on five cognitive states (auditory perception, picture perception, reading perception, speech production, and baseline). Using linear classifiers we were able to robustly decode cognitive states from single-trial FC (i.e. Pearson correlations) of the neural activity patterns, achieving a mean accuracy of 64.4%. These classifiers revealed distinct network signatures underlying auditory and visual perception as well as speech production via stable network connectivity. Importantly, the network signatures included both regions with robust local neural activity and those with minimal or no detectable activation. Such signatures indicate that even low-activity regions contribute critically to differentiating cognitive states. Our findings underscore the significance of functional connectivity analysis as a complementary dimension to investigating local neural activity, and suggest that the functional networks supporting speech extend beyond the most metabolically active regions.

Introduction

Human cognition and behavior is coordinated by a complex network of interconnected brain regions (Sporns and Betzel, 2016; Bassett and Sporns, 2017). A large body of literature has described these networks leveraging functional connectivity (FC) across regions during rest (Biswal et al., 1995; Fox et al., 2005; Greicius et al., 2009) as well as cognitive processing (Friston et al., 1993; Cole et al., 2014, 2021). Resting state data has identified reproducible intrinsic networks of functionally connected regions, such as the default mode, dorsal attention,

and sensorimotor network, that resemble FC patterns observed during tasks (Biswal et al., 1995; Fox and Raichle, 2007; Smith et al., 2009). While task-based FC studies are able to reproduce intrinsic network, they also provide evidence for network reconfiguration during changing cognitive demand (Cole et al., 2014; Shine et al., 2016; Hearne et al., 2017).

One hallmark of human behavior is our ability to produce complex and rapid speech utterances.

However, there are only a select few studies examining functional connectivity during the production of speech and language (Fuertinger et al., 2015; Riecker et al., 2005; Geranmayeh et al., 2014; Ewald et al., 2012). This is mainly due to the severe motor artifacts introduced by the jaw, tongue, and laryngeal movements during speech that are inherent to noninvasive neuroimaging and electrophysiological recordings (Grabski et al., 2012; Abbasi et al., 2021). As a result, the network principles that support the rapid sensorimotor transformations of speech are still poorly understood. However, human invasive electrocorticographic (ECoG) recordings circumvent these motor artifacts. Intracranial signals are obtained during neurosurgical procedures directly from the depth and surface of the brain providing a high spatial resolution and millisecond temporal precision. The vast majority of previous intracranial studies have focused on local high-gamma neural activity as a proxy for population firing (Mesgarani et al., 2014; Pasley et al., 2012; Edwards et al., 2010; Flinker et al., 2015; Chang et al., 2010; Bouchard et al., 2013; Mugler et al., 2014; Cheung et al., 2016). These studies have profoundly advanced our understanding of how local neural activity encodes articulatory gestures and phonetic features (Bouchard et al., 2013; Mesgarani et al., 2014; Chang et al., 2010; Mugler et al., 2014; Cheung et al., 2016), and how speech production sequences involve distinct temporal activation patterns across language-relevant cortical regions (Edwards et al., 2010; Flinker et al., 2015). However, the dynamics of inter-regional connectivity during speech production tasks remain largely unexplored.

Measuring functional connectivity in ECoG typically involves assessing synchronous co-fluctuations in broadband amplitude, or within specific frequency bands, most often high-gamma (i.e. 70-150 Hz frequency band), using pairwise correlation or coherence (Axmacher et al., 2010; Kucyi et al., 2018). Analyses of long-duration resting-state recordings have revealed stable correlation templates that closely mirror canonical fMRI networks (Kramer et al., 2011; Kucyi et al., 2018). During overt speech, high-gamma coherence between inferior frontal gyrus and superior temporal cortex increases selectively during active vocalization relative to passive listening (Kingyon et al., 2015), underscoring the value of correlation-based FC for probing rapid sensorimotor integration. Yet most FC studies in ECoG still rely on long analysis windows or condition-averaged data. This practice can mask the transient network dynamics that support rapid behaviors such as speech. Undirected FC has also been rarely applied to single-trial decoding of cognitive stages, so low-amplitude but behaviorally relevant connectivity patterns are often lost in averaging. As a result, we still do not understand which inter-regional connectivity patterns are specific to different successive stages of speech perception and production, or whether these interactions reveal network structure invisible to analyses that focus only on local activity.

Here, we directly address these gaps by examining single-trial functional connectivity dynamics in ECoG recordings from a cohort of 42 participants performing speech-production tasks. We employ a robust machine learning approach—support vector machine (SVM) classification—to decode cognitive states from trial-specific FC patterns, and we translate the resulting weights into interpretable connectivity signatures using forward model transformations (Haufe et al., 2014). We aim to address several main questions: (i) Are the cortical networks supporting speech perception and production decodable based on connectivity patterns alone? And (ii) are the associated discriminative connections specific to regions with high neural activity, or do they include network structures obscured by analyses focusing solely on activity?

Results

Single-Trial Functional Connectivity

To investigate the dynamics of single trial functional connectivity during speech perception and production, we collected electrocorticography (ECoG) data, which provide high spatiotemporal resolution. We recorded neural activity from 42 participants while performing three word production tasks (see Experimental Tasks and Cognitive States, Figure 1A and B) and defined five cognitive states of interest (Figure 1C): Auditory perception, picture perception, reading perception, speech production, and baseline (production and baseline are shared across tasks).

Analyzing functional connectivity (FC) at the single-trial level can reveal nuanced dynamics, including weak yet consistent interactions, that may be obscured during the common practice of trial-averaging (He et al., 2008; Solomon et al., 2018; Huang et al., 2023). We segmented all singletrial neural activity into state-specific intervals and computed FC for each (see Single-Trial Functional Connectivity). In order to provide a view of single-trial connectivity, we create “connectivity vectors” comprised of the upper-triangular elements of the FC matrices (Figure 2A, left). The entries of these vectors represent all connections between pairs of cortical electrodes. Grouping the connectivity vectors by cognitive state provides a comprehensive view of the connectivity patterns. We illustrate this for one participant, revealing substantial trial-to-trial variability (Figure 2A, right). Some states (e.g. picture and reading perception) show obviously similar frontal–frontal and occipital–frontal connections. However, we were interested in identifying patterns of connectivity that are distinct across states.

In order to test whether these patterns contained sufficient information to differentiate cognitive states we employed a decoding approach. We trained a multi-class Support Vector Machine (SVM) classifier on the connectivity vectors in a representative participant, achieving a mean cross-validated accuracy of 74% (chance level is 20%, Figure 2B). The performance of the model provides evidence for robust state-specific connectivity patterns in this participant. In order to identify these state-specific connections we examined the model weights. We assessed significance of weights after following common practices of transformation (Haufe et al., 2014), to ensure unbiased interpretability (see Decoding Framework). This identified specific networks driving classification performance, for example intra-auditory-cortex connections during auditory perception (Figure 2C). We call these *discriminative connections*, providing a distinction for connectivity patterns that significantly differentiate cognitive states.

State-Specific Connectivity Patterns Across Participants

To test whether the state-specific connectivity patterns observed in the representative participant generalize to the entire cohort, we replicated our decoding pipeline within each of the N=42 participants. Across all participants, the classifiers performed robustly (Figure 3A): perceptual states were decoded with 71.5–74.4% accuracy, speech and baseline with 56.7–59.1%. Participant-wise model accuracies over all states ranged from 52% to 86% (mean = 64.4%; Figure 3B), all well above the 20% chance level for five classes. We then transformed the SVM weights to identify each state’s discriminative connections (Figure 3D) revealing that each state is represented by a small subset of connections (mean across states $\approx 0.002\%$ of all possible connections) largely unique to that state (uniqueness ratio = 0.817; Figure 3C, see Statistical Analyses). Spatially, auditory perception relied on STG–frontal links, visual states on occipital–frontal connections, and speech production on enhanced speech-motor cortex coupling as well as motor–auditory anti-correlations (Figure 3D and Figure 5B). In contrast, a traditional analysis of strongest connections (i.e. correlation magnitude thresholding; see Single-Trial Functional Connectivity) yielded denser, overlapping connections (uniqueness = 0.27; Figure 3C and E). These results show that single-trial FC decoding isolates a highly specific connectivity signature for each cognitive state, highlighting functionally meaningful interactions that are obscured when connectivity is addressed solely by correlation magnitude.

Figure 1. Overview of task and data structure.

(A) Battery of language tasks that all culminate in the same speech utterance. (B) Electrode coverage across participants; left hemisphere shown (right hemisphere is included in [Supplementary Figure 1](#)) (C) The sequence of the cognitive states of interest in a single trial.

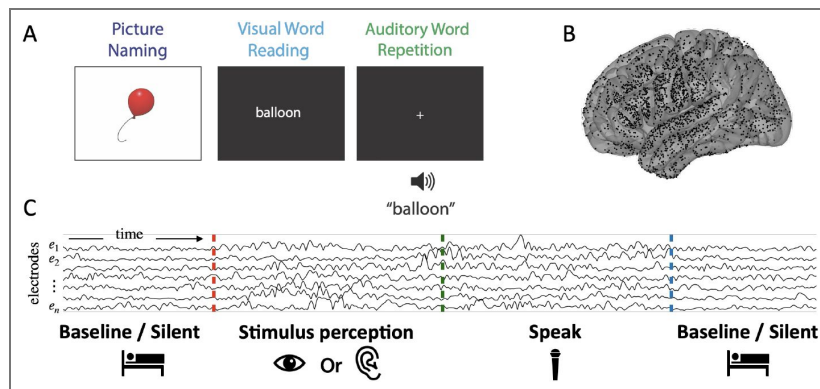
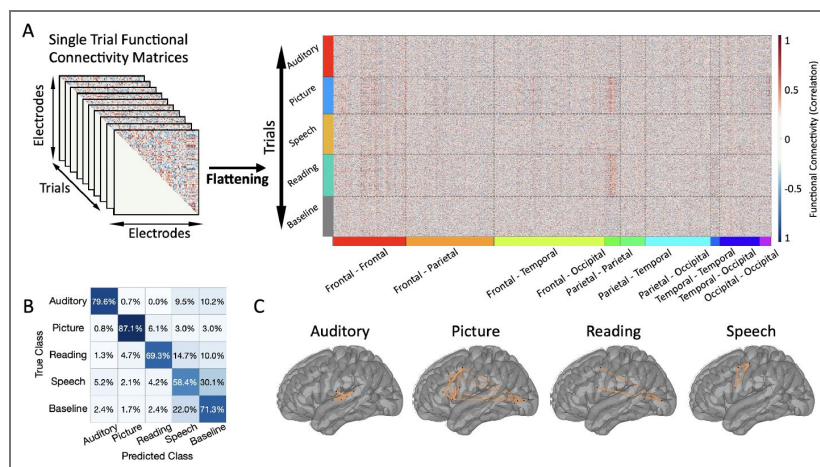


Figure 2. Functional Connectivity analysis for an exemplar participant.

(A) Demonstration of flow of creating the functional connectivity feature and resulting vectors across all states. The values are ordered based on connections between different brain lobes (e.g. Frontal-Frontal, Frontal-Parietal, etc.). The features show clear differences in the connectivity patterns of the cognitive states. (B) Confusion matrix showing high accuracy classification of the connectivity vectors. This matrix was calculated using 5-fold cross-validation on the model for the exemplar participant. (C) Discriminative connections for each cognitive state. Orange lines depict connections whose median absolute deviation of the transformed SVM weights survive a Laplacian tail bound significance threshold; node positions correspond to electrodes.



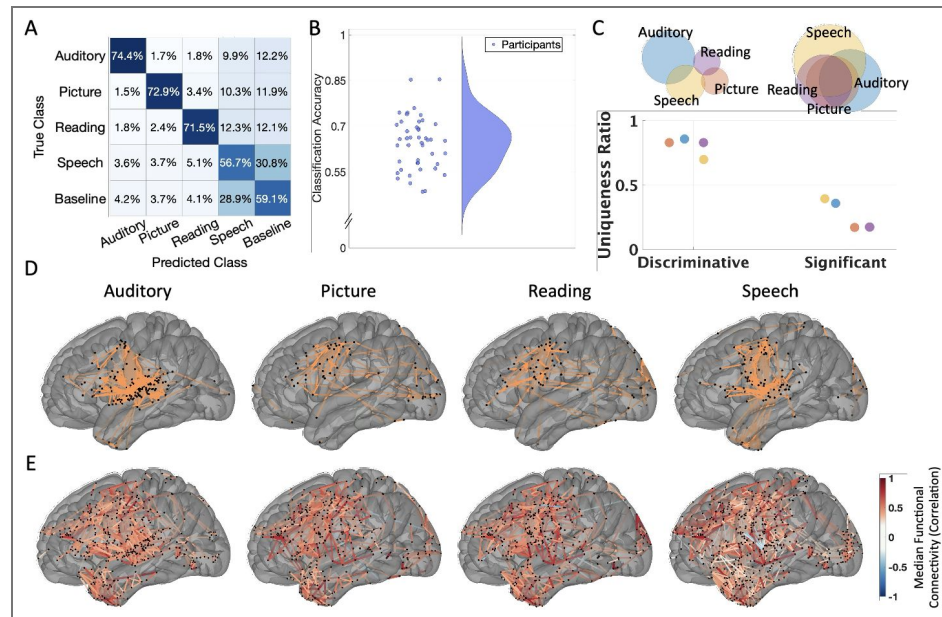


Figure 3. State-Specific Functional Connectivity patterns across all participants.

(A) Confusion matrix obtained from five-fold cross-validated SVM classification, summed over 42 participants. Diagonal cells show per-class accuracies; off-diagonals show misclassification rates. (B) Distribution of participant-wise classification accuracies. The mean accuracy of 64.4% is well above the 20% chance level for five classes. (C) "Uniqueness ratio" for each cognitive state, comparing the sparsity of connections selected by our discriminative approach with those retained after a magnitude threshold (i.e. strongest connections). This ratio is closer to 1 when the connections are more unique in each state, and closer to 0 when they are overlapping across the cognitive states. Discriminative connections are significantly more state-specific than the strongest connections (average uniqueness ratio = 0.817, 0.273 respectively; two-sided permutation test, $p < 0.0001$ for all states). (D) Cortical distribution of discriminative connections for each state, across all participants. The patterns align with our current knowledge of involved regions in these states (e.g., STG-frontal links in auditory perception, motor-auditory decoupling in speech production). (E) Cortical distribution of connections selected solely by magnitude thresholding. The widespread, non-specific pattern contrasts with panel D, underscoring the greater specificity of the discriminative approach. (All brain surfaces are shown in left-hemisphere lateral view; right-hemisphere results are analogous and shown in the Supplementary Figure 2.)

Relationship between discriminative connectivity and local neural activity

Speech production is notoriously difficult to study with non-invasive measures given the inherent motor artifacts. Conversely, intracranial studies have shown great promise in characterizing speech production dynamics, however an overwhelming number of studies have focused on local neural activity alone. We were interested in characterizing the unique contribution of our approach compared with the common practice of analyzing local high-gamma neural activity. During speech production, high-gamma active electrodes (see Statistical Analyses) on the cortex were predominantly distributed over the superior temporal and peri-central cortices (Figure 4A and E). This highly selective distribution has been a hallmark of local activity and is in stark contrast to the widespread distribution of electrodes across cortex that show a strong functional correlation (Figure 4B,D,E). Our decoding approach provides evidence for a more selective set of discriminative functional connections with broad coverage of the language network (Figure 4C,D,E). Our approach reveals a larger ratio of electrodes identified across non-sensory (and non-motor) cortices compared with local activity (permutation test, see Statistical Analyses), notably the inferior temporal ($p = 0.0319$), superior frontal ($p = 0.0114$), parietal ($p = 0.0005$), occipital ($p = 0.0002$), and fusiform cortices ($p = 0.0279$). This indicates that local activity alone may be insufficient for identifying important regions in the language network and a connectivity-based approach is necessary as a complement. While our approach elucidates discriminative connections, we were interested in understanding the relationship between the degree of local activity and discriminative connectivity. To quantify this, we extracted the median correlation for all discriminative connections and the mean neural activity of their respective nodes (for every cognitive state; see Neural Activity versus Connectivity Analysis). The resulting connectivity values span both positive and negative correlations (Figure 5A), yet organize into clear, state-specific patterns when projected onto the cortex (Figure 5B). Node activity shows a similar broad distribution (Figure 5C) with a clear spatial gradient from low to high activity regions (Figure 5D). A natural question is whether nodes with higher neural activity contribute more to functional connectivity. To test this, we correlated the mean connectivity of each node in discriminative connections with its mean activity for every cognitive state and found significant correlations across states (Spearman Correlations, Auditory $\rho = 0.4472$, $p < 0.0001$; Picture $\rho = 0.2925$, $p = 0.0003$; Reading $\rho = 0.4306$, $p < 0.0001$; Speech $\rho = 0.1195$, $p = 0.0254$). When visualizing the relationship (Figure 5E, color-coded by cognitive state), most nodes align along the diagonal, indicating balanced activity and connectivity. More active regions tend to exhibit stronger correlations. However, many electrodes diverge from this relationship: some are highly connected despite low neural activity, whereas others are strongly active but weakly connected. We quantified this imbalance with a connectivity–activity relative-distance index (RDI) and mapped it on the cortex (Figure 5F). The RDI highlights precentral and frontal gyri during auditory perception and speech-motor cortex during picture and reading perception, where connectivity exceeds activity. Conversely, during speech production discriminative nodes include both positive RDI (i.e. low activity and high connectivity) and negative RDI sites (i.e. high activity and low connectivity), particularly within the superior temporal, inferior frontal and precentral gyri. Together, these findings show that discriminative connectivity results in a unique, functionally meaningful network signature that is invisible to activity-only or correlation-magnitude-only views and underscores that connectivity adds a complementary dimension to local activity for differentiating cognitive states.

Discussion

Our study leverages single trial connectivity decoding across a large cohort of patients (N=42) to investigate functional connectivity. Our approach is able to achieve high decoding across five speech-related cognitive states while providing interpretable weights that highlight the discriminative connections. Compared to conventional methods (i.e. local high-gamma activity),

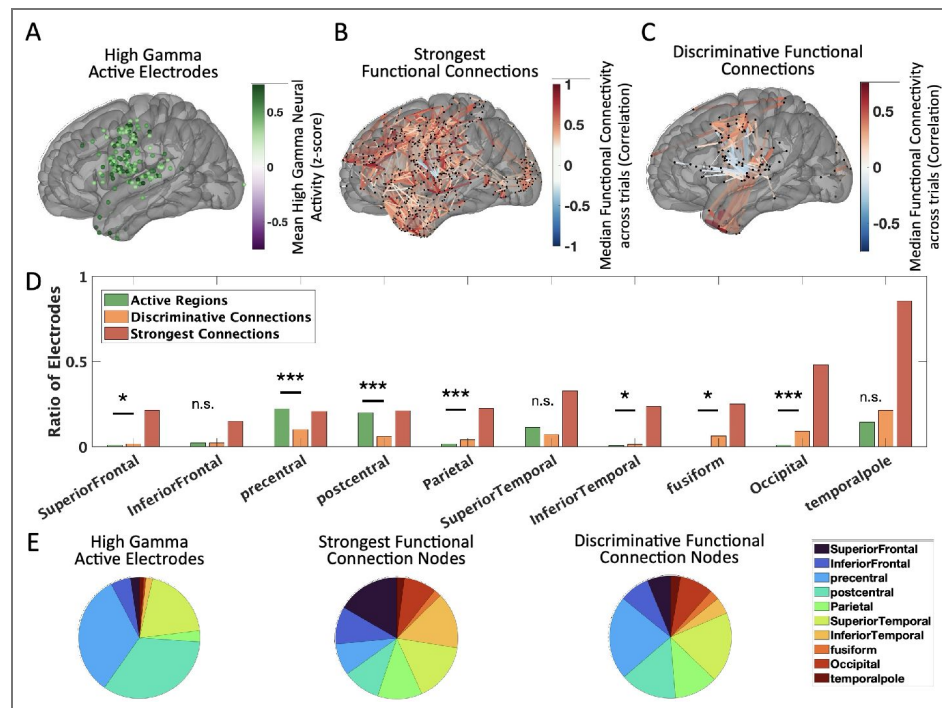


Figure 4. Comparison of maps for Speech production using different methods.

(A) Electrode-wise map of high-gamma activity amplitude (70–150 Hz) during speech production, aggregated across 42 participants and averaged across trials and time. (B) Connections whose median Pearson correlation exceeds a $p < 0.05$ threshold. This magnitude-based connectivity thresholding approach yields a dense, overlapping network. (C) Connections identified by the discriminative SVM transformed weights, resulting in a sparse and state-specific distribution of the connections. (D) Ratio of electrodes identified in each region compared to the total number of electrodes recording in that region, using three different approach. The lower ratios for ‘Active Regions’ and regions involved in ‘Discriminative Connections’ indicate that these methods are more sensitive in identifying relevant electrodes compared to the ‘Strongest Connections’ approach. Stars mark regions where the proportion for discriminative connections differs from active regions (permutation test, p values listed: Superior Frontal $p = 0.0114$, Inferior Frontal $p = 0.0793$, Precentral $p = 0.0001$, Postcentral $p = 0.0001$, Parietal $p = 0.0005$, Superior Temporal $p = 0.1920$, Inferior Temporal $p = 0.0319$, Fusiform $p = 0.0279$, Occipital $p = 0.0002$, Temporal Pole $p = 0.2697$). (E) Venn diagrams summarizing how identified electrodes are distributed among brain regions.

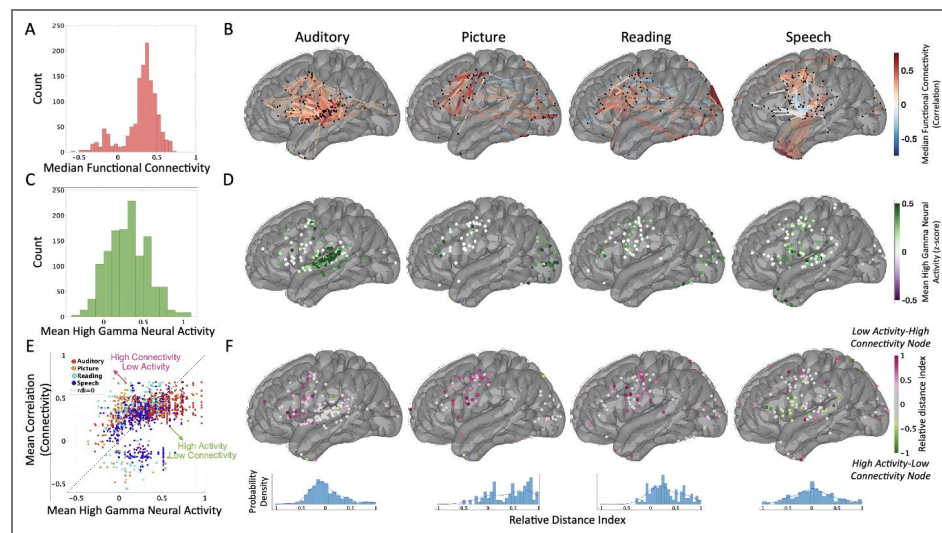


Figure 5. Relationship between discriminative connectivity and local high-gamma activity.

(A) Histogram of FC values for all discriminative edges (pooled across states). While skewed toward stronger correlations, the distribution includes many weak connections that conventional magnitude thresholds would overlook. (B) The cortical distribution of state-specific discriminative connections. The color represents median functional connectivity values, representing the prominent connectivity patterns that remain stable across the trials of these state. (C) Histogram of high-gamma activity, averaged across trials and time at nodes participating in discriminative connections. (D) The cortical distribution of mean high-gamma activity, only for nodes participating in discriminative connections of each state. (E) Scatter-plot of mean connectivity strength versus mean high-gamma activity for the nodes participating in discriminative connections. A positive trend is present, yet many nodes deviate markedly, indicating regions with high connectivity but low signal activity and vice versa. (F) Connectivity-activity relative distance index projected onto the cortex (pink = nodes with relatively higher connectivity than activity; green = nodes with higher activity than connectivity). This map highlights regions whose functional importance is underestimated by activity-only analyses. (All brain surfaces are shown in left-hemisphere lateral view; right-hemisphere results are analogous and shown in [Supplementary Figure 3](#).)

our approach reveals previously obscured cortical sites that discriminate cognitive states. These results are among a select few functional connectivity studies focusing on speech related cortical networks, providing a rare window into the functional networks supporting this function.

Despite valuable insights, most human FC studies in ECoG share design choices that blur fast connectivity dynamics. Many studies estimate connectivity from long windows of >1s (Kucyi et al., 2018; Nir et al., 2008). Investigating connectivity during the transient cognitive states involved in speech perception and production will require a shorter time window, enabling us to capture these state specific characteristics of connectivity. Further, studies often average the signal or connectivity over many repetitions, which eliminates trial-to-trial variability (Casimo et al., 2019; Foster et al., 2015). Averaging signals or correlation matrices can result in robust estimations that highlights the strongest connections. However, this step also blurs the distinction between state specific signals or connections that maintain a steady low value and those that vary drastically. To be able to capture the transient, state-specific connections that are stable across trials regardless of their strength, we compute FC in 500-ms windows and keep every trial separate. This allows us to preserve within-state variability while avoiding the loss of temporal detail. As a result, this framework unveils the fast dynamics of speech perception and production with a resolution that respects both the transient and distributed nature of these networks.

To investigate the discriminative connections underlying speech perception and production, we computed functional connectivity between every pair of electrodes. By leveraging the interpretability of the transformed weights of a linear SVM model, we detect sparse state-specific connections based solely on their ability to differentiate cognitive states (Figure 3D, Figure 5B). As a result, we identify both strong and weak discriminative connections, including ones between regions that fall outside the canonical language areas. In contrast, the standard connectivity magnitude thresholding method results in a widespread and state-agnostic set of connections, masking these distinctions (Figure 3E). A common practice in ECoG-based FC studies that avoids this problem is to restrict analyses to a handful of predefined nodes using seed-based or region-of-interest strategies (Keller et al., 2013). Most often, these seeds are selected based on electrodes with large high-gamma responses or those deemed critical by electrical stimulation mapping (Kinyon et al., 2015; Rolston and Chang, 2018; Fox et al., 2020; Hsieh et al., 2024). In the context of language, seed-based strategies typically target inferior-frontal and auditory cortices, privileging well-established nodes but marginalising others, like middle frontal, precentral, postcentral and temporal pole. While methodologically convenient, this choice significantly narrows the scope of network inference and implicitly reinforces the dominant cortical regions. Moreover, it overlooks potentially informative and functionally relevant regions with lower signal (activity or connectivity), such as those identified by our RDI close to 1 or -1 in Figure 5F. Our results suggest that a more inclusive (e.g. all electrodes) approach coupled with a decoding framework reveals a set of meaningful connections and avoids anatomical blind spots.

Our findings reveal connections across peri-sylvian cortices as well as the temporal pole during shifts from perception to production — a dynamic that has been difficult to capture with previous approaches. While fMRI studies have been instrumental in mapping large-scale networks (Biswal et al., 1995; Smith et al., 2009; Fox et al., 2005; Greicius et al., 2003; Power et al., 2011; Yeo et al., 2011) and in characterizing the language network (Saur et al., 2008; Braga et al., 2020; Tomasi and Volkow, 2012; Branco et al., 2020; Lipkin et al., 2022), most task-based studies focus on listening, reading, or covert speech. This has left overt speech underexplored in fMRI, due to motion artifacts (Birn et al., 1999; Gracco et al., 2005). Moreover, the temporal smoothing of the BOLD response limits fMRI's ability to resolve the rapid state transitions between perception and production of speech. In contrast, ECoG, with its millisecond resolution, allows us to track these fast dynamics. Our approach captures connectivity patterns directly relevant to speech processes, revealing perception-to-production shifts with millisecond resolution. Specifically, we find positive correlations during perception across frontal and relevant sensory regions, however speech production is associated with peri-rolandic and temporal (STG and ATL) networks. Interestingly, the discriminative connections for speech production included many negative correlations (Figure 5B) between STG and ventral frontal cortices (IFG and vPrG) which

likely reflects speech induced suppression during vocalization (Khalilian-Gourtani et al., 2024 [↗](#); Kurteff et al., 2024 [↗](#)). Although ECoG coverage is clinically constrained, it complements the whole-brain approach of fMRI by offering a high-resolution view of speech processing dynamics at behaviorally relevant timescales.

Our results further show that discriminative connections emerge in regions with both high and low neural activity. In the ECoG literature, neural activity is most often measured as the amplitude of the high-gamma (70–150 Hz) frequency range, with task-relevant regions mapped by significant increases above baseline. Numerous studies have shown that high-gamma active regions during speech tasks localize strongly to IFG, precentral gyrus, STG, and MTG (Chang et al., 2010 [↗](#); Edwards et al., 2010 [↗](#); Flinker et al., 2015 [↗](#); Moses et al., 2016 [↗](#)). This approach maps active electrodes but often overlooks distributed connectivity as well regions that are not significantly active. Our connectivity findings provide evidence for connections involving low-activity electrodes, particularly in parts of precentral and inferior frontal cortices during perceptual states (Figure 5F [↗](#)). The fact that we find these connections in addition to discriminative connections between electrodes with high neural activity, suggests that the functional networks supporting speech extend beyond the most metabolically active regions. The identification of both active-to-active and active-to-silent discriminative connections demonstrates that connectivity analyses provide orthogonal information to local high-gamma measures, potentially revealing preparatory or coordinating regions that studies relying on activation alone may overlook.

Together, these findings highlight how single-trial functional connectivity decoding provides a powerful complement to traditional analyses of neural activity. By uncovering state-specific and sparse connections across regions, we reveal a distributed speech network that cannot be captured by focusing on local activation alone or seed-based connectivity. The ability to decode cognitive states from transient connectivity patterns underscores the dynamic and flexible nature of the underlying cognitive processes and allows for mapping the full cortical networks involved in speech perception and production.

Methods and Materials

Participants

We used intracranial data from 42 neurosurgical patients undergoing surgical monitoring for Epilepsy (20 females, mean age: 30.38 ± 11.75 yo, 18 right grid, 24 left grid coverage). Patients were selected based on sufficient electrode coverage over temporal, parietal, frontal, and occipital cortices relevant to language processing and their ability to perform the experimental tasks. The electrode arrays included grids and strips placed directly on the cortical surfaces. The implantation and location of the electrodes were guided solely by clinical requirements. All participants provided informed consent following approval from the NYU Langone institutional review board. Surface reconstructions, electrode localization, and Montreal Neurological Institute coordinates were extracted by aligning postoperative brain imaging (MR or CT) to preoperative brain MRI using previously published methods (Yang et al., 2012 [↗](#)).

Experimental Tasks and Cognitive States

Participants completed three tasks that elicited production of the same target words from auditory or visual stimuli (Figure 1A [↗](#)). The tasks were auditory word repetition (repeat an auditorily presented word), visual word reading (read a visually presented written word), and picture naming (name a word from a visually presented line drawing). Each task comprised 100 trials drawn from an identical set of 50 words that appeared twice across different modalities. For each task and trial, the stimulus was randomly presented. Each trial began with a silent baseline of at least 500ms, followed by stimulus presentation, and then speech production (Figure 1C [↗](#)). Participants are instructed to produce the word as soon as they are ready without a go signal (Shum et al., 2020 [↗](#); Yu et al., 2025 [↗](#)). We defined five cognitive states using 500 ms windows time-locked to event markers: auditory perception (auditory stimulus onset), picture perception

(picture stimulus onset), reading perception (written word stimulus onset), speech production (speech onset; shared across tasks), and baseline (pre-stimulus presentation period, also shared across tasks).

ECoG Data Acquisition and Preprocessing

ECoG neural signals were recorded at 2048 Hz with the Neuroworks Quantum Amplifier (Natus Biomedical, Appleton, WI) and were downsampled to 512 Hz during export. Electrodes exhibiting seizure activity or excessive noise identified clinically were excluded from further analysis. Data were re-referenced using a common average referencing scheme to mitigate common-mode noise. We band-passed signals into eight logarithmically spaced sub-bands from 70–150 Hz and averaged them to isolate high-gamma activity. We adopted this multi-band extraction to avoid dominance of lower frequencies (Hamilton et al., 2021 [↗](#); Moses et al., 2016 [↗](#)). We computed analytic amplitude as the absolute value of the Hilbert transform of the filtered signal in each band. We then normalized the data (i.e., z-score) and averaged across bands.

Single-Trial Functional Connectivity

For computing functional connectivity, we segmented the ECoG high-gamma signals into 500 ms epochs for each trial and cognitive state, aligned to task event markers described above. For every epoch, we computed pairwise Pearson correlations of high-gamma analytic amplitude between all electrodes, producing a symmetric functional connectivity matrix per trial and state. To avoid redundancy, we vectorized the upper-triangular off-diagonal of each matrix to obtain a trial-specific connectivity vector for each state. Each vector contains the correlation for all possible electrode pairs (features), with the sign preserved.

In the analysis to identify the strongest connections (correlation magnitude-thresholding, Figure 3E [↗](#)), we first summarized each state's connectivity matrix by computing the median value of each connection across trials. We then evaluated how much each connection's median deviated from the overall distribution of medians. Connections that showed significantly high or low values (beyond what we would expect by chance, after accounting for multiple comparisons, $\alpha < 0.05$) were retained. All others were set to zero. After this thresholding step, we reconstructed the participant- and state-specific connectivity matrices using only the significant connections. Finally, we combined these matrices into a block-diagonal group matrix, preserving individual participant structure while enabling pooled network analysis.

Decoding Framework

We classified trial-specific connectivity vectors into cognitive states using a linear Support Vector Machine (SVM) in MATLAB (MathWorks). To address class imbalance, we applied the Synthetic Minority Oversampling Technique (SMOTE, Chawla et al., 2002 [↗](#)) within each participant and training fold to avoid leakage. We evaluated performance with stratified five-fold cross-validation per participant, averaged accuracy across folds, and derived confusion matrices. We estimated chance levels as theoretical chance (20% for five states, after accounting for SMOTE) and verified this estimate with a permutation approach (i.e. shuffling state labels 10000× within participant). To identify discriminative connections in Figure 2 [↗](#) and Figure 3D [↗](#), we transformed SVM weights from the decision boundary hyperplanes using the Haufe forward model (Haufe et al., 2014 [↗](#)). This transformation enables interpretation of classifier weights by accounting for feature dependencies and mapping them back to neural sources. We normalized the resulting weights using their L_2 norm, and then evaluated how far each transformed weight deviated from the median of the distribution, using the median absolute deviation (MAD) as a robust scale estimator. We set to zero all weights whose deviation from the median did not exceed a threshold derived from a Laplacian tail bound ($\alpha < 0.05$). We selected this threshold to reflect the heavy-tailed distribution of weights. We defined discriminative connections as those whose weights exceeded this threshold, indicating they contributed most strongly to the separation of cognitive states in the

classifier. To quantify the specificity of the identified connections for each state, we computed a uniqueness ratio. This ratio represents the proportion of connections uniquely associated with a given cognitive state relative to all connections identified for that state.

Neural Activity versus Connectivity Analysis

For the analysis in Figure 5 [↗](#), we focused on electrodes that participated in the discriminative connections. For each such electrode and state, we quantified local activity as the mean high-gamma analytical amplitude across trials and time points. For each discriminative connection, we quantified connectivity strength as the median Pearson's correlation across trials of that state. We then computed a connectivity–activity relative distance index (RDI) at the electrode level:

$$RDI = \frac{(C - A)}{|C| + |A|},$$

Where A denotes average local activity and C denotes average connectivity. RDI ranges from -1 (high activity, low connectivity) to +1 (low activity, high connectivity), with values near zero indicating balance. We projected RDI onto each participant's cortical surface to visualize its spatial distribution.

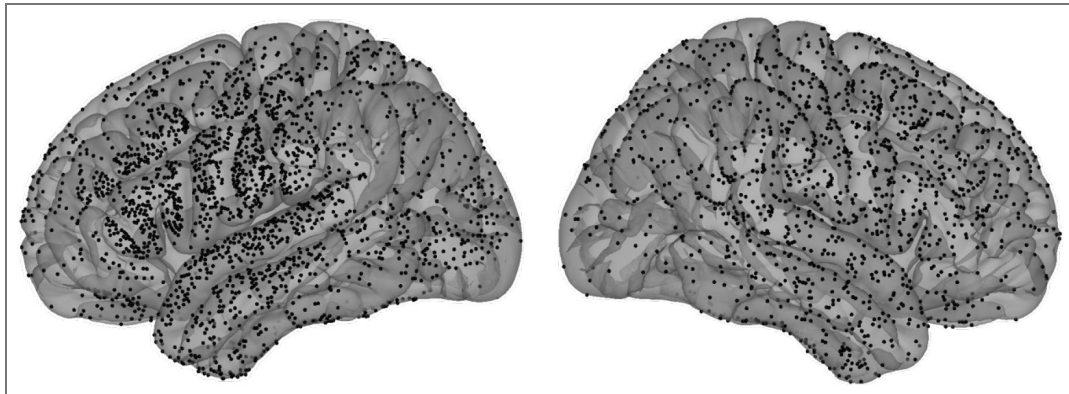
Statistical Analyses

For assessing the significant weights and connections (i.e. Decoding Framework and Single-Trial Functional Connectivity, respectively), We performed two-sided hypothesis tests at the single participant level. To control the family-wise error rate (FWER) across multiple comparisons, we applied a Bonferroni correction, maintaining an FWER of $\alpha = 0.05$. For active electrode selection, we compared the high-gamma neural activity of each trial averaged over time, with the distribution of high-gamma neural activity during baseline, and used a one-sided threshold with $\alpha = 0.05$ of the baseline to label an electrode as active on that trial.

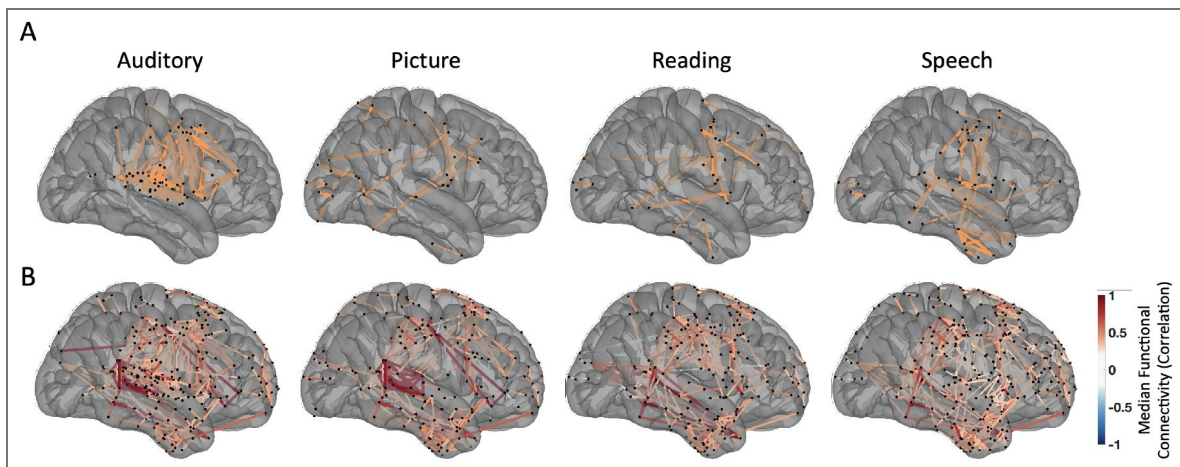
To compute the significance of the difference between uniqueness ratios (Figure 3C [↗](#)), we performed permutation test, randomly swapping the connections identified across the two methods (for each connection, values are 1 for significant/discriminative connection and 0 otherwise, then swapped between methods with probability 0.5), with 10,000 permutations. We controlled for multiple comparisons using the false-discovery rate for a $p < 0.05$ two-sided significance (Benjamini and Hochberg, 1995 [↗](#)).

To identify brain regions where the two methods yielded different results (Figure 4D [↗](#)), we compared the fraction of electrodes identified by the discriminative FC method against the fraction identified by the neural signal-only method. For each state s and region r , we defined the fraction(ratio) as the number of identified electrodes in r divided by the total electrodes recorded in r . This was statistically compared to a null hypothesis distribution by randomly permuting region labels across electrodes (preserving each region's total electrode count) while holding fixed which electrodes were identified by that method, recomputing the ratio difference $\Delta r = \text{ratio}_r^{\text{disc}} - \text{ratio}_r^{\text{sig}}$ in each region for 10,000 permutations. Two-sided p-values used the permutation tail; For each region and state, we controlled for multiple comparisons using the false-discovery rate (Benjamini and Hochberg (1995 [↗](#)), $\alpha = 0.05$).

Supplementary Information

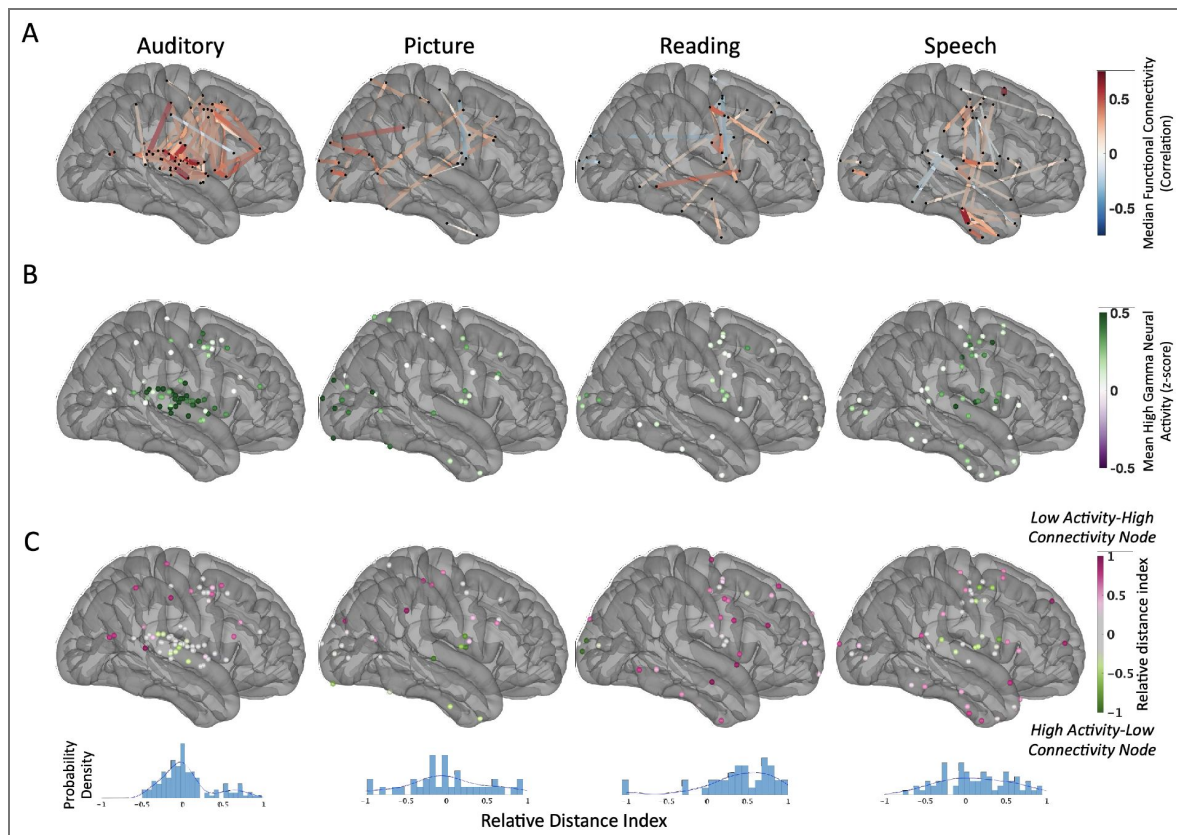


Supplementary Figure 1. The spatial electrode coverage across participants, showing both right and left hemisphere.



Supplementary Figure 2. Functional Connections identified using two methods, for participants with *right hemisphere* coverage.

(A) Cortical distribution of discriminative connections for each state. Orange lines depict connections whose median absolute deviation of the transformed SVM weights survive a Laplacian tail bound significance threshold; node positions correspond to electrodes. (B) Cortical distribution of connections selected solely by magnitude thresholding. The widespread, non-specific pattern contrasts with panel A, underscoring the greater specificity of the discriminative approach.



Supplementary Figure 3. Relationship between discriminative connectivity and local high-gamma activity, for participants with right hemisphere coverage.

(A) The cortical distribution of state-specific discriminative connections, visualized on the right lateral view of an average brain. The color represents mean functional connectivity values, representing the prominent connectivity patterns that remain stable across the trials of these state. (B) The cortical distribution of mean high-gamma activity, only for nodes participating in discriminative connections of each state. (C) Connectivity-activity relative distance index projected onto the cortex (pink = nodes with relatively higher connectivity than activity; green = nodes with higher activity than connectivity). This map highlights regions whose functional importance is underestimated by activity-only analyses.

Data availability

All code will be available under the Flinker Lab GitHub, and data will be available upon request.

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Peer reviews

Reviewer #1 (Public review):

In this study, the authors took advantage of a powerful method (iEEG) in a large participant cohort (N=42) to demonstrate specific functional connectivity signatures associated with speech. The results highlight the complementary utility of functional connectivity analysis to the more traditional iEEG approaches of characterizing local neural activity.

Strengths:

This is an interesting study on the important topic of cortical mechanisms of speech perception and production in humans. The authors provide strong evidence for specific functional connectivity signatures of speech-related cortical activity.

Weaknesses:

A potential issue of the work is the interpretation of the five studied experimental conditions as representing distinct cognitive states, where "task conditions" or "behavioral states" would have been more appropriate.

<https://doi.org/10.7554/eLife.109566.1.sa2>

Reviewer #2 (Public review):

Summary:

This study, conducted by Esmaeili and colleagues, investigates the functional connectivity signatures of different auditory, visual, and motor states in 42 ECoG patients. Patients performed three tasks: picture naming, visual word reading, and auditory word repetition. They use an SVM classifier on correlation patterns across electrodes during these tasks, separating speech production from sensory perception, and incorporating baseline silence as another state. They find that it is possible to classify five states (auditory perception, picture viewing, word reading, speech production, and baseline) based on their connectivity patterns alone. Furthermore, they find a sparser set of "discriminative connections" for each state that can be used to predict each of these states. They then relate these connectivity matrices to high-gamma evoked data, and show largely overlapping relationships between the discriminative connections and the active high-gamma electrodes. However, there are still some connectivity nodes that are important in discriminating states, but that do not show high evoked activity, and vice versa. Overall, the study has a large number of patients, and the ability to decode cognitive state is compelling. The main weaknesses of the work are in placing the findings into a wider context for what additional information the connectivity analysis provides about brain processing of speech, since, as it stands, the analysis mostly reidentifies areas already known to be important for speaking, listening, naming, and visual processing.

Strengths:

- (1) The authors were able to assess their connectivity analysis on a large cohort of patients with wide coverage across speech and language areas.
- (2) The use of controlled tasks for picture naming, visual word reading, and auditory word repetition allows for parcellating specific components of stimulus perception and speech production.
- (3) The authors chose not to restrict their connectivity analysis to previously identified high amplitude responses, which allowed them to find regions that are discriminative between different states in their speech tasks, but not necessarily highly active.

Weaknesses:

- (1) Although the work identifies some clear connectivity between brain areas during speech perception and production, it is not clear whether this approach allows us to learn anything new about brain systems for speech. The areas that are identified have been shown in other studies and are largely unsurprising - the auditory cortex is involved in hearing words, picture naming involves frontal and visual cortical interactions, and overt movements include the speech motor cortex. The temporal pole is a new area that shows up, but (see

below) it is important to show that this region is not affected by artifacts. Overall, it would help if the authors could expand upon the novelty of their approach.

(2) Because the connectivity is derived from single trials, it is possible that some of the sparse connectivity seen in noncanonical areas is due to a common artifact across channels. The authors do employ a common average reference, which should help to reduce common-mode noise across all channels, but not smaller subsets. Could the authors include more information to show that this is not the case in their dataset? For example, the temporal pole electrodes show strong functional connectivity, but these areas can tend to include more EMG artifact or ocular artifact. Showing single-trial traces for some of these example pairs of electrodes and their FC measures could help in interpreting how robust the findings are.

(3) The connectivity matrices are defined by taking the correlation between all pairs of electrodes across 500-ms epochs for each cognitive state, presumably for electrodes that are time-aligned. However, it is likely that different areas will interact with different time delays - for example, activity in one area may lead to activity in another. It might be helpful to include some time lags between different brain areas if the authors are interested in dynamics between areas that are not simultaneous.

(4) In Figure 3, the baseline is most commonly confused with other categories (most notably, speech production, 22% of the time). Is there any intuition for why this might be? Could some of this confusion be due to task-irrelevant speech occurring during the baseline / have the authors verified that all pre-stimulus time periods were indeed silent?

(5) How similar are discriminative connections across participants? Do they tend to reflect the same sparse anatomical connections? It is not clear how similar the results are across participants.

(6) The results in Figure 5F are interesting and show that frontal electrodes are often highly functionally connected, but have low evoked activity. What do the authors believe this might reflect? What are these low-evoked activity electrodes potentially doing? Some (even speculative) mention might be helpful.

(7) One comparison that seems to be missing, if the authors would like to claim the utility of functional connectivity over evoked measures, is to directly compare a classifier based on the high gamma activity patterns alone, rather than the pairwise connectivity. Does the FC metric outperform simply using evoked activity?

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Reviewer #3 (Public review):

I read this manuscript with great interest. The purpose of this paper is to use human intracranial recordings in patients undergoing routine epilepsy surgery evaluation to investigate speech production and perception during five specific and controlled tasks (auditory perception, picture perception, reading perception, speech production, and baseline). Linear classifiers were used to decode specific states with a mean accuracy of 64.4%. The interpretation of these findings is that the classifiers reveal distinct network signatures "underlying auditory and visual perception as well as speech production." Perhaps the most interesting finding is that the network signatures, including both regions with robust local neuronal activity and those without. Further, this study addresses an important gap by examining functional connectivity during overt speech production.

The abbreviation ECoG is used throughout the manuscript, and the methods state that grids and strips were placed, though many epilepsy centers now employ intracerebral recordings. Does this manuscript only include patients with surface electrodes? Or are depth electrodes

also included? The rendering maps show only the cortical surface, but depth recordings could be very interesting, given that this is a connectivity analysis.

Also interesting, given both the picture and reading task, is whether there is coverage of the occipitotemporal sulcus?

A major strength of the chosen paradigm is the combination of both perception (auditory or visual) and production (speech). Have the authors considered oculomotor EMG artifacts that can be associated with the change in visual stimuli during the task (see Abel et al. for an example PMID: 27075536, but see also PMID: 19234780 and PMID: 20696256).

I'm very interested in the findings in Figure 4D, with regard to the temporal pole. I would recommend that the authors unpack what it means that the ratio of electrodes with the strongest connections is highest, but active and discriminative is perhaps the lowest. We (I think many groups!) are interested in this region as a multimodal hub that provides feedback in various contexts (like auditory or visual perception).

Given the varieties of tasks and the fact that electrodes are always placed based on clinical necessity, are there concerns about electrode sampling bias?

This manuscript makes an important contribution by demonstrating that functional connectivity analysis reveals task-specific network signatures beyond what is captured by local neuronal activity measures (LFP). The finding that low-activity regions are engaged in task-specific classifications has important implications for future human LFP connectivity work.

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