Elucidating relations between fMRI, ECoG and EEG through a common natural stimulus

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Human brain activity can be studied at different spatial and temporal scales using fMRI, ECoG and EEG. To assess how reliably these imaging methods reflect brain responses related to a complex audio-visual stimulus and how similar stimulus-related responses are across methods, we presented a movie clip twice to three different cohorts of subjects (N_{EEG} = 45, N_{fMRI} = 11, N_{ECoG} = 5) and assessed correlations across viewings and imaging methods within a standardized brain space. Grand-average broad-band EEG and low-frequency (4–28 Hz) EEG power reached similar levels of inter-subject reliability as grand-average fMRI and single-subject high-frequency (28–116 Hz) ECoG power. ECoG power was negatively correlated with fMRI in low frequencies and positively correlated in high frequencies in temporal and occipital brain areas. Low-frequency EEG power was negatively correlated with fMRI in occipital and parietal, but positively correlated in temporal areas. We also observed strong correlations between fMRI and infra-slow EEG voltage fluctuations.

fMRI | EEG | ECoG | inter-subject correlation | inter-method correlation
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Introduction

The ability to measure human brain activity at high temporal and spatial scales is of vital importance in many branches of neuroscience. The most frequently-used neuroimaging techniques are functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). Both approaches are complementary in that fMRI provides high spatial but low temporal resolution, while the opposite is true for EEG. Invasive methods such as electrocorticography (ECoG) combine high temporal resolution with relatively high spatial resolution; however, such procedures are only used in small cohorts of neurological patients, where the coverage of the implanted electrodes is constrained and guided by purely clinical considerations. ECoG, EEG and fMRI also differ in their underlying neurophysiological origin, and are susceptible to different noise sources (e.g., artifacts, pathological activity). ECoG electrodes pick up the summed electric activity of neurons within a range of millimeters (Logothetis, 2003), while scalp EEG electrodes are sensitive to synchronous activity of larger populations of pyramidal neurons on the centimeter scale. The blood-oxygen-level dependent (BOLD) signal measured by fMRI, on the other hand, reflects the brain's indirect hemodynamic response to neural activity.

Thus, each imaging method provides a unique window into human brain functioning, and there is increasing interest in combining these methods and studying relations between them. The predominant approach to multi-modal neuroimaging are concurrent recordings. Simultaneous ECoG–fMRI recordings in animals (Logothetis et al., 2001; Magri et al., 2012) and simultaneous EEG–fMRI in humans (Moosmann et al., 2003; Ritter et al., 2009; Ritter and Villringer, 2006; Scheeringa et al., 2009) have successfully established links between ECoG/EEG power and the BOLD signal. The main findings of these studies are that high-frequency power in the ECoG correlates positively with BOLD, and that ECoG and EEG power in low frequencies correlates negatively with BOLD. These effects are, however, not uniformly distributed across the cortex, but display frequency-dependent spatial topographies (Scheeringa et al., 2009), in line with theoretical models (Hermes et al., 2017). Thus, there exists a rather fragmented body of evidence derived from distinct experimental paradigms and species, but no study yet has provided a comprehensive spatio-spectral account of the relations between human fMRI, ECoG and EEG. Here, we aim to narrow this gap in a study combining all three measurement techniques.

To circumvent the technical challenges associated with concurrent multi-modal recordings, data from three different cohorts of subject were acquired, where only a single measurement technique was used per cohort. Each subject was presented with the same audio-visual movie, which allowed us to temporally align data of different subjects (cohorts), and to quantify their similarity using inter-subject correlations (ISC, Hasson et al., 2010, 2004). The richness of the movie stimulus thereby ensured that not only auditory, visual and multi-sensory systems were engaged in the viewing task, but also a host of higher-level cognitive functions such as language, memory, and attention. The use of ISC further allowed us to rule out correlations induced by physiological or artifactual fluctuations not related to the task, which would be present in concurrent multi-modal recordings. The degree of ISC can, therefore, be regarded as a measure of the reliability of the stimulus-related response or, alternatively, of the signal-to-noise ratio (SNR) of stimulus-related versus stimulus-unrelated activity. Inter-subject correlations have previously been used to study cognitive processes with fMRI (Chen et al., 2017; Jääskeläinen et al., 2008; Mantini et al., 2012), ECoG, (Honey et al., 2012), EEG (Cohen and Parra, 2016; Dmochowski et al., 2012; Ki et al., 2016), and MEG (magnetoencephalography, Lankinen et al., 2014), but not to elucidate the relations *between* these measurement tech-

niques.

Here, we use ISC to address two questions. First, how reliably can stimulus-related responses across different brain structures and spectral regimes be picked up by each single imaging technique? To study this, we assessed temporal correlations between brain signals recorded during two identical renditions of the stimulus *within* the same subject cohort. Second, how similar are the responses picked up by different techniques? That is, to what extent do they reflect the same stimulus-related activity? We address this question by studying correlations *between* subject cohorts in a common anatomical space. To allow meaningful comparisons of correlations across methods, we harmonized the spatial and temporal scales of the different datasets using spatial co-registration and the standardization of correlation coefficients using data-dependent null distributions.

Signal-to-noise ratio can be substantially enhanced by averaging across subjects, which is straightforward for EEG and fMRI but not ECoG data. The present analysis focuses on the pragmatic question of how much stimulus-related information can be extracted in a neuroimaging experiment with a typical sample size. We therefore report 'population-SNR' obtained from 'grand-average' signals in the main text. In contrast, one may also ask a more basic question; namely, what is the SNR of the signal generators in the brain, comparing, say, electric fields with metabolic activity. In this case the more relevant quantity is the SNR of single subjects, which we report in the supplement.

Results

Three separate cohorts of subjects were presented with a 325 s long segment of a feature film (Dog Day Afternoon; previously used by Honey et al., 2012) two times, and neural activity was recorded with EEG (N = 45 subjects), fMRI (N = 11) and ECoG (N = 5). We analyzed correlations of 'raw' broad-band signals of all imaging methods as well as of EEG/ECoG power fluctuations in five frequency bands: θ (4–8 Hz), α (8–12 Hz), β (12–28 Hz), γ (28–56 Hz) and the high frequencies (HF, 64–116 Hz). As our emphasis is not on single-subject prediction but on quantifying the effects that can be obtained from entire cohorts of realistic sizes, we performed grand-averaging (GA) of the EEG and fMRI (after spatial normalization) data. In ECoG, this averaging across subjects is not possible, as electrode montages differ between subject; we therefore combined the ECoG channels of all subjects into a single dataset.

Reliability of responses within imaging methods

To assess the *reliability* of stimulus-related brain activity for each method, we calculated the correlation of the continuous neural responses across the two renditions of the stimulus, which we refer to as the inter-viewing correlation (ISC). Correlations were assessed separately for each anatomical location using Pearson's r, and their statistical significance was assessed by comparing observed values to a null distribution obtained from surrogate data. The resulting z-scores correct for unequal variances of the estimated correlation coefficients that arise from different sampling frequencies and data-dependent auto-correlation spectra. While z-scores with absolute values greater than 1.96 classically indicate significance at an alpha level of 5%, we here also interpret their values as objective measures of how much the observed correlations stand out against random fluctuations in the data.

In practice, the choice of the 'right' metric depends on one's analysis goals. Strong correlations (if significant) are useful if one wants to predict one time course from another, where stronger correlations imply better predictability. This could, for example, be of practical relevance if one wanted to approximate ECoG activity from non-invasive EEG measurements. In contrast, if one is interested in how correlation values fluctuate over time, or between conditions, then the relevant metric is the z-score. For example, one may want to test if inter-subject correlations are statistically significant, or if they differs between task conditions. In those instances the relevant question is not how large or small the correlations are, but rather, how stable they are in the face of chance fluctuations. There, a high z-score is more relevant than a large r-value.

We observed strong and highly significant ISC of neural activity for all three imaging methods (Fig. 1). The grand-average fMRI BOLD signal reaches a maximum ISC of $r_{max} = 0.79$, where strongest correlations are observed in temporal, parietal, occipital and fronto-temporal areas known to implement auditory and visual processing hierarchies. Without averaging, the maximum ISC for single subjects reaches only $r_{max} = 0.39$ with a similar spatial distribution (Fig. 1–Suppl. 4). Significant ISCs of single-subject ECoG band-power traces were observed in very similar areas in all studied frequency bands. In contrast to fMRI, significant ISC are also present in central sensori-motor areas, while the lack of ECoG electrode coverage in parietal regions (see Fig. 3) prevents ISC analysis in these regions. The strongest ISC are in the same range as those observed for GA-fMRI ($r_{max} = 0.77$), and were observed in the superior temporal gyrus for high-frequency oscillations. These results reproduce what has been reported by (Honey et al., 2012) on the same ECoG data. GA-EEG band-power in the lower frequency bands (θ, α, and β) reaches maximal ISC levels only slightly below what is observed for ECoG and GA-fMRI ($r_{max} = 0.72$). Grand-averaging is particularly effective for EEG (compare Fig. 1 with Fig. 1–Suppl. 4). Without grand-averaging ISC for single-subject EEG only reach values around 0.1 (notice that the color map has been enhanced to show these smaller value). These smaller ISC are consistent with previous reports in EEG and MEG (Dmochowski et al., 2012; Lankinen et al., 2014). The levels of ISC are comparable when computed on scalp sensor data and on cortical sources estimated using a linear solution to the EEG inverse problem (Pascual-Marqui, 2007, eLORETA,). In both cases, the topography of significant effects shows a broad global pattern, with diminished values observed only in fronto-temporal regions. High-frequency and γ-band activity hardly show any significant effect, speaking to the susceptibility of the EEG signal

to movement artifacts and the relative weakness of coherent brain activity reaching scalp sensors in these frequency ranges.

To ensure compatibility with fMRI and previously published ECoG results (Honey et al., 2012), the ISCs between EEG and ECoG band-power traces shown in Fig. 1 were obtained on data reduced to the fMRI sampling rate of 0.67 Hz. When evaluated at a higher sampling rate of 256 Hz, ISCs dropped to a maximum of r_{max} = 0.23 for ECoG and r_{max} = 0.53 for EEG (c.f. Fig. 1–Suppl. 2). However, no such differences were observed when statistically assessing how much the observed ISCs departed from the null distribution with the same spectral content (Figs. 1–Suppl. 1 and 1–Suppl. 3). An explanation for this stability is that the noise (non-stimulus-related activity) above 0.33 Hz diminishes inter-subject correlations as well as correlations that arise under the null hypothesis to the same extent, limiting the variance of the latter. Removing that noise through low-pass filtering increases ISC, but to the same extent also correlations that could arise under the null hypothesis, leading to the same level of significance (see also Fig. 1–Suppl. 5). If anything, maximal z-scores were higher for EEG power fluctuations in the θ-, α-, and β-bands when sampled at 256 Hz (z_{max} = 15.9) as compared to 0.67 Hz (z_{max} = 9.2). The same was observed for HF-ECoG oscillations (z_{max} = 15.3 for 256 Hz compared to z_{max} = 10.5 for 0.67 Hz sampling rate). This increase in correlation suggests that stimulus-related amplitude fluctuations in these data are predominantly occurring at frequencies below 0.33 Hz (see Fig. 1–Suppl. 5). However, downsampling reduces z-scores because a substantial amount of reliable activity occurs above 0.33 Hz, as verified when applying a spectrally-resolved inter-subject coherence analysis (Fig. 1–Suppl. 5).

Inter-subject correlations of raw broad-band EEG and ECoG voltage fluctuations were assessed at a sampling frequency of 256 Hz, and reached maximal values of r_{max} = 0.56 in GA-EEG and r_{max} = 0.26 in ECoG (Fig. 1). The topography of EEG-ISC is most similar to the topography obtained with EEG θ-band power, while the ECoG-topography closely resembles the ISC distribution observed in HF-ECoG. These correlations are highly significant (z_{max} = 23.4 for both, see Fig. 1–Suppl. 1).

Similarity of responses between imaging methods

To assess the *similarity* of responses between imaging methods, we measured the *inter-method correlation (IMC)* after spatial co-registration (see Spatial registration and Mappings between fMRI, ECoG and EEG spaces for technical details). As before, results for fMRI and EEG were computed with the signal averaged across subjects (grand-average). We observed significant correlations of stimulus-related responses between all three neuroimaging methods (Fig. 2). These are strongest between the fMRI BOLD signal and ECoG band-power with absolute values exceeding r_{max} = 0.61 in all frequency bands. ECoG power in the lower frequency bands (θ, α, β) was negatively correlated with BOLD in virtually all cortical areas with significant ISC (θ: r_{min} = -0.72, α: r_{min} = -0.72, β: r_{min} = -0.70). In contrast, γ- and HF-ECoG power in the same areas was positively correlated with fMRI (γ: r_{max} = 0.61), HF: r_{max} = 0.72), the only exception being γ-power in the sensorimotor-areas, which were negatively correlated with fMRI. Unlike ECoG, EEG band-power in the lower frequencies shows diverse effects. θ- and α-power fluctuations in temporal areas are positively correlated with fMRI BOLD (θ: r_{max} = 0.46, α: r_{max} = 0.35), while α- and β-power fluctuations in occipital and parietal areas were negatively correlated with fMRI (r_{min} = -0.58 for both). θ-band EEG power in parietal areas also showed a negative correlation with fMRI (r_{min} = -0.38). EEG and ECoG power in lower frequency bands were predominantly positively correlated, with strongest correlations observed in occipital cortex between α-band EEG and β-band ECoG (r_{max} = 0.45). Note that correlations between fMRI, EEG band-power and ECoG band-power were again assessed on data sampled at 0.67 Hz (Fig. 2). Assessing correlations between EEG and ECoG band-power at 256 Hz sampling frequency diminished correlations but slightly increased the detectability of the correlations in terms of z-scores (see Figs. 2–Suppl. 1–2–Suppl. 3). Significant, yet small correlations were also observed between raw broad-band EEG and ECoG voltage fluctuations (r_{max} = 0.05) at 256 Hz sampling rate. Furthermore, we observed significant correlations between the fMRI signal and raw infra-slow EEG below 0.33 Hz (Fig. 2), which were localized predominantly in temporal areas. A similar IMC analysis between raw ECoG and fMRI was not possible due to a high-pass filter of 0.6 Hz that was applied to the ECoG data at recording time.

Discussion

Our analyses identified brain areas related to the processing of a complex audio-visual narrative in temporal, occipital, parietal and sensori-motor areas, in line with previous reports (Honey et al., 2012; Jacques et al., 2016). Reliable stimulus-related activity in these areas was found not only in fMRI BOLD signals and high-frequency power of the ECoG, but also in low-frequency EEG and ECoG rhythms as well as in raw broad-band EEG and ECoG voltage fluctuations. The regions involved in stimulus-related processing are strikingly consistent between fMRI and ECoG, suggesting that both methods pick up similar brain responses as previously established in Logothetis (2003). This finding was further corroborated by studying correlations between methods. In line with results obtained in simultaneous fMRI-ECoG recordings (Logothetis et al., 2001; Mukamel et al., 2005; Niessing et al., 2005; Nir et al., 2007), we observed positive correlations between fMRI and high-frequency ECoG activity, but negative correlations between fMRI and low-frequency ECoG, suggesting that HF-oscillations are more directly linked to BOLD than other brain rhythms (Magri et al., 2012). We also observed negative correlations between EEG band power and BOLD in parietal, occipital and rolandic areas in line with previous reports on simultaneous recordings (Moosmann et al., 2003; Ritter et al., 2009) and separate recordings linked through a common task

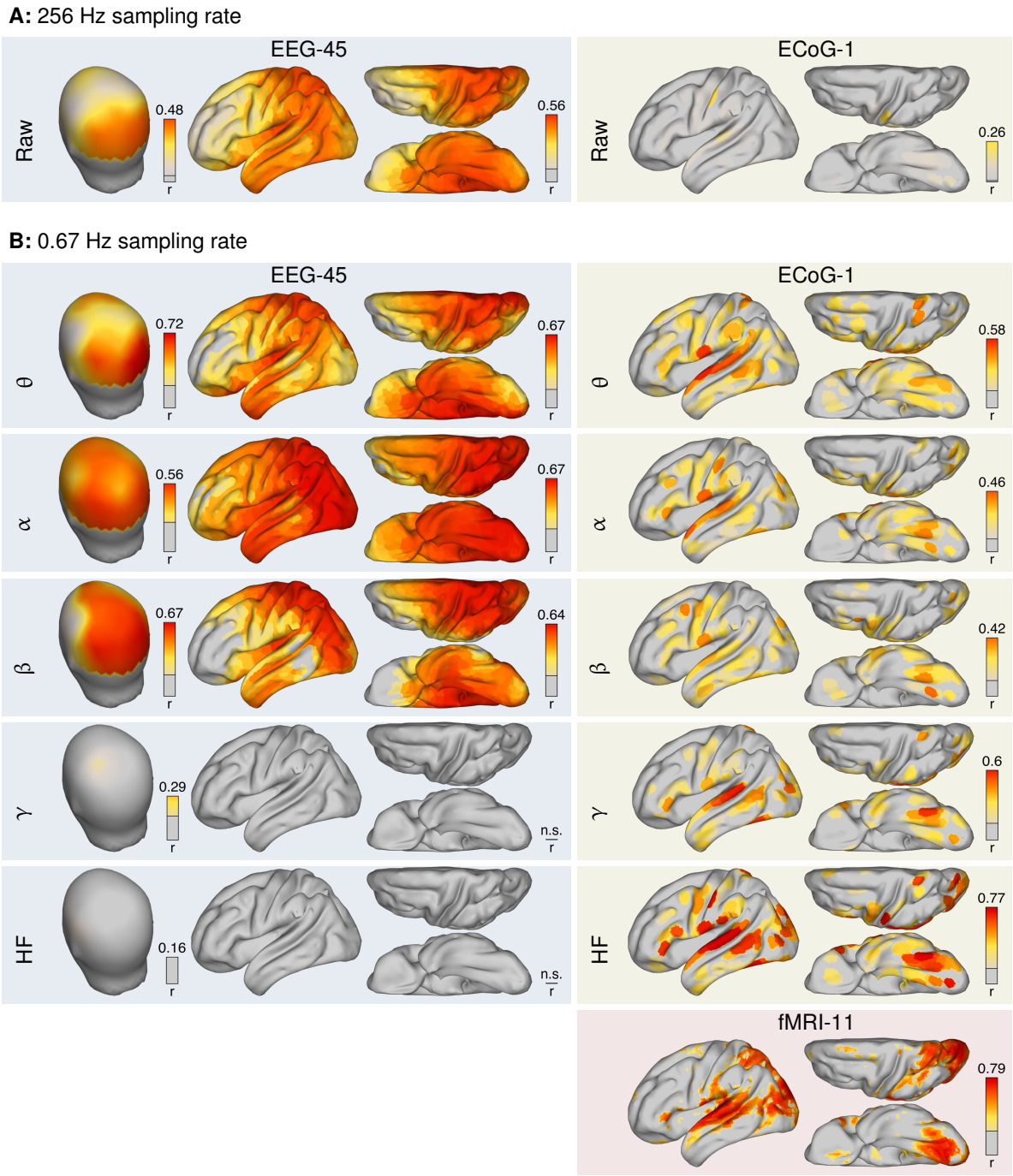

Fig. 1. Reliability of stimulus-related brain activity measured with EEG, ECoG and fMRI BOLD as assessed in terms inter-subject correlations (ISC), r of signals acquired during two separate viewings of a 325 s long audio-visual movie stimulus. EEG data were analyzed at 32 sensors and 2,004 cortical locations after source reconstruction by eLORETA. fMRI data were analyzed at 16,037 cortical locations, while ECoG data were analyzed at 511 cortical locations representing the pooled set of electrodes in five subjects. 'Raw' broad-band EEG and ECoG voltage fluctuations were analyzed at 256 Hz sampling frequency (panel **A**). In addition, the instantaneous log-power of EEG and ECoG oscillations in the following frequency bands were analyzed at the same sampling frequency as fMRI (0.67 Hz, panel **B**): θ (4–8 Hz), α (8–12 Hz), β (12–28 Hz), γ (28–56 Hz) and high-frequency (HF, 64–116 Hz). EEG data of 45 subjects and fMRI data of 11 subjects were grand-averaged before ISC analysis. ISC was measured in terms of Pearson correlation, r, and plotted onto the outer head surface (sensor-space EEG) or the smoothed cortical surface of the left brain hemisphere (ECoG, fMRI, source-space EEG, shown from left, top, and bottom). Statistically significant values (surpassing results on phase-randomized surrogates with $p < 0.05$, uncorrected) are shown in color, whereas gray areas indicate non-significant ISC. Numbers above the color bars indicate maximal correlation values. As ECoG data do not provide a full coverage of the cortex (see Fig. 3), gray areas also mark the absence of any electrode within 12 mm distance.

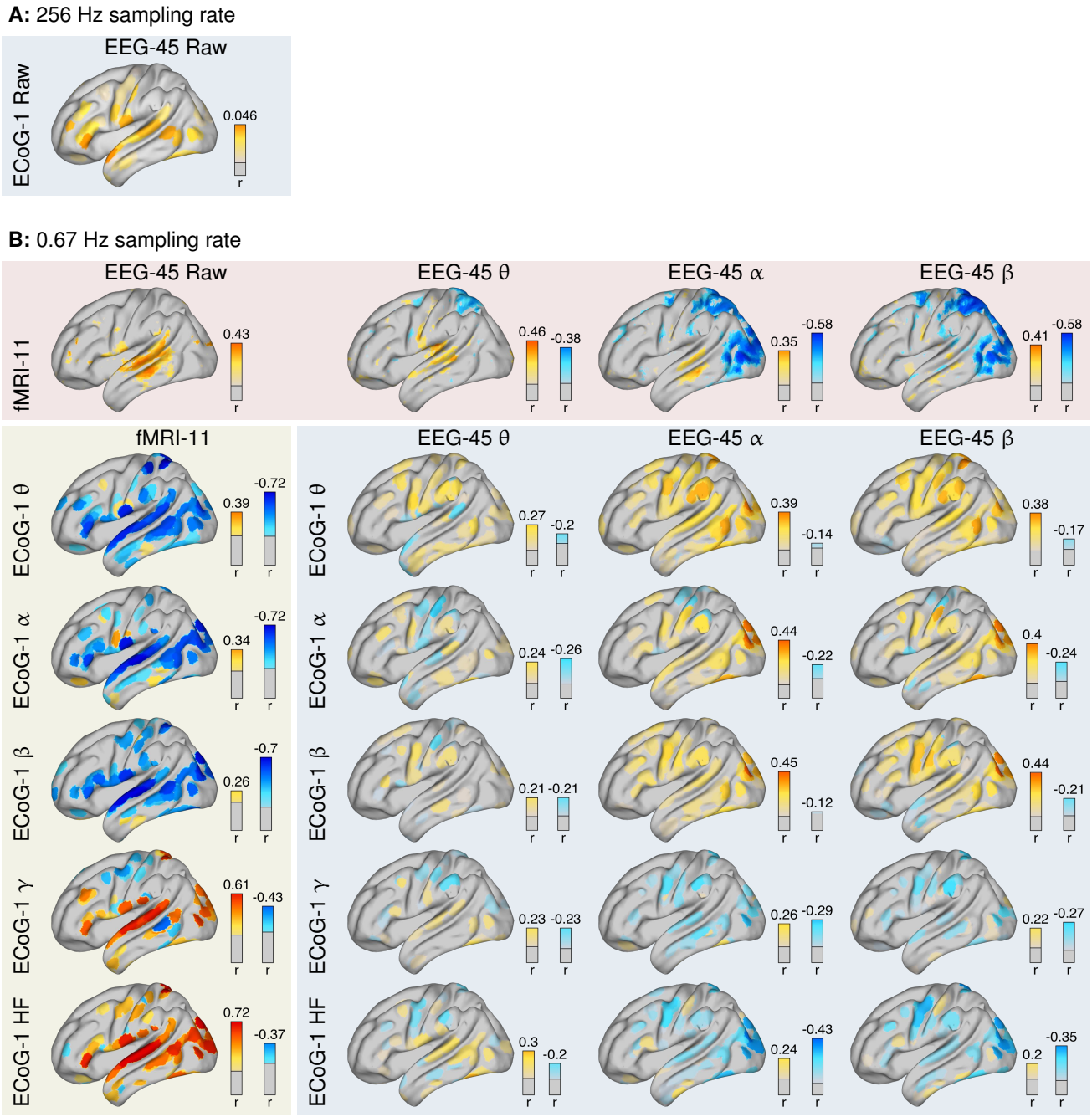

Fig. 2. Similarity of stimulus-related brain activity between EEG, ECoG and fMRI BOLD as measured in terms of inter-method correlations (IMC) between co-localized single-subject ECoG, grand-average EEG and grand-average fMRI BOLD activity. IMC was assessed in terms of Pearson correlation, r, between 'raw' broad-band EEG and ECoG voltage fluctuations at 256 Hz sampling rate (panel **A**, notice the different color scale compared to panel B) as well as between fMRI and raw EEG, between fMRI and EEG band-power, between between fMRI and ECoG band-power, and between EEG and ECoG band-power (panel **B**) at 0.67 Hz sampling rate. Frequency bands are the same as in Fig. 1. Matching of co-localized ECoG electrodes and cortical fMRI voxels was based on Euclidean distance. Source-reconstructed EEG activity (eLORETA) was matched with ECoG electrodes/fMRI voxels based on maximal IMC with a 5 cm radius. Statistically significant IMC values (surpassing results on phase-randomized surrogates with $p < 0.05$, uncorrected) are shown in color, whereas gray areas indicate non-significant IMC. Numbers above color bars indicate maximal correlation values.

(Scheeringa et al., 2009; Yuan et al., 2010).

Interestingly, temporal areas showed predominantly positive correlations between fMRI and EEG in the θ and α-bands, while negative correlations were observed in occipital cortex in the α and β-bands. This selectivity in the α-band suggests a modality-specific role of alpha oscillations in audio-visual processing. Further analyses are, however, required to rule out that this mixed polarity is not driven by anti-correlated fMRI activity in visual and auditory cortex.

Another interesting observation is that, within the lateral temporal lobe, correlations involving α-power are seemingly inconsistent: fMRI correlates positively with α-power in ECoG and EEG, yet the latter two are negatively correlated. Mixed signs in the correlations of three variables can, however, arise when these variables contain different mixtures of underlying signals. For example, there could be a 'local' signal that is picked up by fMRI and ECoG (with opposing signs), but not EEG. If this local signal is superimposed by a 'global' signal that is pickup up by all three methods with the same sign, one obtains the observed mixed correlation patterns. A testable prediction of this model is that the negative correlation between ECoG and fMRI would increase if EEG is regressed out of ECoG and fMRI.

A noteworthy result of the present study is that we identified strong stimulus-induced correlations of the BOLD signal and the infra-slow EEG signals below 0.33 Hz (Fig. 2, panel B). Previous links between hemodynamic responses and infra-low EEG had been associated with resting-state fluctuations (Hiltunen et al., 2014), the slow-cortical potential (He and Raichle, 2009), and arterial blood pressure (Nikulin et al., 2014). Most studies in this field used simultaneous recordings; correlated activity could therefore be the result of common physiological or artifactual confounds such as heart beat, breathing, etc. Here, we could exclude the presence of any confounds unrelated to the cognitive task. The observed correlations between infra-slow EEG and fMRI were most pronounced over temporal areas, suggesting auditory and speech perception processes as drivers.

Benefits and limitations of inter-subject correlations

Our analyses relied on correlations between separately-acquired but synchronized recordings within and across imaging methods. This framework allowed us to assess the similarity of signals from different imaging methods without multi-modal recordings, while at the same time preventing task-irrelevant brain processes from driving our results (Hasson et al., 2004; Mukamel et al., 2005). An additional advantage of this approach is that one can prevent the technical complications and significant signal-loss resulting from simultaneous recordings. For example, concurrent EEG–MRI recordings are severely affected by artifacts of the fMRI gradient and the ballisto-cardiogram, while the combination of ECoG with other measurements is made difficult by safety considerations as well as susceptibility artifacts in the fMRI around the electrodes. While this approach is well-suited for the present investigation, the scope of studies in which it can be applied is limited by the requirement that identical timings of relevant events must be enforced in all experiments. As an intended side effect, all correlations reported here exclusively relate to brain processes involved in processing the audio-visual narrative. The spatial distribution of reliable brain activity reported here must, therefore, be interpreted exclusively in terms of that cognitive task, and should not be mistaken as representative of all brain signals captured by the different imaging methods.

Cohort size and impact of grand-averaging

EEG and fMRI data presented here were averaged across subjects before assessing the reliability of the task-related responses they contain. This form of 'grand-averaging' is well established to analyze evoked potentials in EEG and has recently also been used in fMRI (Schmaelzle et al., 2017). We did not average across subjects in ECoG due to inconsistent electrode montages in each of the five subjects. Using grand-averaging in EEG and fMRI, the SNR could be increased to reach similar levels of reliability as in single-subject ECoG. Without grand-averaging, the observed reliability of fMRI was lower than in ECoG. This drop was even more pronounced in EEG. Note that the sample sizes used here are typical in research studies, and are indicative of the ease of obtaining these data for the different methods. The obvious disadvantage of averaging is the potential loss of spatial (and functional) resolution due to anatomical or functional misalignment across subjects, as well as the loss of subject-level information. Whether or not grand-averaging is a useful approach in a given neuroimaging study will depend on this trade-off between (functional) resolutions and signal-to-noise ratio as well as the general analysis goal.

Among the various signals analyzed here, raw EEG/ECoG times series were somewhat less reliable across stimulus repetitions, but were highly significant compared to chance fluctuations (for the EEG, after grand-averaging). Raw stimulus-evoked EEG activity has traditionally been studied by averaging brain responses across many repetitions of a simple stimulus within highly controlled experiments (Luck, 2014). More recently it has been used with naturalistic stimuli by correlating activity between subjects (Cohen and Parra, 2016; Dmochowski et al., 2014; Ki et al., 2016). Given the large z-scores observed here, these signals may have been generally under-appreciated, as they remain largely unexplored, with a few notable exceptions (e.g., He and Raichle, 2009; He et al., 2010; Hiltunen et al., 2014).

Identifying the most reliable time-scale

We analyzed amplitude fluctuations in EEG and ECoG at the original sampling rate of 256 Hz as well as at 0.67 Hz. Low-pass filtering to the lower sampling rate substantially increased inter-subject correlations. Slow fluctuations below 0.33 Hz were found to capture most of the stimulus-related signal in these amplitude traces. Interestingly, z-scores were found to be larger before low-pass filtering, while corresponding inter-subject correlations increased. This suggests that z-scores are less sensitive to the power-spectrum of the signal, and a drop in z-scores indicates that reliable activity

has been removed.

Comparing reliability between imaging methods

An important advantage of z-scores over r-values is that they allow direct comparison between data sets. For homogeneous datasets consisting of a fixed number of independent samples, there is a monotonous relationship between r-values and z-scores. Thus, comparisons of datasets in either of the two metrics lead to the same conclusion. This is not anymore the case if the number of samples differs between datasets, as correlations estimated on fewer samples are more variable and therefore reach statistical significance less easily. The same effect is caused by dependencies between samples, which lead to increased variance by decreasing the *effective* number of samples. Such dependencies are naturally present in all neurophysiological time series, and are expressed in the dataset-specific autocorrelation spectrum. Testing for significant correlation between auto-correlated time series: simulation) provides numerical demonstration that z-scores as computed here achieve correct false-positive rates (p-values) despite different number of samples and autocorrelation spectra. Thus, z-scores are suitable to compare ISC in EEG, fMRI and ECoG despite differing numbers of samples and differing spectra of these signals.

Spatial heterogeneity

The EEG, ECoG and fMRI datasets studied here strongly differ in the number of simultaneously-acquired measurements, as well as in the spatial domains sampled by these measurements. EEG was measured at 32 scalp sites, whereas ECoG and fMRI were assessed at about 100 intra-cranial electrodes and thousands of brain voxels, respectively. In this light, one of the most interesting findings of this study is that EEG signals reached absolute levels of reliability that are comparable to levels achieved by ECoG and fMRI. A likely explanation for the competitive performance of EEG is again the larger number of subjects entering the grand-average, as discussed above.

Computation of inter-method correlations was hampered by different spatial coverages. fMRI signals were available from the entire brain, but only cortical activity was used for inter-method comparisons. EEG sensors pick up mixtures of activities of sources located all across the brain, and therefore often suffer from low SNR and the lack of straightforward anatomical localization. To increase SNR, and to visualize and relate EEG to ECoG and fMRI activity in a common anatomical space, scalp EEG data were mapped to the cortical surface using an inverse source reconstruction technique. The blurring observed in EEG source estimates could in principle be reduced by making prior assumption on the spatial focality of the underlying brain sources (e.g., Haufe et al., 2008, 2011). However, it was accepted here as being reflective of the low spatial resolution of the scalp-level data. ECoG electrodes were available at superficial cortical locations of the left hemisphere, with little coverage for large parts of the right hemisphere, the medial surface of the left hemisphere, and several larger patches of the occipital, parietal, central and frontal cortex of the left hemisphere. Inter-method correlations involving ECoG were thus only assessed at those locations.

Future work

Two restrictions of the present study are that we assessed only linear relationships and only looked at co-localized anatomical structures. Future studies may assess task-related interactions between different brain structures (Simony et al., 2016) across imaging methods and use non-linear measures of functional connectivity in order to better characterize the mechanisms linking the neurophysiological phenomena picked up by different methods. Using partial correlation analysis and information theory, future studies may also attempt to dissociate task-related signals that are method-specific from signals that are reflected by multiple imaging methods. Specific multivariate techniques (e.g., Bießmann et al., 2010; Dähne et al., 2015; Dähne et al., 2014; Dmochowski et al., 2012; Lankinen et al., 2014; McIntosh and Lobaugh, 2004) could, moreover, be used to identify brain networks characterized by maximal ISC/IMC in optimal data-driven ways.

Conclusion

Our results provide a comprehensive spatio-spectral account of the neural correlates of natural audio-visual stimulus processing in fMRI, ECoG and EEG, three of the most widely used neuroimaging methods in humans. All three methods reached similar levels of signal-to-noise ratio when data were averaged across the subjects of each cohort.

Experimental procedures

ECoG data used in this study have been described in detail in Honey et al. (2012); we here largely recapitulate these details. The EEG data with 32 electrodes ($N = 30$ subjects) has previously been used by Dmochowski et al. (2017). The additional EEG dataset with 128 electrodes ($N = 15$ subjects) and the fMRI data have not been previously published.

Study subjects

fMRI—Eleven subjects (six female; 20-35 years old) participated in the fMRI experiment. All subjects were in good health without history of psychiatric or neurological disorders and gave their informed consent to participate in the study and consent to publish in accordance with procedures approved by the Princeton University Institutional Review Board and with ethical standards set out by the Federal Policy for the Protection of Human Subjects (or 'Common Rule', U.S. Department of Health and Human Services Title 45 CFR 46). Subjects had normal or corrected-to-normal visual acuity. All subjects were experienced MRI subjects that were well trained to lay still during scans. There were no specific recruitment goals with respect to gender or race/ethnicity; however, fluency in English was required.

ECoG—Five patients (four female; 20–47 years old) experiencing pharmacologically refractory complex partial seizures were recruited via the Comprehensive Epilepsy Center of

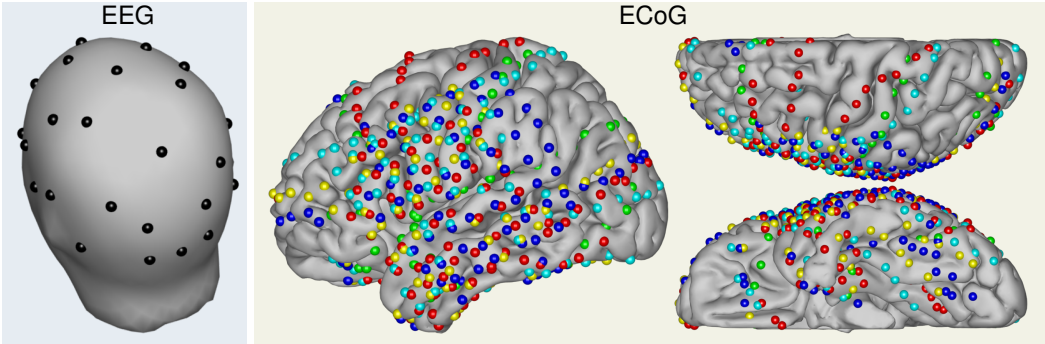

Fig. 3. Location of EEG and ECoG electrodes on the scalp/cortical surfaces. ECoG electrodes are drawn in a different color for each of the five subjects.

the New York University School of Medicine. Patients had elected to undergo intracranial monitoring for clinical purposes and provided informed consent both pre- and post-electrode implantation in accordance with National Institutes of Health guidelines administered by the local Institutional Review Board. For each patient, electrode placement was determined by clinicians based on clinical criteria. We focus here on patients with entirely or predominantly left-lateralized coverage, all of whom had left-lateralized language function, excluding data from two patients with right-hemisphere only coverage.

EEG—Data were obtained from two separate batches. In the first batch, thirty healthy subjects with no history of neurological disorders or impairments (fifteen male; 19–31 years old) were recruited. Procedures were approved by the Western Institutional Review Board (Puyallup, WA). In the second batch, 15 healthy subjects were recruited from the campus of City College (nine male; 18–28 years old). All procedures for this cohort were approved by the Institutional Review Board of the City University of New York. Prior to the start of the experiments, all subjects gave written informed consent. There were no specific recruitment goals with respect to gender or race/ethnicity; however, fluency in English was required.

Experimental setting

The audiovisual stimulus was a 325 s long movie clip selected from the 1975 commercial film Dog Day Afternoon (DDA, Lumet, 1975).

fMRI—subjects viewed two repetitions of intact, coarse, and fine DDA clips. Presentation order was randomized across individuals. The Psychophysics Toolbox in MATLAB was used to display the movie clips and synchronize the movie onset with the MRI data acquisition. Audio for the movie was delivered via in-ear headphones. Movie clips subtended 20° horizontally and 16° vertically.

ECoG—subjects viewed DDA in alternation with two more movie clips (two presentations per clip) at bedside on a MacBook laptop located 40–60 cm from their eyes. PsychToolbox Extensions (Kleiner et al., 2007) for MATLAB (MathWorks, Natick, MA) were used to display the movies and trigger their onsets. In addition to original (intact) clips, two manipulated variants, in which the scene order was randomized either on a coarse or fine level, were presented. The order of presentation was fixed: intact, coarse, intact, fine, coarse, fine. Presentation of each clip was preceded by a 30 s period in which subjects fixated on a central white square (< 1° visual angle) on a black background.

EEG—subjects of the first batch watched two repetitions of the intact movie interspersed with single presentations of the manipulated version: intact, coarse, fine, intact as used in Honey et al. (2012). In-house software (Neuromatters LLC, NY) was used for video playback. Only data recorded during presentation of intact stimuli (two viewings per subject and imaging method) were analyzed in the present study. subjects of the second batch watched the intact DDA clip twice, with each exposure separated by approximately 45 min, at the beginning and the end of an unrelated experiment. The video clip was presented via a custom version of mplayer (Mplayer media player, http://mplayerhq.hu), modified to generate parallel port triggers oncer per second.

Signal acquisition

fMRI—Data were acquired with a 3T Skyra magnetic resonance imaging (MRI) scanner (Siemens, Munich, Germany) using a 16-channel head coil. All functional acquisitions used a gradient echo, echo planar sequence with a 64 square matrix (slice thickness of 4 mm, interleaved acquisition) leading to an in-plane resolution of 3×3 mm^2 (field of view [FOV], 192×192 mm^2, GRAPPA iPAT = 2, 27 slices per volume; repetition time [TR] = 1.5 s; echo time [TE] = 30 ms; flip angle = 72 degrees). High resolution structural scans were acquired in each scan session for registration to surface anatomical images (MPRAGE sequence; 256×256 matrix; 240×240 mm^2 FOV; TR = 1.9 s; TE = 2.1 ms; flip angle = 9 degrees; $0.9375 \times 0.9375 \times 0.9375$ mm^3 resolution).

ECoG—Signals were recorded from 922 electrodes across all five subjects. Subdural arrays of platinum electrodes embedded in silastic sheeting (8×8 square grids, 4×8 rectangular grids, or 1×8 strips) were placed purely according to clinical criteria. Electrodes had an exposed diameter of 2.3 mm and were spaced 10 mm center-to-center. Depth recordings were not analyzed in the present study. Screws in the skull served as reference and ground. Signals were sampled at 30 kHz using a custom-built digital acquisition system (based on the open-source NSpike framework (L.M. Frank and J. MacArthur, Harvard University Instrument Design Laboratory, Cambridge, MA) that included a 0.6 Hz high-pass filter in hardware.

EEG—EEG data were recorded with a BioSemi Active Two

system (BioSemi, Amsterdam, Netherlands) at a sampling frequency of 2,048 Hz. subjects of the first batch were fitted with a standard, 32-electrode cap following the international 10/20 system, while subjects in the second batch were fitted with a 128-electrode cap according to an equiradial system (Biosemi). Six additional electrooculogram (EOG) electrodes were placed around the eyes to record and allow for the removal of eye-movement artifacts. Sony MDR 7506 headphones were used for audio playback during video viewing for the first batch of subjects, whereas the second batch of subjects were presented the audio over a pair of studio monitors, each situated at a 45° angle to the subject (e.g., left/right side) and at a distance of approximately 1 m (Fostex, PM0.3 Active monitors, Tokyo, Japan).

For this investigation, we pooled the data of the two EEG batches. To this end, 32 out of 128 electrodes used in the second batch of recordings were matched with the 32 electrodes used in the first batch of recordings based on nearest Euclidean distance of their standardized locations. This yielded N = 45 recordings with 32 EEG and six EOG electrodes available in each.

Spatial registration

All data were processed using in-house MATLAB code unless otherwise noted.

fMRI—Data were preprocessed using AFNI (Cox, 1996). Subject-wise data were transformed to MNI standard space using a two-step linear and nonlinear registration (AFNI's 3dAllineate and 3dQWarp), and re-sampled to a common rectangular grid at 4 mm resolution using linear interpolation. Data were then spatially smoothed using a Gaussian kernel (full-width-at-half-maximum: 10 mm; with less smoothing ISC were lower and areas above significance more disconnected). After extraction of the brain volume, 32,798 voxels were retained. Volumetric data were further mapped to the cortical surface of the 'New York Head' (Huang et al., 2016), a high resolution anatomical template extending the ICBM152 head (Fonov et al., 2011), based on minimum Euclidean distance. This resulted in the selection of 16,037 grey matter voxels (8,080 in the left hemisphere) to be analyzed.

ECoG—T1-weighted MR images were acquired from each subject both before and after the implantation of electrodes. Electrodes were localized on the individual cortical surfaces using a combination of manual identification in the T1 images, intraoperative photographs, and a custom MATLAB tool based on the known physical dimensions of the grids and strips (Yang et al., 2012). Subsequently, the individual-subject T1 images were non-linearly registered to an MNI template using the DARTEL algorithm via SPM (Ashburner, 2007), and the same transformation was applied to map individual electrode coordinates into MNI space. Out of 573 artifact-free labeled and MNI-registered electrodes used in Honey et al. (2012), only those 511 located in the left hemisphere were retained (see Fig. 3 for a depiction of the electrode locations). Data of all five subjects were pooled and subsequently treated as one single dataset.

EEG—For plotting purposes, electrode coordinates were aligned with the surface of the New York Head (Huang et al., 2016) using MNI coordinates provided by EEGLAB (Delorme et al., 2011) (see Fig. 3 for electrode locations). Source reconstruction (see EEG source modeling) was conducted in order to map EEG activity to cortical anatomy in MNI standard space.

Data preprocessing

fMRI—Functional data were slice-time and motion corrected (AFNI's 3dvolreg). The remaining data were linearly detrended, and high-pass filtered at 0.01 Hz using the discrete Fourier transform (DFT) and its inverse. In addition to the subject-level data, a grand-average (GA) was computed by averaging across subjects.

ECoG—Data were preprocessed using mean regression and down-sampling to 400 Hz (see procedures described in Honey et al., 2012). In order to facilitate comparisons between ECoG and EEG data, ECoG data were further decimated to 256 Hz after appropriate low-pass filtering using anti-aliasing finite impulse response filters (8th order Chebyshev Type I, MATLAB's resample function).

EEG—Data were decimated to 256 Hz using MATLAB's resample. Data were then high-pass filtered at 0.5 Hz and notch-filtered between 59 and 61 Hz using third order Butterworth infinite response (IIR) filters. Activity from six electrooculogram (EOG) channels was removed from all EEG channels through multivariate linear regression and subtraction. Artifact channels, defined as those with unusually small or large standard deviations (SD < 1 μ V or SD > 50 μ V or SD $> \text{mean}_{\text{ch}}(\text{SD}) + 2\ \text{SD}_{\text{ch}}(\text{SD})$, where SD_{ch} are mean and standard deviations over channels, respectively) were set to zero. A grand-average dataset was computed by averaging the preprocessed EEG time courses (here referred to as 'raw' as opposed to log band-power time series (see Calculation of EEG/ECoG band-power) across subjects.

In all datasets, the first 15 and the last 13 seconds were excluded, leaving a period of 297 seconds to be analyzed. The initial time is typically removed to allow the scanner to get to a steady state and avoid any potential evoked responses due to scanner onset. In this paradigm we also wanted to remove a strong visual, non-specific response. There was also a brief blank screen period at the end of the recording. The number of EEG/ECoG samples at 256 Hz sampling rate was T = 76,032, while the number of fMRI samples (TR's) at 0.67 Hz was T = 198.

EEG source modeling

For source analysis, EEG data at 32 channels were mapped to 2,004 locations covering the entire cortical surface (1,002 in the left hemisphere) by inverting a precise standardized volume conductor model of current flow in an average human head (Huang et al., 2016). This step was performed on grand-average signals for analyses of raw broad-band EEG time courses, while it was performed separately for each subject for analyses of the log-power of brain oscillations (see below). Prior to source imaging, data and head model were transformed into common average electrical reference. The

inversion was carried out using eLORETA (Pascual-Marqui, 2007). The regularization parameter λ was adjusted on grand-average raw EEG data using two-fold cross-validation. To this end, electrodes were split into two subsets comprising 19 and 13 electrodes, respectively, both covering the whole scalp. Sources were first estimated based on the subset of 19 electrodes for 11 logarithmically spaced choices of the regularization parameter (λ). The resulting source activity was projected back to the scalp using the volume conductor model. The resulting scalp potentials were evaluated at the 13 remaining channels, and the discrepancy to the potentials actually recorded at those electrodes was measured in terms of the mean-squared error (MSE). Using the value of λ that minimized this MSE, sources were re-estimated based on all 32 electrodes. This choice of λ was used in all subsequent source analyses.

Three-dimensional source current estimates were further reduced to scalar activations. This was done by projecting the current vector using location-specific 3D projection vectors that were designed to maximize the correlation of the grand-average raw EEG signal between the first and the second viewing (Dmochowski et al., 2012). These projection vectors were computed once and used throughout all source analyses.

Calculation of EEG/ECoG band-power

In addition to the raw broad-band EEG and ECoG signals (preprocessed as described above), we also calculated the instantaneous amplitude in five common frequency bands. These bands included θ (4–8 Hz), α (8–12 Hz), β (12–28 Hz), γ (28–56 Hz) and a high-frequency band (HF, 64–116 Hz). subject-level data were filtered in each band using third-order Butterworth IIR filters. We applied the Hilbert transform to obtain the complex-valued analytic signal, the absolute value of which provides the instantaneous band-amplitude. For single-subject analysis (see Fig. 1–Suppl. 4), the logarithm was applied directly. Grand-average instantaneous log band-power was obtained by taking the mean of the subject-wise squared amplitudes across subjects, and applying the logarithm on the mean. Additional down-sampled datasets were obtained by reducing the EEG and ECoG band data to the fMRI sampling rate of 0.67 Hz using resample.

Inter-subject correlation (ISC) within imaging methods

Raw and log band-power EEG data (at the level of 32 sensors as well as at 2,004 source locations) were linearly detrended. Correlations between time series recorded during the first and second movie viewing were assessed using the Pearson product-moment correlation coefficient, yielding one inter-subject correlation (ISC) coefficient per channel and imaging method.

Mappings between fMRI, ECoG and EEG spaces

In order to study correlations *across* imaging methods we selected channels (electrodes/cortical locations) that were co-located. The procedures to match channels between methods as well as to harmonize the temporal scale of the data for each pair of methods are outlined below.

ECoG–fMRI—For each of the 511 ECoG channels, corresponding BOLD activity was defined as the average of the activity of all cortical fMRI voxels within a 6 mm radius around that ECoG electrode. The down-sampled ECoG log band-power data at 0.67 Hz sampling rate were convolved with a canonical hemodynamic response function (HRF, SPM package, Penny et al., 2011). ECoG data were then detrended, high-pass filtered at 0.01 Hz using the Fourier transform, and cropped to the common 297 s interval. For both measurement methods, the grand-average data were also averaged across the two viewings.

EEG–ECoG—EEG channels pick up activity from the entire brain as a result of the spread of neuronal electrical activity in the head. It is, therefore, impossible to associate individual EEG channels with ECoG/fMRI counterparts, which is why we worked on EEG source estimates obtained as described above. To account for the enhanced spatial variability of EEG source estimates, source locations were not mapped to ECoG electrodes based on minimum Euclidean distance. Instead, for a given ECoG electrode, the EEG source with maximally correlated activity within a 5 cm radius around that electrode was sought. Correlation was assessed between the first viewing in ECoG and the second viewing in EEG, and vice versa (training combinations), and averaged across the two combinations. After selecting the EEG source location with maximal correlation, the activity at that location was correlated to the ECoG data using previously unused (test) combinations of viewings (first viewing in ECoG to first viewing in EEG, second viewing in ECoG to second viewing in EEG), and averaged across the two combinations. Using this procedure, the matching of EEG sources to ECoG sensors could not artificially inflate the measured correlations due to the preferential electrode selection. All correlations were assessed at the original EEG/ECoG sampling rate of 256 Hz. In addition, correlations between log band-power were also assessed on down-sampled datasets at 0.67 Hz sampling rate.

EEG–fMRI—EEG source log band-power traces at 0.67 Hz sampling rate were convolved with a canonical HRF, detrended, high-pass filtered at 0.01 Hz, and cropped. Similar to the EEG–ECoG case, EEG sources were matched with fMRI voxels based on maximal correlation within a 5 cm radius. Correlations were calculated using the previously unused combinations of viewings, and averaged across combinations.

Inter-method correlation (IMC) analysis

For each of the three pairs of measurement techniques, correlations between the appropriately mapped time courses were assessed using Pearson's product-moment correlation, yielding one inter-method correlation (IMC) value per channel and pair of imaging techniques.

Statistical significance of correlations

As neurophysiological time series are auto-correlated, correlations between them cannot be assessed using standard analytical tests assuming independent and identically distributed samples. Instead, the distribution of observed cor-

relations under the null hypothesis of zero true correlation needs to be estimated empirically. Correlation values r obtained on original and surrogate data were mapped to the interval $[-\infty, \infty]$ using the Fisher z-transform $\rho = \text{atanh}(r)$, where atanh is the hyperbolic tangent. For each channel, we confirmed that the null distribution of the z-transformed correlation scores is consistent with a Gaussian distribution using the Kolmogorov-Smirnov test ($p < 0.05$). Means μ_0 and standard deviations σ_0 estimated from surrogate data were used to standardize correlation coefficients observed on the original data, yielding z-scores $z = (\rho - \mu_0)/\sigma_0$. We derived p-values assuming that these z-scores are standard normal distributed under the null hypothesis. We demonstrate the exactness of this approach empirically with numerical simulations in Testing for significant correlation between auto-correlated time series: simulation.

As we did not expect any negative inter-subject correlations, right-tailed tests were used for all ISC analyses. In contrast, inter-method correlations were assessed using two-tailed tests. Only correlations with corresponding p-values falling below the alpha level of $\alpha = 0.05$ are reported. Our goal here was not to establish statistical significance in any particular location, but rather to provide a broad overview of the effect sizes observed. Thus, we did not correct for multiple comparisons when preparing the topographic maps of r-values or z-scores.

Visualization

Color-coded z-scores were rendered onto the surface of either the outer head surface or the cortical surface of the 'New York Head' (Huang et al., 2016). EEG sensor-space results were projected onto the outer head surface using a spherical harmonics expansion interpolation. fMRI results as well as results of EEG–fMRI IMC analyses were mapped to the cortical surface using to the nearest-neighbor rule, where distance was measured along the geodesics of the cortical manifold. ECoG results as well as results of ECoG–fMRI and EEG–ECoG IMC analyses were mapped onto the cortical surface by coloring all surface nodes within 6 mm distance of those ECoG channels reaching statistical significance. Cortical surfaces were smoothed for display purposes. Electrodes/voxels with z-scores significant at $\alpha < 0.05$ are shown in color, while non-significant locations are shown in gray. Identical r-values/z-scores are displayed in identical colors in all plots throughout the paper except for panel A of Fig. 1 and Fig. 1–Suppl. 4. To cover the entire range of values observed, we used non-linear saturating color scales. For each analysis, a colorbar is plotted that shows the range of attained significant r-scores/z-scores.

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APPENDIX

Testing for significant correlation between auto-correlated time series: simulation

We assessed the validity of the statistical test for non-zero correlations between auto-correlated time series introduced in the Statistical significance of correlations section. Two independent time series were generated either as univariate third-order linear auto-regressive (AR) processes, as Gaussian-distributed pink noise, or as squared (non-Gaussian distributed) pink noise. The number of samples was set to either N = 198 or to N = 76,032, amounting to a recording of 297 s length at the fMRI and EEG/ECoG sampling frequencies, respectively. For each pair of time series, 100 surrogate datasets were constructed using phase randomization, and a p-value was derived. An alternative p-value was derived using MATLAB's corr() function under the assumption that samples are independent. For this approach, correlation scores were transformed into a Student-t distributed test statistic, which gave rise to an analytic solution for the p-value.

Each experiment was repeated 2,000 times. From the distribution of the p-values we derived the empirical false-positive rate (FPR) as a function of the required FPR (alpha-level). For a statistical test to be exact, it is important that the relation between the two is close to identity, while undershoots of the empirical FPR are generally more tolerable than inflated FPR's. Results shown below (Fig. A1) indicate that the statistical test based on surrogate data is faithful to the desired alpha level for all possible FPR's and in all tested scenarios. In contrast, the standard analytic test is characterized by highly inflated FPR's in the alpha ranges of interest in practice ($\alpha = 0.01$, $\alpha = 0.05$). This behavior is more pronounced for pink noise than for auto-regressive processes, and for longer compared to shorter time series. In extreme cases, FPR's of up to 92% (pink noise data, N = 76,032) are observed at a nominal alpha level of 5%.

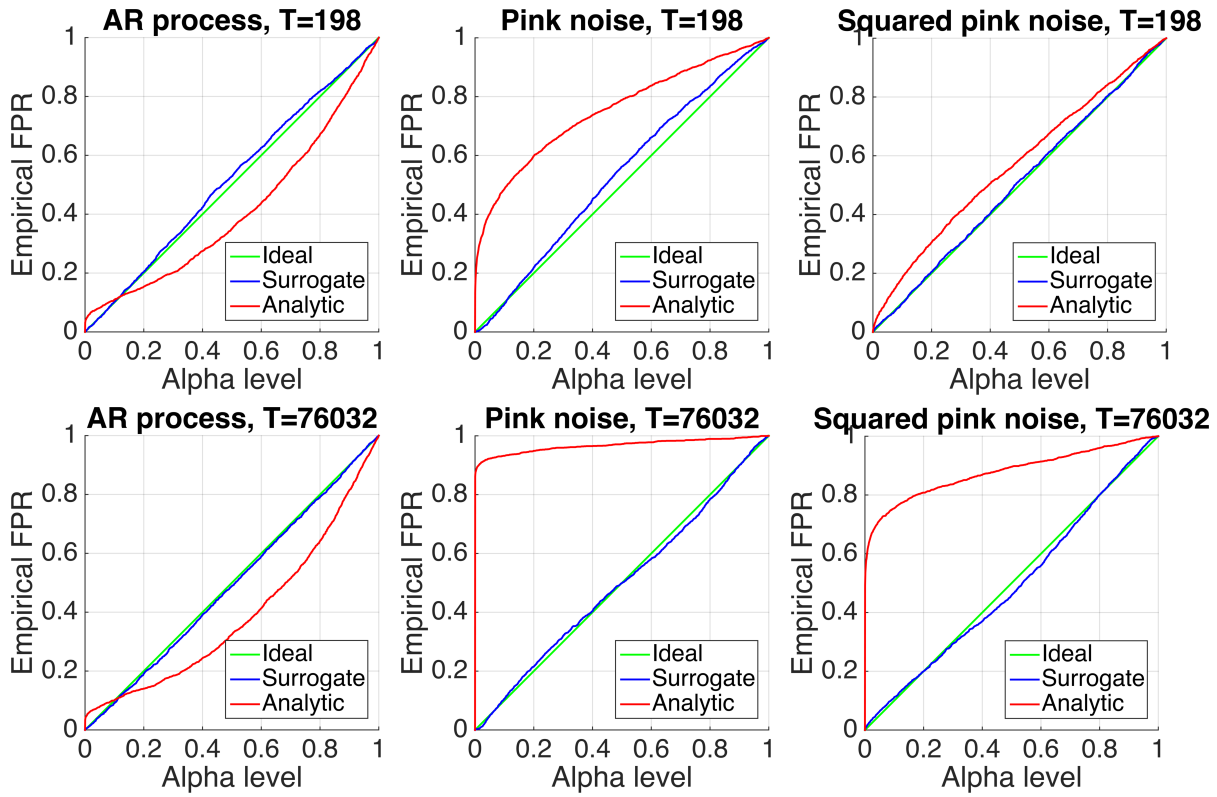

Fig. A1. Comparison of two approaches to test the statistical significance of correlations between auto-correlated time series: the surrogate data based approach used throughout this paper (see Statistical significance of correlations section) and the conventional analytic approach assuming independent samples. The surrogate based approach leads to empirical false-positive rates (FPR) that are close to the desired FPR (alpha level) regardless of the sample size or temporal dynamics of the time series, while the conventional approach leads to strongly inflated FPR's in the practically relevant alpha ranges ($\alpha = 0.01$, $\alpha = 0.05$) in all cases.

SUPPLEMENTARY FIGURES

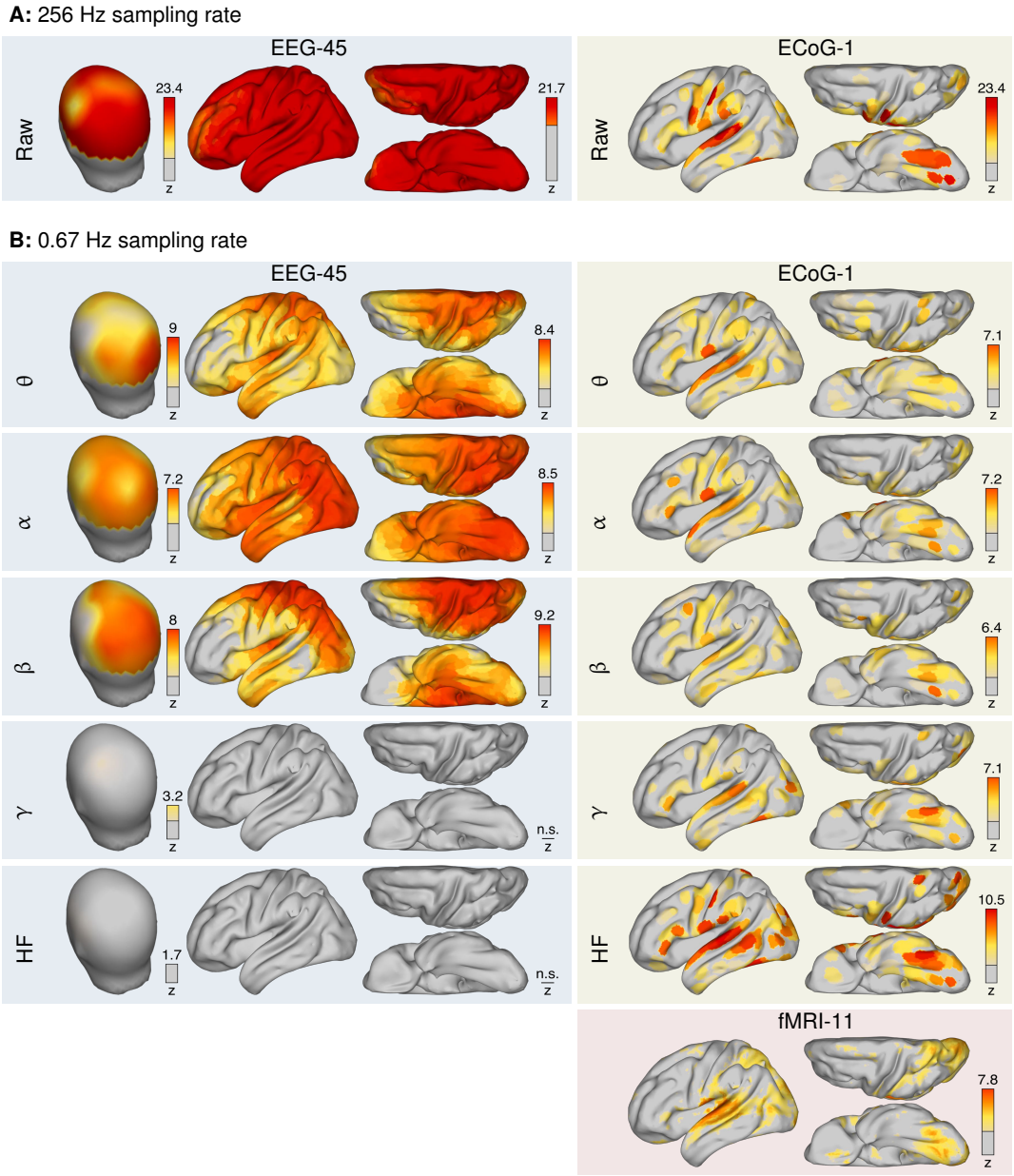

Fig. 1–Suppl. 1. Statistical significance of inter-subject correlation (ISC) coefficients. Observed correlations, r, were standardized based on the mean and standard deviation of a null distribution established from phase-randomized surrogate data, yielding a standard normal distributed z-score for each scalp/cortical location. z-scores exceeding 1.645 are significant at alpha level 0.05 (uncorrected) according to a one-sided hypothesis, and are drawn in color. The figure shows that even small ISC values observed for 'raw' broad-band EEG/ECoG voltage fluctuations (c.f., panel **A** of Fig. 1) are highly significant when compared to surrogate time series with identical autocorrelation spectrum but no ISC. Numbers above the color bars indicate maximal correlation values.

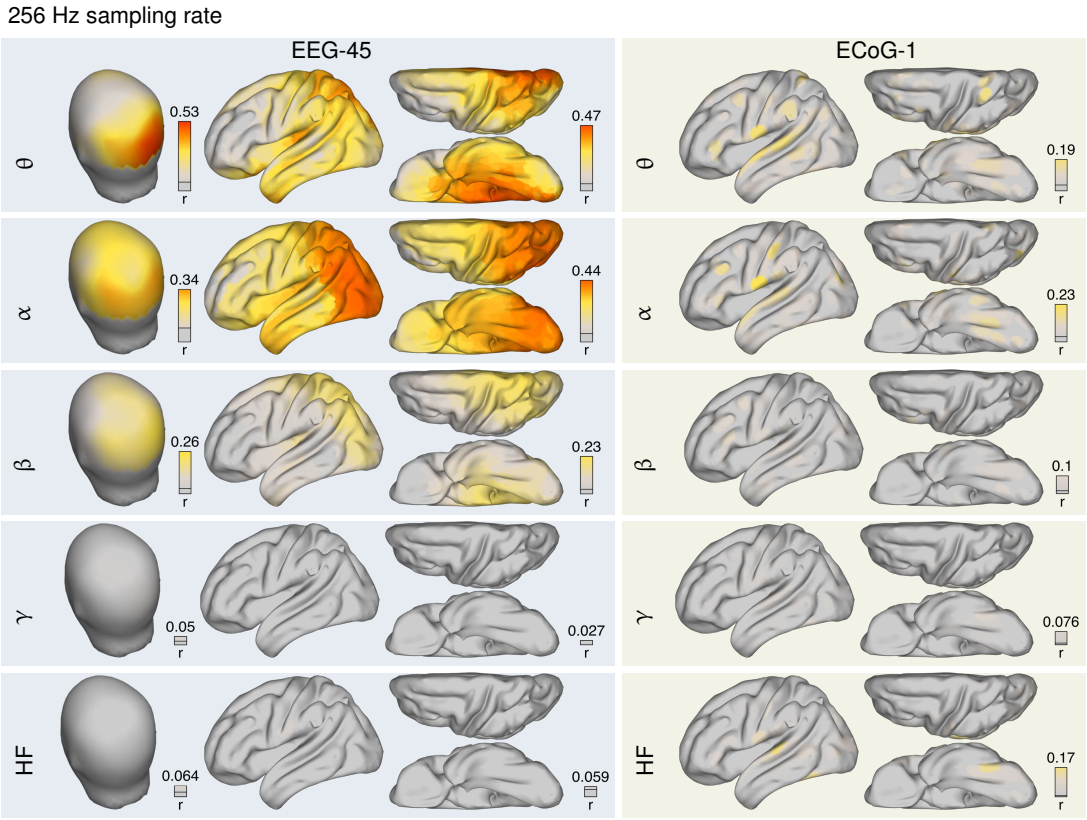

Fig. 1–Suppl. 2. Inter-subject correlation of EEG/ECoG band-power computed at **256 Hz sampling rate**, i.e., without low-pass filtering the instantaneous log band-power. Observed ISC values are smaller than for down-sampled data, but exhibit similar spatial topographies.

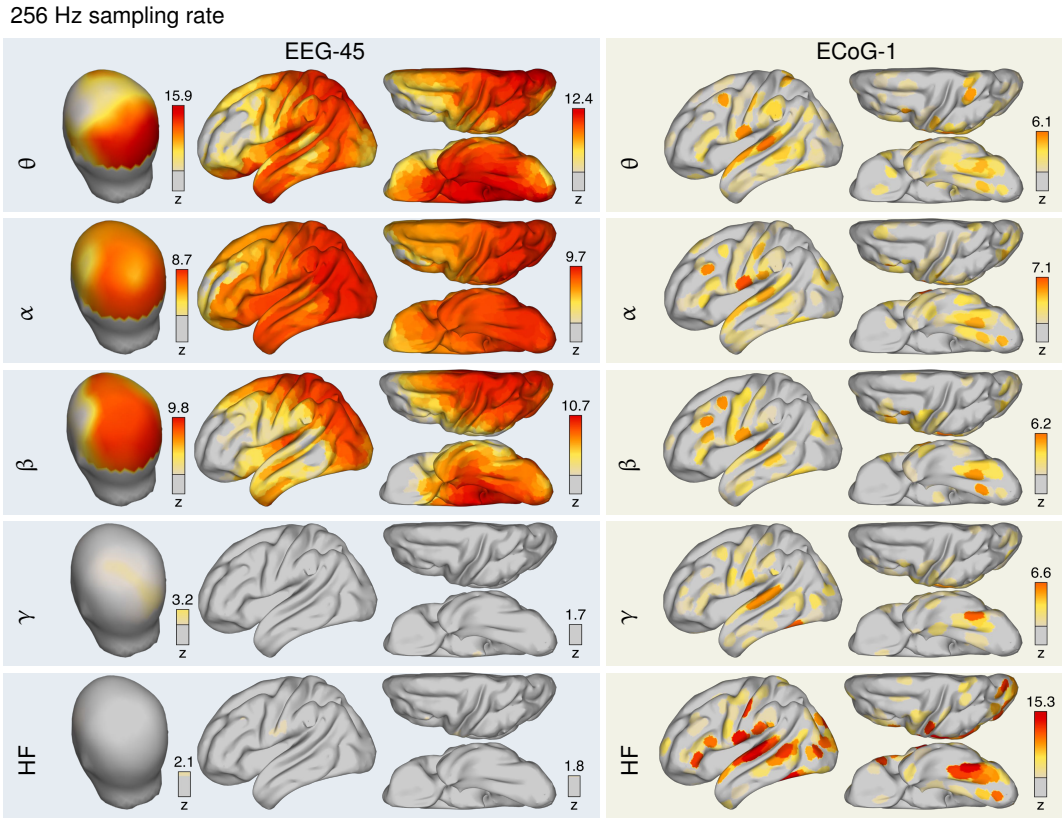

Fig. 1–Suppl. 3. Statistical significance of EEG/ECoG band-power inter-subject correlation at **256 Hz sampling rate**. Note that even small ISC values (as, e.g., observed for high-frequency ECoG data, c.f. Fig. 1–Suppl. 2) are highly significant.

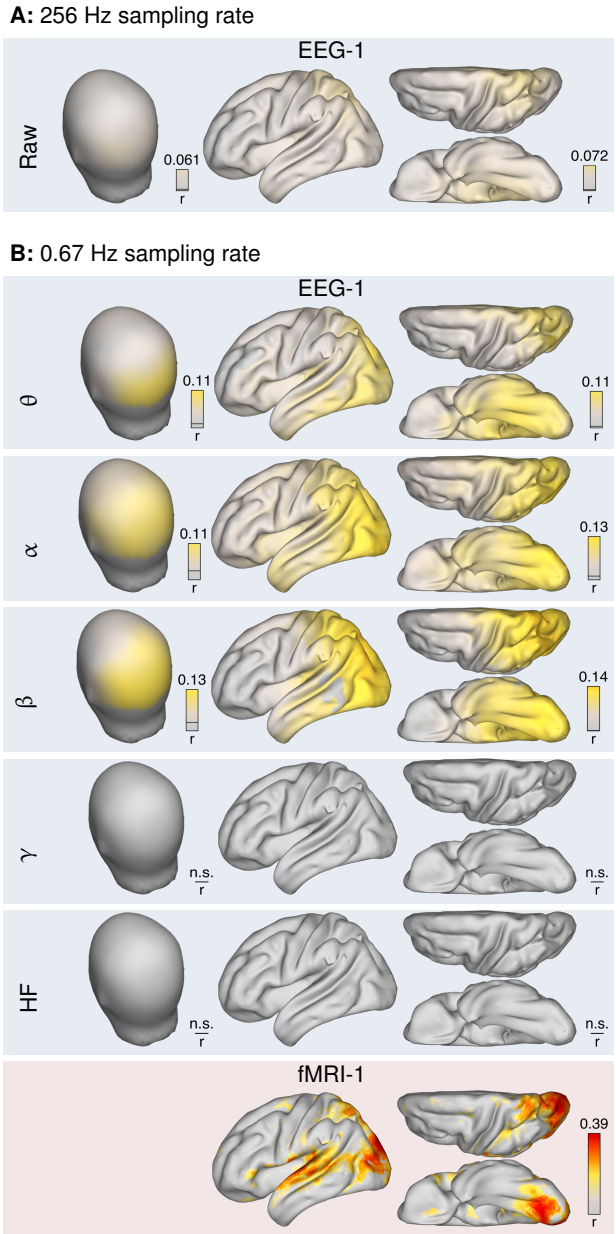

Fig. 1–Suppl. 4. Average EEG and fMRI inter-subject correlations observed within single subjects. ISC scores, r, were computed in each subject, and averaged across subjects. No statistical testing/thresholding was performed. Observed ISC scores are smaller than those observed on averaged data (c.f., Fig. 1, but notice the different color scale here), yet exhibit similar topographies.

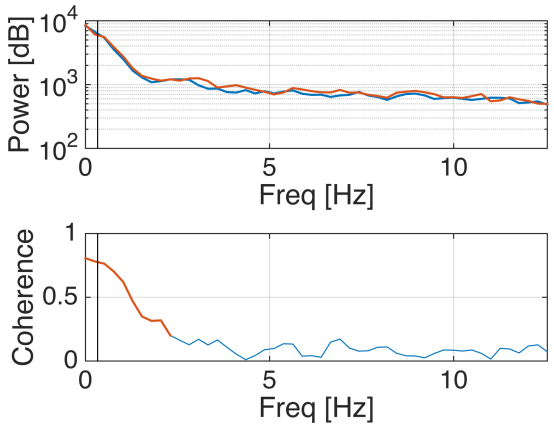

Fig. 1–Suppl. 5. Analysis of inter-subject coherence (frequency-resolved correlation) of high-frequency (56–116 Hz) ECoG band-power fluctuations for the ECoG electrode exhibiting highest ISC in the HF band. Top panel shows the power spectrum for first and second viewing. The HF power signal is dominated by activity below 2 Hz. The coherence spectrum shows significant correlation (red bold line) also below 2 Hz. The black vertical line indicates the low-pass filter at 0.33 Hz that is applied when sampling at the fMRI resolution of 0.67 Hz. For this signal, an inter-subject correlation of r = 0.17 (z = 15.3) was observed at 256 Hz sampling rate. After low-pass filtering and down-sampled to 0.67 Hz, IV correlation increased to r = 0.77, but was slightly less significant (z = 10.5). This drop in significance is explained by the fact that the low-pass filter removes correlated signal components that do not exist in random surrogate data. On the other hand, restricting the signal content to the strongest and most correlated portion through the low-pass filter increases inter-subject correlation, as less correlated signal parts are removed.

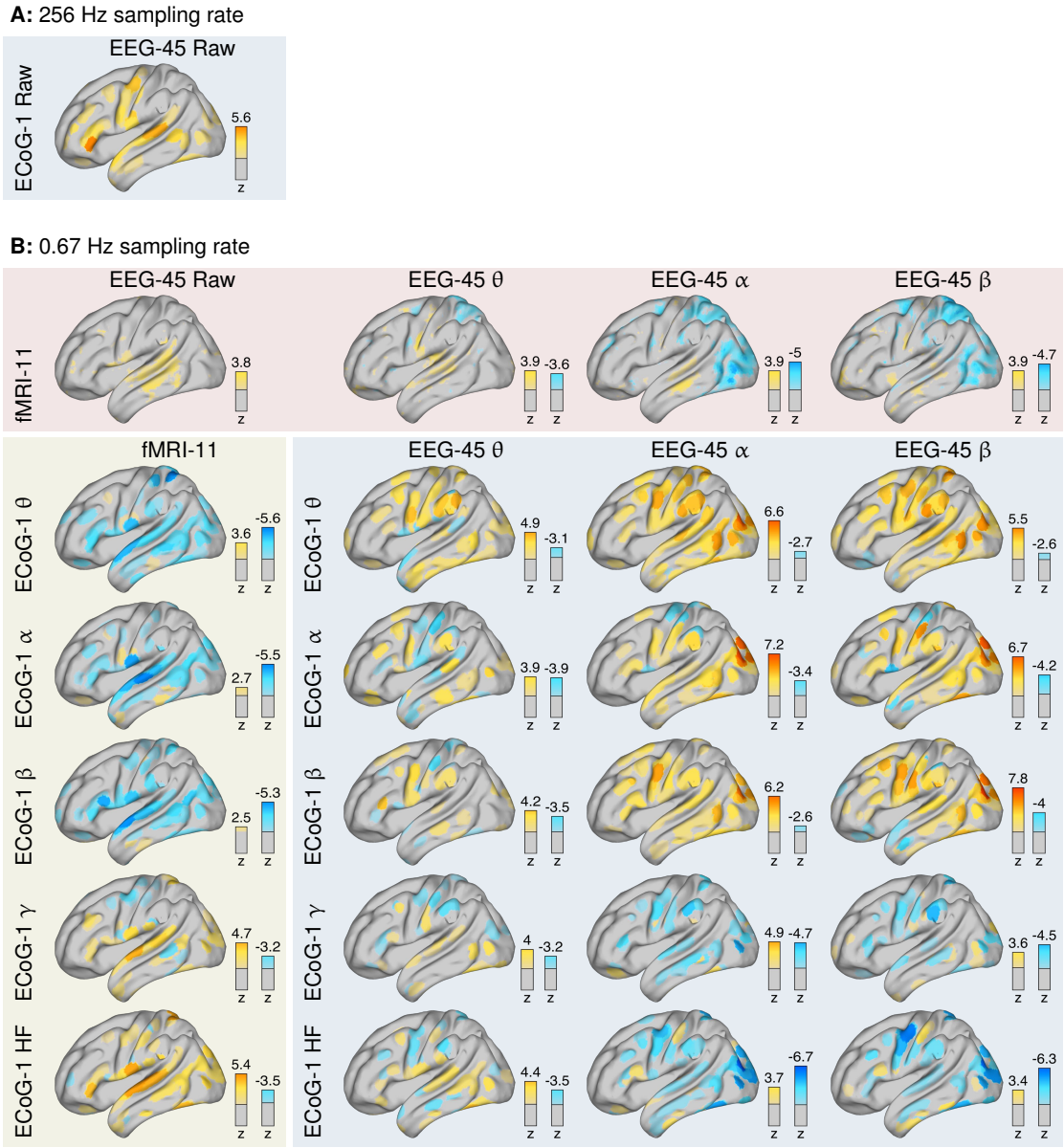

Fig. 2–Suppl. 1. Statistical significance of inter-method correlations between single-subject ECoG, grand-average EEG and grand-average fMRI BOLD activity. Using a null distribution established from phase-randomized surrogate data, observed correlations were transformed into standard normal distributed z-scores. z-scores exceeding absolute values of 1.96 are significant at alpha level 0.05 (uncorrected) according to a two-sided hypothesis, and are drawn in color.

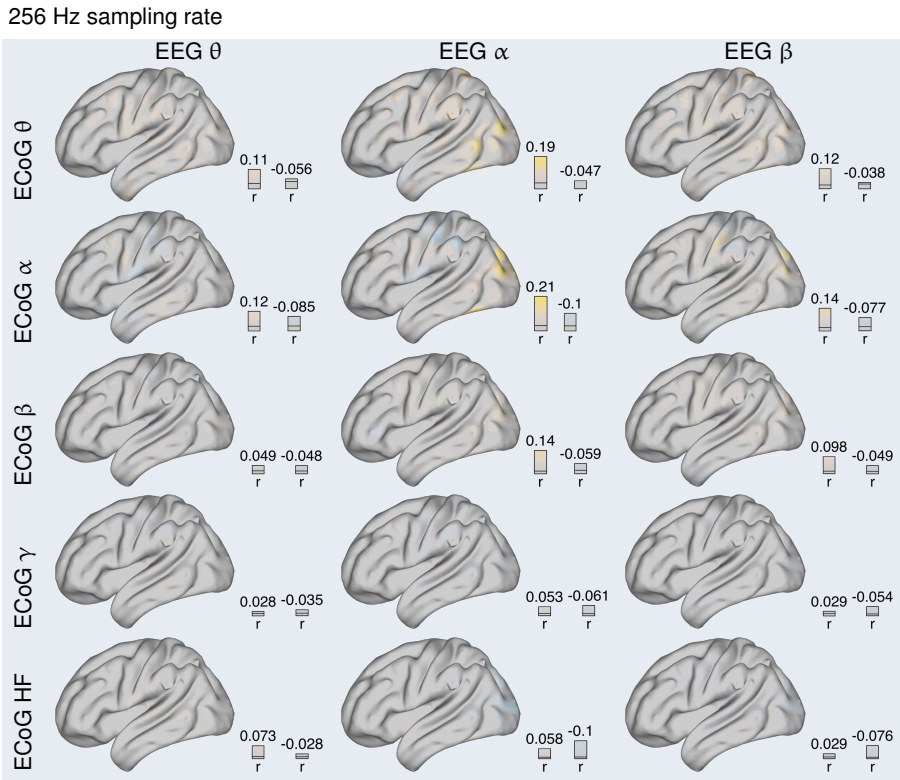

Fig. 2–Suppl. 2. Inter-method correlation (IMC) between the instantaneous log-power of EEG and ECoG oscillations in the θ (4–8 Hz), α (8–12 Hz), β (12–28 Hz), γ (28–56 Hz) and high-frequency (HF, 64–116 Hz) bands **at 256 Hz sampling rate**.

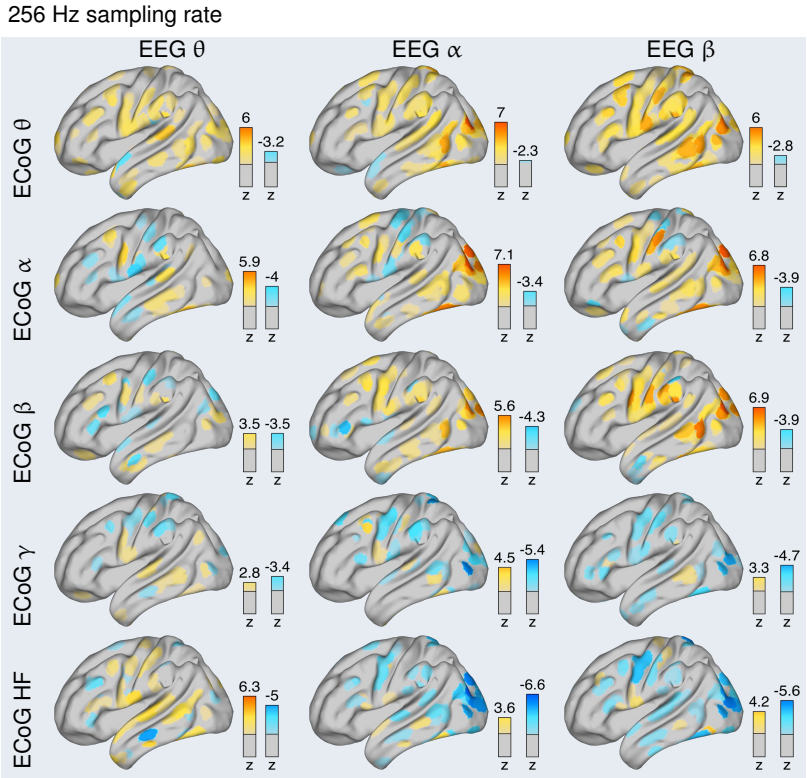

Fig. 2–Suppl. 3. Statistical significance of inter-method correlations between EEG and ECoG band-power at **256 Hz sampling rate**. While correlation values are much smaller than for 0.67 Hz sampling rate, they remain equally significant as compared to null distributions.