Do neural oscillations reconfigure their networks to support adaptive listening behavior?

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Abstract:

Recently we provided a large-scale brain network account of adaptive listening behavior. Our study illustrated how modular reconfiguration of cortical networks derived from brain hemodynamic responses shape individuals' listening behavior, and accordingly posed an important question: Do frequency-specific neural oscillations reconfigure their networks at large-scale as they get engaged in active listening? Here we address this question by combining source imaging of scalp electrophysiological signals with frequency-resolved graph-theoretical network analysis. We first show that power-envelope correlation between neural oscillations within alpha/beta frequency band can be reliably measured during both resting and listening states. These correlations show a good agreement with those derived from brain hemodynamic responses. However, we find that there is no one-to-one correspondence between the modularity of hemodynamic brain networks and amplitude-coupled neural oscillations at a specific frequency. Our results suggest that precise spectral and topological characterization of amplitude-coupled neural oscillations requires frequency- and connection-resolved investigation.

Keywords: neural oscillations; amplitude coupling; network modularity; adaptive listening; EEG

Introduction

In noisy, multi-talker situations, listening turns into a challenging cognitive task for our brain. Under such circumstances, listening is often facilitated by a stronger engagement of auditory spatial attention ('where' to expect speech) and context-dependent semantic prediction ('what' to expect). It is plausible to assume that these neurocognitive strategies require a fine-tune configuration of distributed cortical networks in order to support listening success.

We recently provided a large-scale brain network account of adaptive listening behavior (Alavash et al., 2018). In our study, 49 participants underwent fMRI during resting state and a challenging speech comprehension task. We found that, in adaptation to the listening task, resting-state brain networks were reconfigured towards more localized cortical processing–predominantly within a fronto-temporal auditory-control network–and displayed higher modularity during the listening task. Importantly, the degree to which modularity of this auditory-control network increased relative to its resting state baseline predicted individuals' speech comprehension success.

An important question which remained unanswered is how coupling between frequency-specific neural oscillations underlies this task-specific reconfiguration. To answer this question, in the present study we combined source imaging of scalp electroencephalography (EEG) signals recorded during resting state and the same listening task with frequency-resolved graph-theoretical network analysis. Previous work suggest that task-specific cortical networks rely on neural interactions at slow time scale (<0.1 Hz) (Siegel et al., 2012). Specifically, power envelope of neural oscillations within alpha and beta frequency bands exhibit this characteristic, and their coupling–as measured by their envelope correlation over time–has been suggested as one network mechanism underlying behavior (Engel et al., 2013). Accordingly, the present study aims at spectral characterization of large-scale cortical networks during resting state and active listening, and asks whether the resting brain neural oscillations reconfigure their connectivity and modularity in adaptation to listening.

Materials and Methods

Participants Here we report the results based on the data of forty-nine healthy adult participants from an ongoing large-scale study entitled "The listening challenge: How ageing brains adapt (AUDADAPT)". Each participant completed seven runs of EEG recording: eyes-open resting state (~5 min) followed by six blocks of a challenging speech comprehension task (~10 min each). Out of these forty-nine participants,

twenty-four had also completed fMRI on a separate day, whose data have been used in (Alavash et al., 2018).

Listening task As the focus of the present study is on spectral characterization of large-scale cortical networks at resting and listening states, we here provide only a brief description of the listening task and refer the reader to (Alavash et al., 2018) for details. During the task, participants listened to two competing, dichotically presented sentences and were probed on the sentence-final word in one of the two sentences. Sentence presentation was preceded by two cues that informed participants about the to-be-probed side (spatial cue) and the semantic category of the two sentence-final nouns (semantic cue). The participants had the task to choose the final word of the to-be-probed sentence form a visual response array.

EEG recording and analysis Electroencephalogrphy was conducted using 64 active cap electrodes. EEG data were analyzed using EEGlab and Fieldtrip Matlab toolboxes (Delorme and Makeig, 2004; Oostenveld et al., 2011). Independent component analysis (ICA) was used to remove all non-brain signal components. This procedure was applied to the concatenated rest and task data. The continuous EEG was band-pass-filtered (0.3 –180 Hz). Task data were cut into epochs –2 to 8 s relative to the onset of the spatial cue to capture cue presentation and the entire auditory stimulation. Resting state data were similarly cut into 10-sec continuous epochs. Spectrotemporal estimates of the sensor signals were obtained within each epoch, at frequencies ranging from 8 to 32 Hz (Morlet's wavelets).

EEG source imaging Individual forward head models were created using each participant's T1 MRI. The fit of digitized head surface points to individuals' reconstructed head surfaces were optimized using rigid-body transformation. Individual anatomical images were spatially normalized to the standard Connectome Workbench template. The inverse of these operations were applied to a cortical surface grid in the same template space to obtain subject-specific cortical surface grid points. The physical relation between sources and sensors for all grid points was estimated using boundary element method. Next, a frequency-domain beamforming approach, namely partial canonical coherence (PCC) (Schoffelen and Gross, 2009) was applied to the concatenated rest and a 5-min task data to obtain a common spatial filter. Finally, the sensor-level complex-value wavelet estimates were projected to source space using the spatial filters.

Cortical parcellation and connectivity analysis Nodes of the networks were defined according to a multimodal parcellation encompassing 362 cortical nodes (Glasser et al., 2016). This template was used to average time-frequency estimates across grid points within each node. To assess frequency-specific neural interactions, we computed Pearson's r between the log-transformed powers of all pairs of nodes separately for resting state and listening task. To eliminate the trivial common co-variation in power measured from the same sources, we used the orthogonalization approach proposed by (Hipp et al., 2012). This gave us frequency-specific 362-by-362 correlation matrices per subject, for each rest and task condition.

Network analysis Brain graphs were constructed based on connectivity matrices by including links in the graph according to the rank of their absolute correlations. The number of links in each brain graph was fixed at 10% of network density. Mean connectivity was defined as the average of upper-diagonal correlations within the sparse matrices. Network modularity was quantified using Newman's optimization algorithm as implemented in the Brain Connectivity Toolbox (Rubinov and Sporns, 2010).

Reliability analysis of EEG source connectivity The signal-to-noise ratio (SNR) poses a serious but often neglected potential confounding factor in assessments of neuronal interactions. This is an important issue in the present study as we compare connectivity under two conditions, i.e., resting state and listening task, each of which is potentially measured at different levels of SNR. Therefore, we first asked at which frequency and cortical node connectivity can be measured reliably in both conditions. As a measure of reliability, we used between-subject correlation of connectivity patterns (columns of correlation matrices) across rest and task. This correlation is underestimated in the presence of noise. Thus, we applied Spearman's correction for attenuation to account for differences in SNR, similar to (Hipp and Siegel, 2015). At a given frequency and node, estimation of connectivity was considered reliable if the attenuation-corrected correlation was consistently positive across all participants.

Relation to fMRI For those participants with both EEG and fMRI, we assessed the correlation between mean connectivity and network modularity across the two imaging modalities using Spearman's rank correlation.

Results

EEG power-envelope correlations can be reliably measured within alpha/low-beta bands

Power-envelope correlations estimated under resting state and the listening task showed consistently positive between-subject correlations in node-to-all connectivity within the frequency range 4–32 Hz (Fig. 1A).
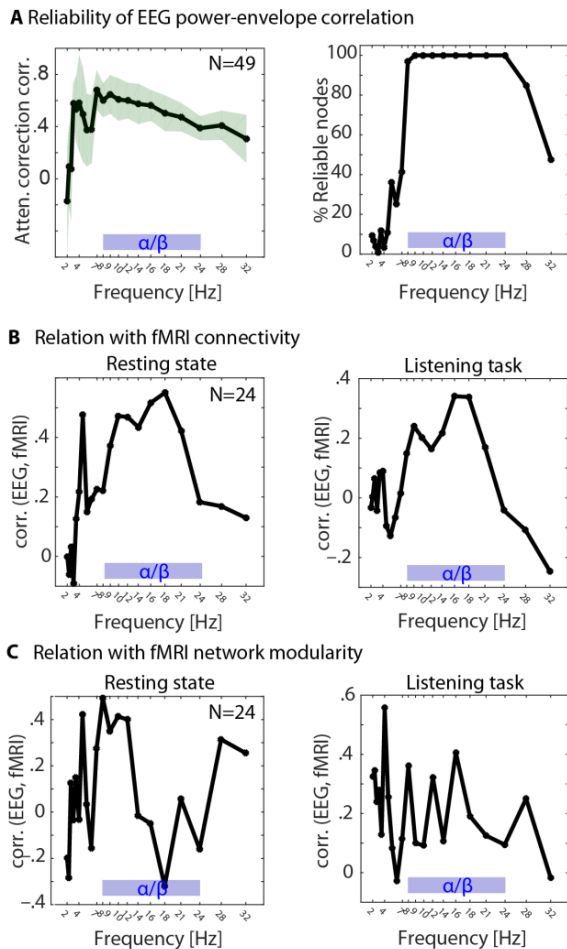
A Reliability of EEG power-envelope correlation

B Relation with fMRI connectivity

C Relation with fMRI network modularity

Figure 1: Reliability of EEG source connectivity and its correspondence with fMRI under resting and listening states. Shaded errors in A: ±SEM across cortical nodes.

As these correlations were averaged across all cortical nodes, we next quantified percentage of nodes which showed this relationship. We found that within the frequency range 8–24 Hz (alpha/low-beta) envelope-correlation was measured reliably across all cortical nodes under both resting state and listening task (Fig. 1A).

Correspondence between EEG and fMRI connectivity within alpha/low-beta range

Twenty-four participants out of 49 were those who also completed the same experiment inside fMRI scanner. For these participants, we found consistently positive correlations between EEG and fMRI whole-brain connectivity within high-alpha/low-beta bands. These positive correlations were found for both resting state

and listening task conditions, and peaked at frequencies ~16 Hz (Fig. 1B).

No one-to-one correspondence between EEG and fMRI network modularity

The correlation between network modularity across the two imaging modalities did not show a consistent spectral profile. For resting state, this correlation was positive in the range 8–12 Hz (r~0.4) and turned negative in the range 16–24 Hz (r~–0.2; Fig. 1C). In the case of the listening task, this correlation fluctuated but remained positive within the range 8–24 Hz.

Spectral profile of cortical networks differ between resting and listening states

We next focused on the connectivity and network modularity derived from EEG power-envelope correlations under each rest and task condition. For connectivity, the spectral profile peaked at 10 Hz in the case of resting state, and it plateaued within 8–21 Hz in the case of the listening task (Fig. 2AB, left). Within this range, the strength of mean connectivity was weaker in the case of listening task as compared to resting state (Fig. 2C, left). This difference was significant only at 10 Hz (permutation test, p=0.03, Cohen's d=−0.25). For modularity, the difference was the strongest at 8 and 16 Hz (permutation test, p<0.01, Cohen's d=−0.75).

Discussion

Our results suggest that power-envelope correlations within alpha/low-beta ban can be reliably measured using source imaging of conventional 64-channel EEG signals during resting state and task. The strength of these correlations showed a good correspondence with those derived from brain hemodynamic responses below 0.1 Hz. This is in good agreement with previous studies (Hipp and Siegel, 2015).

However, when modularity in these large-scale networks is compared between the two imaging modalities, a direct correspondence seems lacking. Network modularity is a topological metric which depends on the connection patterns across the network rather than the correlations per se. It has been previously suggested that correlations between brain hemodynamic responses reflect different electrophysiological processes in different frequencies (Hipp and Siegel, 2015). Importantly, it has been shown that this dependency is different across cortico-cortical connections. Accordingly, we argue that the topology of cortico-cortical neural interactions as measured by power-envelope correlation depends on the cortical site and frequency of the interacting nodes.
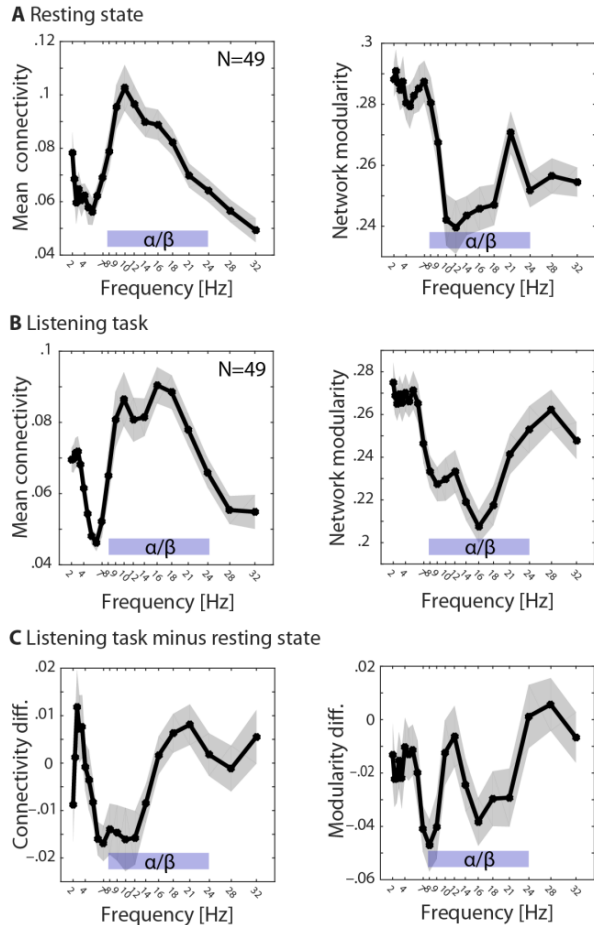
A Resting state

B Listening task

C Listening task minus resting state

Figure 2: Spectral profile of whole-brain connectivity and network modularity under resting and listening states. Shaded errors: ±SEM across N=49 participants.

Here we additionally compared connectivity and modularity of large-scale networks of amplitude-coupled neural oscillations between resting state and listening task. Based on our recent fMRI study we expected a degree of reconfiguration in these networks, particularly within alpha/low-beta band. The connectivity and modularity of resting and listening brain networks within this range were indeed different. In line with our prediction, this difference was more pronounced for network modularity, particularly at 16 Hz. However, the direction of this network alteration was opposite to what we had found in fMRI: modularity decreased during listening as compared to resting state. This finding again suggests that there is no one-to-one correspondence between the topology of hemodynamic brain networks and amplitude-coupled neural oscillations at a specific frequency.

In sum, our results support the view that amplitude-coupling of neural oscillations at alpha/beta band can be used as a proxy for brain-wide network

communication at different cognitive states. However, the precise spectral and topological characterization of these networks requires frequency- and connection-resolved investigation.

Acknowledgments

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