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The spatospectral characterization of brain networks: fusing concurrent EEG spectra and fMRI maps

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Abstract

Different imaging modalities capture different aspects of brain activity. Functional Magnetic Resonance Imaging (fMRI) reveals intrinsic networks whose BOLD signals have periods from 100s (0.01 Hz) to about 10s (0.1 Hz). Electroencephalographic (EEG) recordings, in contrast, commonly reflect cortical electrical fluctuations with periods up to 20 ms (50 Hz) or above. We examined the correspondence between intrinsic fMRI and EEG network activity at rest in order to characterize brain networks both spatially (with fMRI) and spectrally (with EEG). Brain networks were separately identified within the concurrently recorded fMRI and EEG at the aggregate group level with group independent component analysis and the association between spatial fMRI and frequency by spatial EEG sources was examined by deconvolving their component time courses. The two modalities are considered linked if the estimated impulse response function (IRF) is significantly non-zero at biologically plausible delays. We found that negative associations were primarily present within two of five alpha components, which highlights the importance of considering multiple alpha sources in EEG-fMRI. Positive associations were primarily present within the lower (e.g. delta and theta) and higher (e.g. upper beta and lower gamma) spectral regions, sometimes within the same fMRI components. Collectively, the results demonstrate a promising approach to characterize brain networks spatially and spectrally, and reveal that positive and negative associations appear within partially distinct regions of the EEG spectrum.

Keywords

EEG-fMRI; ICA; intrinsic connectivity networks; deconvolution

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1.1 Introduction

Differences in cognition and perception are thought to emerge from differences in the dynamic activity of functional brain networks (Siegel et al., 2012; Varela et al., 2001). These brain networks exist over a broad range of spatial and temporal scales and the subset of networks identified in a given study depends on the constraints of the imaging modalities used. Functional magnetic resonance imaging (fMRI), for example, reveals a series of intrinsic networks whose blood-oxygenation level dependent (BOLD) signal covaries over time scales between approximately 0.01 to 0.1 Hz (Biswal et al., 1995; Raichle et al., 2001). Electroencephalographic (EEG) recordings, in contrast, reveal cortical electrical fluctuations of up to 50 Hz or above (Buzsaki, 2006; Nunez and Srinivasan, 2006) (for clarification see Vanhatalo et al., 2005). Combining information obtained within these different modalities can provide an improved characterization of brain networks both spatially (with fMRI) and spectrally (with EEG). This improved spatio-spectral characterization of brain networks may inform the degree in which individuals can perform tasks, and may be related to differences in healthy and clinical populations.

A common approach to EEG-fMRI integration during rest has been to associate the BOLD fMRI response with concurrent EEG responses within a particular frequency band (for multiple frequencies see De Munck, et. al., 2009; Mantini, et. al., 2007; Scheeringa et al., 2011). The EEG time course is first converted to its frequency representation along intervals that correspond to each fMRI acquisition. The EEG spectral information is then associated with BOLD fMRI by correlating the two time courses or using the spectral time course as a predictor in a general linear model (GLM) analysis. Initial studies focused on the BOLD fMRI responses related to the EEG alpha band (e.g. between 8–12 Hz) since it demonstrates a robust peak within the EEG frequency spectrum (Goldman et al., 2002; Laufs et al., 2003; Laufs et al., 2003; Moosmann et al., 2003). Subsequent studies also focused on BOLD fMRI networks associated with the EEG theta band (4–8 Hz) (Mizuhara et al., 2004; Sammer et al., 2007; Scheeringa et al., 2008). However, it is important to consider multiple EEG frequency bands in EEG-fMRI integration. For example, multiple frequency bands may be associated with a particular fMRI response and a constellation of fMRI and EEG networks are likely present at any given moment (De Munck et al., 2009; Mantini et al., 2007; Scheeringa et al., 2011).

A potential difficulty with examining EEG-fMRI networks throughout the EEG spectrum is that it contains the combined contribution of multiple distinct networks which may overlap spectrally and/or spatially. This is particularly evident within the 8 – 12 Hz alpha band, which has been subdivided by its upper and lower frequencies, and which overlaps in frequency with the central mu rhythm. The different alpha sources demonstrate distinct spatial topographies, spectral peaks, and/or sensitivities to experimental manipulation (Niedermeyer, 1997; Nunez et al., 2001), and the average 8 – 12 Hz activity represents the combined contribution of these multiple independent sources. The presence of multiple sources with overlapping spectral characteristics is also suggested by the difficulty indentifying the boundaries between EEG frequency bands within the average EEG spectrum (with exception to peak between 8 and 12 Hz that appears above EEG's characteristic 1/f spectra (Pritchard, 1992)) and the presence of high correlations between the different frequency bands (De Munck et al., 2009; Mantini et al., 2007).

The combined contribution of multiple distinct EEG spectral sources (within an individual frequency band) motivates blind source separation (BSS) approaches such as spectral independent component analysis (ICA) (Wu et al., 2010), principle component analysis (PCA), and temporal ICA (for a review see Makeig et al., 2004), as well as semi-BSS approaches such as functional source separation (FSS) (Di Pino et al., 2012; Porcaro et al.,

2008; 2010; 2011). Spectral ICA was used in the current study in order to decompose the overlapping independent contributions of the EEG spectrum into its distinct sources, potentially revealing the sources that correspond to the traditional EEG bands as well as the distinct sources present *within* a frequency band. This data-driven approach validates that distinct EEG frequency bands are present within a given dataset and may improve the ability to link fMRI with the EEG activity specific to each band and/or brain network. However, ICA (or other source separation approaches) is commonly applied to one modality (usually fMRI) while the other modality remains mixed. Thus, the majority of EEG-fMRI studies link the unmixed sources from one modality with the mixed sources from the other modality (Eichele et al., 2009).

The present study combines the spatial information of fMRI with the frequency and spatial information of concurrent EEG during eyes open and eyes closed rest. Brain networks were independently identified within the concurrent fMRI and EEG at the aggregate group level with group ICA and the spatial fMRI and frequency by spatial EEG sources were linked by deconvolving their component time courses. Conducting an independent group ICA within each modality can provide an improved measure of fMRI or EEG network activity, while also helping to incorporate as much information as possible within each modality without creating an unmanageable number of statistical comparisons. The approach reduces the need to restrict the analysis to only a subset of fMRI networks (e.g. the default mode), or to restrict analysis to a subset of EEG electrodes or frequencies. The resulting linked sources reveal brain dynamics with improved spatio-spectral resolution.

2.1 Methods

2.1.1 Participants and Procedures

Twenty-five individuals (mean age 29 $\pm$ 8 years, 17 males) were recruited to participate in a single experimental session. Each individual had normal or corrected to normal vision and had no family history of neurological disease. Individuals provided informed written consent at the Mind Research Network, and were compensated for their participation. The experimental session consisted of an initial structural MRI scan (7 min), followed by simultaneous recording of EEG and BOLD fMRI while individuals rested first with their eyes closed (8.5 min), then with their eyes open (8.5 min). A total of 50 simultaneous EEG/fMRI recordings were acquired (25 subjects with 2 recordings per subject). The individuals were instructed to fixate on white cross-hairs presented against a black background during eyes open rest. Individuals were instructed to relax, lie still, and remain awake for the duration of each recording. The participants, experimental paradigm, and acquisition details are also described in a previous report (Wu et al., 2010).

2.1.2 EEG acquisition

EEG was recorded with a 32-channel BrainAmp MR-compatible system (Brainproducts, Munich, Germany) and a BrainCap electrode cap (Falk Minow Services, Herrsching-Breitbrunn, Germany). The Ag/AgCl electrodes were placed according to the international 10–20 system. Electrocardiogram (ECG) and eye movement (EOG) signals were recorded in separate channels, reducing the number of scalp electrodes to 30. The EEG signals were sampled at 5 kHz, and the EEG acquisition was synched to each fMRI acquisition (i.e TR).

2.1.3 EEG preprocessing

EEG preprocessing was conducted in Matlab (<http://www.mathworks.com>) using custom functions, built-in functions, and the EEGLAB toolbox (<http://sccn.ucsd.edu/eeqlab>). The EPI gradient artifact was attenuated by calculating the average artifact template (across 2 s epochs) separately for each channel, and subtracting the template from the individual epochs

within that channel. The EEG data was down-sampled to 1 kHz, band-pass filtered (.01 to 50 Hz), and average referenced. Additional artifacts (e.g. ballistocardiogram, eye movement, and residual EPI gradients) were attenuated by conducting a temporal ICA decomposition on the individual recordings (Srivastava et al., 2005). Thirty components were estimated using the extended Infomax algorithm implemented in EEGLAB (Bell and Sejnowski, 1995; Lee et al., 1999). Artifactual components were identified by visual inspection of the component time-course, topographic distribution, and frequency spectrum and removed from the back reconstructed time-course (Jung et al., 2000). Seventeen components were eliminated on average (min 11, max 23).

2.1.4 Group spectral ICA of EEG

The preprocessed EEG data was variance normalized, segmented into 2 second epochs and converted to the frequency domain by the fast Fourier transform (FFT) ($\Delta f = 0.5 \text{ Hz}$). The complex valued Fourier coefficients were absolute valued (i.e. converted to the amplitude spectrum) and values corresponding to 1 – 35 Hz were concatenated from the 2D channel $\times$ frequency matrix into a 1D vector. The 1D (length = 2070 = 30 channels $\times$ 69 frequency bins) vectors were concatenated into a single matrix for each epoch generating a 256 (epochs) $\times$ 2070 matrix for each recording (see Fig 1a). The individual data matrices were entered into a Group ICA analysis implemented in the EEGIFT toolbox (<http://mialab.mrn.org/software/eegift/>). (For a detailed description of the Group ICA implementation, please see: Calhoun et al., 2001; Eichele et al., 2009; Eichele et al., 2011) Group ICA provides a formal procedure for integrating the individual EEG recordings into aggregate group independent channel $\times$ frequency EEG components. Group ICA alleviates issues with aligning sources from independent ICA decompositions while enabling evaluation of individual subject differences via individual back-reconstructed components (Beckmann and Smith, 2005; Calhoun et al., 2001; Erhardt et al., 2011).

Separate source and mixing matrices were generated for each recording by back-reconstructing the group components (as demonstrated in Calhoun et al., 2001) (Fig 1 b,c). The individual mixing matrices capture the contribution of the frequency by channel component at each 2 s epoch. Twelve group components were estimated. The group components were relatively stable with model orders of 8, 10, 12, 16, and 20 components, except that there was a more detailed decomposition of the alpha components with model orders above 10 (Supp. Fig. 1). Group spectral components were selected for further analysis if they contained one or more peaks in their spectral response. The EEG source time courses were converted to z-scores for subsequent analysis.

2.1.5 fMRI acquisition and preprocessing

Anatomical and functional images were acquired with a 1.5 T Siemens Sonata scanner. The high resolution anatomical image was acquired with a 3D MPRAGE T1 sequence (sagittal; TR, 12 ms; TE, 4.76 ms; flip angle, 20°; voxel size, 1 mm $\times$ 1 mm $\times$ 1.5 mm; fov 256 mm). Functional images were acquired with an echo planar imaging (EPI) free induction decay (FID) sequence (TR, 2 s; TE, 39 ms; flip angle, 80°; voxel size, 3.5 $\times$ 3.5 $\times$ 3 mm; fov 224 mm; gap 1 mm; slices, 27; ascending). fMRI data was preprocessed using SPM5. Images were realigned using INRIAlign (Freire and Mangin, 2001), spatially normalized to MNI space (Friston et al., 1995), and smoothed with a Gaussian (full width half maximum (fwhm), 8 $\times$ 8 $\times$ 8 mm) kernel. The data was subsampled to a voxel size of 3 $\times$ 3 $\times$ 3 mm, resulting in a 53 $\times$ 63 $\times$ 46 volume. The first four volumes were discarded.

2.1.6 Group Spatial ICA of fMRI

The preprocessed fMRI data was entered into a group spatial ICA implemented in GIFT (<http://mialab.mrn.org/software/gift/>). Seventy-eight group components were estimated,

providing a detailed separation of components (Abou-Elseoud et al., 2010; Allen et al., 2011; Kiviniemi et al., 2009; Smith et al., 2009). The group components were back reconstructed onto the individual recordings in the same manner as the EEG data. Biologically plausible components were selected based upon visual inspection of the group sources, and visual inspection of the time course and spectrum of the back reconstructed individual source time courses. Twenty-two components were identified as artifactual, and the remaining 56 components were used in the subsequent analysis. The components were characterized according to their MNI coordinate and Talairach labels generated from the Talairach Demon (TD) atlas (after z-scoring and thresholding at $z > 3.5$) (Lancaster et al., 1997, 2000). The anatomical labels acronyms were obtained from the BrainInfo portal (<http://braininfo.rprc.washington.edu/>). Inflated surface maps were generated using AFNI and SUMA <http://afni.nimh.nih.gov/afni/suma> with the MNI template (Cox et al., 1996; Saad and Reynolds, 2012).

2.1.7 EEG and fMRI component deconvolution

Brain networks may be characterized with improved spatial and temporal resolution by fusing concurrent EEG and BOLD fMRI. The separate modalities were fused by deconvolving the z-scored fMRI component time-courses with the z-scored EEG spectral map time-courses, generating an estimated impulse response function (IRF) for each of the 560 component pairs (56 fMRI components $\times$ 10 EEG components). Specifically, let tc_{eeg} and tc_{fmri} represent the EEG and fMRI source time courses, respectively (length = 256). The convolution matrix A was constructed with tc_{eeg} from epochs 1 to 244 (using matlab's `convmtx` function). The IRF was estimated as the product of the pseudoinverse of A and tc_{fmri} (e.g. $\text{IRF} = \text{pseudoinverse}(A) \times tc_{\text{fmri}}$). Small singular values of the convolution matrix (e.g. < 0.5) were discarded since the deconvolution amplifies noise in proportion to their inverse. The IRF's were estimated up to 26 seconds.

Deconvolution treats the BOLD fMRI modulation as the output of the EEG spectral modulation and an estimated linear time invariant filter. The estimated filter, or IRF will be non-zero if the EEG spectral source modulation acts as an "impulse" for the corresponding fMRI spatial source. The deconvolution approach has been implemented previously with fMRI (Eichele et al., 2008) and EEG-fMRI (De Munck et al., 2007; Wu et al., 2010). The approach is akin to examining the cross-correlation of the separate components. Similarly, the BOLD fMRI time course may also be correlated with the EEG time course after convolution with a canonical hemodynamic response function (HRF) (Goldman et al., 2002; Laufs et al., 2003). This is less than optimal, however, since it does not account for variability in the hemodynamic response across brain regions and individual subjects (Aguirre et al., 1998; Handwerker et al., 2004; Steffener et al., 2010), leading to reduced statistical sensitivity and an increase in false negative test results.

The IRF's were pooled together across eyes-open and eyes-closed recordings since the pattern of results were consistent across the two conditions (Supp. Fig. 2). We examined significant deviations in the estimated average IRF at 4 time points along the IRF using a bootstrap test (Efron and Tibshirani, 1993). The 50 individual estimated IRFs were resampled with replacement and averaged, generating a single bootstrapped IRF curve. This procedure was repeated over 2.5×10^5 bootstrapped resamples. The IRF significantly deviates from zero at an individual point if 99.995 % of the bootstrap resampled values at that point are either above or below zero (i.e. $p < .000045$; $\alpha = .05$). This statistical threshold Bonferroni corrects for the total number of component pairs (e.g. 56 fmri components $\times$ 10 EEG components). We focused our analysis on the 4 time points corresponding to delays of 4, 6, 8, and 10 seconds since they correspond to the physiological delay in the hemodynamic response.

3.1 Results

3.1.1 Group Spectral ICA of EEG

The temporal modulation of the [epoch by [frequency by channel]] EEG source (indicated by the mixing matrix) represents the contribution of the source over epochs. For example, if a group component is restricted to a narrow frequency range (e.g. 10–11.5 Hz) then the temporal modulation of the component represents the contribution of the 10–11.5 Hz spectral component at each EEG epoch (which corresponds to the concurrent fMRI acquisition). Components were selected for further analysis if they demonstrate a distinct peak within one or more regions of the spectrum (between 1 and 35 Hz) within the 4 channels with the largest amplitude. Ten out of the 12 components were selected for further analysis. The excluded component contained either a uniform spectrum or EPI artifact.

The 10 selected group components each demonstrate a peak response that approximately corresponds to one of the characteristic EEG frequency bands (Fig 2). We describe the frequency range of each component by the upper and lower frequency at half the maximum value. A single frontal component contained peak responses within the delta band (1 – 1.5 Hz) and one component contained a peak response within the theta band (2.5 – 5 Hz over central midline electrodes). Five components contained a peak response within the alpha band. The components show a peak response over occipital and/or parietal electrodes with frequencies between 6.5 – 8.5 Hz, 8.5 – 10 Hz, 9 – 10.5 Hz, 10 – 11.5 Hz, and 11.5 – 13 Hz. One component corresponds to the lower beta band (13 – 15.5 Hz, over frontal electrodes) and another corresponds to the upper beta band (25 – 29 Hz, over right temporal electrodes). The remaining component corresponds to the lower gamma band (31.5 – 35 Hz, over frontal and temporal electrodes) (Fig 2).

3.1.2 Group Spatial ICA of fMRI

The BOLD fMRI data was decomposed into 78 group components. Twenty-two of the 78 components were excluded from further analysis due to either a peak response within a vascular region, due to movement artifacts (e.g. edge effects), and/or due to the predominance of high frequency activity (e.g. from 0.15 to 0.25 Hz) within the component time course. Fifty-six group components were included in the subsequent analysis (Fig. 3a). The group components were visually organized according to their approximate spatial location as suggested by the Talairach label of the component peak response and its MNI coordinates. Organizing the components visually in this manner allows us to determine whether spatially similar subsets of BOLD fMRI components demonstrate similar relationships to the concurrent frequency by spatial EEG components.

3.1.3 EEG and fMRI component deconvolution

The 56 spatial fMRI component time courses were deconvolved with the 10 frequency by spatial EEG component time courses for each recording. This approach treats the fMRI component time course as the output of the frequency by channel EEG source time course convolved with an (estimated) IRF. Significant deviations in the estimated IRF indicate that changes in the EEG response are associated with (subsequent) changes in BOLD fMRI, linking frequency by spatial EEG network modulations with spatial fMRI network modulations.

The average estimated IRF is shown in figure 4 for a BOLD fMRI component with a peak response within the cuneus (Cun) (Fig 4a). The IRF's show significant positive deviations from zero within the EEG components corresponding to the delta, theta, upper beta, and lower gamma bands and significant negative deviations within the EEG components corresponding to the lower/upper alpha boundary, the upper alpha, and the lower beta band

(Fig 4b). This pattern is generally present within the larger set of 56 fMRI components, as demonstrated in Fig. 3b for each of the 560 component pairs. One-hundred and twenty five of the 560 component pairs demonstrate a significant non-zero deviation in the estimated IRF. Seventy-six of the estimated deviations were positive and 49 were negative. A more detailed parcellation of fMRI components and their relationship to EEG is demonstrated in table 1 (for negative relationships) and table 2 (for positive relationships).

The majority of positive associations are present within the EEG components corresponding to the delta and theta frequency bands (demonstrating 21 and 23 significant IRF's, respectively). Positive associations are present within delta and theta over frontal (SFG, MedFG, MFG, IFG, and PrG), parietal (PoG and IPL), temporal (STG and FuG), limbic (PcgC and CgG), and occipital regions (Cun, IOG, and LiG). Negative associations were present at each frequency within fMRI components with peak responses within frontal (MedFG) and subcortical (Cd and Th) regions (Fig. 3b).

The 9 – 10.5 Hz “low / high alpha” and 10–11.5 Hz “high alpha” EEG components share negative associations with fMRI components with peak responses within the middle frontal gyrus (MFG), superior temporal gyrus (STG), fusiform gyrus (FuG), cuneus (Cun), inferior occipital gyrus (IOG), and lingual gyrus (LiG). The 9 – 10 Hz “low / high alpha” component additionally shows negative associations within frontal (MedFG and IFG), parietal (PoG and IPL), limbic (PcgC), and occipital (PCu) regions. Many of these negatively associated components (e.g. MedFG, MFG, IFG, PoG, and Cun) are also negatively associated with the 13–15 Hz “low beta” EEG component. Positive associations were present within the 9 – 10.5 Hz alpha component within the medial frontal gyrus (MedFG) and the thalamus (Th). The thalamic component was also positively associated with the 13 – 15.5 Hz “low beta” band (Fig. 3b).

The “high beta” and “low gamma” EEG components contain 15 and 11 significant positive associations with fMRI, respectively. The positive associations are present within fMRI components with peaks within frontal (SFG, MedFG, MFG, and IFG), parietal (PoG and IPL) and occipital locations (Cun). The EEG components each share negative associations with the parahippocampal gyrus (PHG), caudate (Cd), and thalamus (Th) (Fig 3b). The general pattern of associations is shown in figure 5, where the “linked” fMRI components are displayed on a composite inflated surface for each EEG component.

A subset of the fMRI components individually demonstrate the pattern described, with positive associations within the lower (e.g. delta or theta) and upper (e.g. upper beta, or lower gamma) frequencies and a negative association with the “low / high alpha” component. These fMRI components contained peak responses within the medial frontal gyrus (MedFG), middle frontal gyrus (MFG), inferior frontal gyrus (IFG), postcentral gyrus (PoG), inferior parietal lobule (IPL), superior temporal gyrus (STG), fusiform gyrus (FuG), and the Cuneus (Cun) (Fig. 4). The opposite pattern of responses were present within the thalamus (Th), with negative associations with delta, theta, upper beta, and lower gamma, and positive associations with the “low / high alpha” component.

4.1 Discussion

The current study characterized dynamic patterns of brain activity by combining the spatial information of fMRI with the spectral information of EEG. Brain networks were independently identified within each modality at the aggregate group level with group ICA and the spatial fMRI and frequency by spatial EEG sources were linked by deconvolving their component time courses. The resulting spatio-spectral networks reveal an interesting pattern, with positive and negative associations with fMRI within partially distinct regions

of the EEG spectrum. Positive associations were primarily observed within the lower (i.e. delta and theta) and upper (i.e. upper beta, and lower gamma) EEG frequency bands and negative associations appeared predominantly within the alpha band.

Approaches to source separation

It is possible that the observation of multiple alpha sources in the current study may have been facilitated by incorporating both frequency and spatial information within the EEG spatospectral decomposition. For example, some of the alpha sources appear to separate based upon differences in their spectral peaks, while demonstrating similar spatial locations (e.g. the “low / high alpha” source and the “high alpha / low beta” source in Fig. 2b) while other alpha sources appeared to have different spatial locations, but similar spectral peaks (e.g. the “low / high alpha” source and the “low alpha” source in Fig 2b). Decomposing the 2 dimensional frequency by channel EEG amplitude spectra thus appears to facilitate the ability to separate sources that are independent considering both space and frequency. We found in the current study that these sources demonstrate different relationships with spatially independent fMRI sources. Further studies may further explore the EEG-fMRI sources revealed by different unmixing assumptions or constraints. For example, ‘tensor ICA’ can incorporate a second dimension in ICA, which imposes different constraints in the source decomposition (Zhang, et al. 2008).

The EEG sources observed in the present study implicitly focus on widespread or global EEG responses. Higher resolution EEG recordings (e.g. with 128 channels) enable the ability to spatially filter EEG responses with current source density (CSD) or surface Laplacians (for review see Srinivasan, 2005), enabling the ability to additionally examine the relationship between fMRI and local EEG sources. This may be particularly applicable in further efforts to distinguish fMRI networks associated with different sources within the alpha band, since they may be observed globally, regionally, or locally in EEG (Nunez et al., 2001), and since they demonstrate different functional properties and origins in local field potential and multiunit activity (MUA) recordings (Bollimunta et al., 2011; Mo et al., 2011).

The spatospectral EEG ICA approach in the current study was able to isolate independent sources using Fourier amplitudes corresponding to different channels and frequencies. The sources appear to correspond well with the characteristic EEG frequency bands and they were identified in a data driven manner from 1 to 35 Hz. The ability to incorporate information over a wide range of frequencies is important for recordings during “rest” since it likely consists of a range of cognitions operating over multiple frequency bands. The advantages of semi-BSS approaches have been demonstrated to be useful when an a priori emphasis can be placed on a particular range of frequencies. For example, Di Pino et al., 2012 used functional source separation (FSS) to preferentially isolate spectral sources between 8 – 25 Hz since they have been implicated in movement intention and execution. Thus, further EEG-fMRI integration studies may also utilize semi-BSS approaches in order to place emphasis on an individual spectral or temporal EEG sources (Di Pino et al., 2012; Porcaro et al., 2010).

FMRI and alpha

We found negative associations between frontal, parietal, temporal, and limbic fMRI regions and EEG alpha. Positive associations with alpha were present within the thalamus and medial frontal gyrus. These results are in agreement with prior findings in the EEG-fMRI literature indicating that alpha (and sometimes beta) is negatively correlated with occipital, frontal and temporal activity and positively correlated thalamic activity (De Munck et al., 2007; DiFrancesco et al., 2008; Feige et al., 2005; Goldman et al., 2002; Laufs et al., 2003; Laufs, Kleinschmidt, et al., 2003; Moosmann et al., 2003). The negative relationship

supports the notion that alpha increases are paralleled by reduced cortical metabolism, as suggested by increased alpha activity during eyes closed rest (Moosmann et al., 2003).

Examining responses over a fixed frequency range (and subset of electrodes) in previous studies, however, combines the contribution of multiple alpha sources. This leaves open the possibility that different alpha sources may be related to BOLD fMRI in a different manner (Sadaghiani et al., 2010). This possibility is suggested by the presence of five alpha sources in the current study and the finding that the negative relationship with fMRI was present in only two of the five sources. Interestingly, the two components were negatively associated with many of the same occipital components, but the 9 – 10.5 Hz component was the only one to additionally show negative associations with frontal, temporal, and parietal regions (Fig 3b). This suggests that the lower 9 – 10.5 Hz region of the alpha band may contribute to the negative association with these areas in previous studies (De Munck et al., 2007; DiFrancesco et al., 2008; Goldman et al., 2002; Gonçalves et al., 2006; Laufs et al., 2003; Laufs et al., 2003) and highlights the importance of considering multiple alpha sources in concurrent EEG and fMRI.

FMRI and delta / theta

The relationship between fMRI and EEG theta activity has been well studied, but the results are generally less consistent. Scheeringa et al., 2008 indicates that frontal theta activity is negatively correlated with many fMRI regions during rest, including inferior frontal, medial frontal, inferior parietal, and medial temporal areas. The negative correlation with theta and medial frontal areas is also supported by (Mizuhara et al., 2004). This finding is in agreement with the negative relationship between theta and the medial frontal gyrus observed in the present study.

Positive associations between theta and fMRI have been reported primarily while individuals perform mental arithmetic tasks (Mizuhara et al., 2004; Sammer et al., 2007). The spatial location of these associations (e.g. over frontal and temporal locations) qualitatively agrees with the locations of a subset of the positive associations with theta in the current study. In general, however, the associations with theta that we observed were more widespread. The widespread nature of our findings may be related to improved measurements of theta activity by decomposing the underlying EEG sources at the group level and by relaxing the assumption of a fixed relationship (e.g. the assumption of a canonical HRF) between EEG and fMRI (as in De Munck et al., 2007, 2009). A potential source of inconsistency between theta and fMRI in previous studies may be due to violations in the assumption of a fixed impulse response. This possibility is supported by the finding that estimated theta IRF's less clearly resemble the canonical HRF (De Munck et al., 2007) and that theta IRF's tend to be more variable across subjects compared to the alpha band (De Munck et al., 2009).

Physiological implications

The functional role of the different EEG spectral bands has been well studied. Gamma activity has been implicated in sensory processing and the binding of sensory information either externally in visual perception (Eckhorn et al., 1988; Gray, et al., 1989), or internally in episodic memory representations (Sederberg et al., 2006; van Vugt et al., 2009). Theta activity has been implicated in episodic memory and additional complex processes, including decision making (for a review see Nyhus and Curran, 2010). The general consensus, therefore, is that low frequency theta and high frequency gamma oscillations are involved in "active" or complex processes. This contrasts with the inhibitory influence of alpha activity which is suggested by its reduced amplitude during sensory stimulation (Klimesch et al., 2007). The present findings demonstrate a subset of fMRI networks that are

positively modulated by delta/theta and upper beta/lower gamma EEG responses and negatively modulated by EEG alpha. Thus, the frequencies separate in their association with fMRI in a similar manner as they separate functionally in previous studies. The findings add to a growing body of literature utilizing EEG or MEG recordings to examine the frequency characteristics of resting state networks (Brookes et al., 2011; Hipp et al., 2012; Mantini et al., 2007). It should be noted, however, that it is difficult or impossible to determine the functional role of these networks directly in the absence of an explicit task. “Resting state” is not a unique cognitive function on its own. Instead, it likely incorporates the broader range of cognitions than may occur when cognition is unconstrained by an experimental task.

The observation of common positive associations within the lower and upper regions of the EEG spectrum is intriguing in light of the findings that these regions of the spectrum may be functionally coupled in cognition and behavior (for review, see Schroeder and Lakatos, 2009; Siegel et al., 2012). For example, theta phase is coupled with the amplitude of high frequency gamma band responses (e.g. 80 – 150 Hz) in subdural electrocorticography (EcoG) (Canolty et al., 2006) as well as with lower frequency EEG gamma band responses (Demiralp et al., 2007; Schack et al., 2002). The present findings demonstrate fMRI networks within occipital, temporal, parietal, and frontal areas which show positive associations within a similar region of EEG frequencies (e.g. delta, theta, upper beta, and lower gamma). These fMRI networks demonstrate the intrinsic spectral properties that are prerequisite for integration across different frequency bands.

5.1 Conclusion

This study combined the spatial information of fMRI with the frequency and spatial information of concurrent EEG during rest. Brain networks were independently identified within each modality at the aggregate group level. This approach unmixes the independent sources within each modality, allowing examination of the correspondence between fMRI and EEG without restricting analysis to a subset of the data (e.g. a subset of fMRI spatial locations or a subset of EEG electrodes or frequency bands). The fMRI source time course was treated as the output of the frequency by spatial EEG source time course convolved with an estimated IRF. The deconvolution approach relaxes the (potentially constrained) assumption of a fixed canonical HRF. With this approach, we demonstrate that the positive and negative relationship between EEG and fMRI appear within somewhat distinct regions of the EEG spectrum. Widespread positive associations were observed within the lower (e.g. delta and theta) and upper frequencies (e.g. upper beta and lower gamma), sometimes within the same fMRI components. Negative associations were primarily present within a subset of EEG alpha sources. The negative relationship between occipital fMRI and the alpha band was present within two of the five alpha sources, while the negative relationship between frontal, temporal, and parietal fMRI sources was restricted to the single 9 – 10.5 Hz “lower alpha” component. These results highlight the importance of considering multiple alpha sources in EEG and fMRI. Together, the results reveal that positive and negative associations are present within different EEG frequency bands, demonstrating that fMRI networks may segregate according to their intrinsic spectral properties.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Fusing EEG and fMRI by deconvolving group component timecourses. Group ICA is conducted separately on the frequency by spatial EEG (a) and spatial BOLD fMRI (d) data. The 2D EEG (a) or fMRI (b) data is converted into an [frequency $\times$ channel] amplitude spectra vector or voxel magnitude vector, respectively (represented by the red lines in a and b). The vectors are concatenated across epochs forming a 2D data matrix for each individual (represented by the boxes in a and b). The separate group ICA (implemented with GIFT software) generates an individual time course and source matrix for the EEG (b and c) and fMRI recording (e and f). The first level group components are fused by deconvolving the individual EEG source time course and the individual fMRI source time course (g). Deconvolution (as implemented here) treats the BOLD fMRI component time course as the output of the EEG component time course convolved with an unknown (estimated) impulse response function (IRF). Linked EEG-fMRI sources are identified when the estimated IRF significantly deviates from zero. The two time courses shown (in g) correspond to the time course from a segment of a recording for the EEG group component representing the upper alpha band (e.g. 10–11.5 Hz) (in c) and a group fMRI component with a peak response over occipital cortical regions (in f). The negative peak in the estimated IRF (bottom right) demonstrates that increases in the upper alpha band are associated with a subsequent reduction in the occipital BOLD response.

Figure 2.

Frequency by channel EEG sources. The 2D frequency (y-axis) by channel (x-axis) EEG sources are demonstrated in a for the 10 selected components. The components are organized from lowest peak frequency (upper left) to the highest peak frequency (lower right). The x axis denotes the electrodes corresponding to occipital (O), parietal (P), temporal (T), central (C), and frontal (F) locations. The characteristic EEG frequency bands are indicated by the horizontal bars at 4, 8, 10, 12, 20, and 30 Hz. The values represent the normalized (i.e. z-scored) source values. The peak response and topography of the 2D sources is represented in b. The upper plot indicates the average normalized spectrum of the four channels (indicated in white) with the largest normalized (i.e. z-scored) peak amplitude.

The topographic plot indicates the average normalized spectrum for each channel across frequencies.

Figure 3.

Spatial fMRI components and their relationship to frequency by spatial EEG. The 56 selected BOLD fMRI components are z-scored, thresholded at $z > 4$ and displayed in (a). The components are organized in the composite maps according to the approximate spatial location of their peak response. The relationship between each BOLD fMRI component and the 10 EEG components (shown in Fig 2) is indicated in (b). Significant positive associations are indicated along the white grayscale axis and significant negative associations are indicated along the black grayscale axis. White and black pixels indicate the regions with the largest positive or negative peak in the IRF, respectively. Non-significant relationships are in gray. The solid lines in (b) separate the components according to their

grouping in (a) and the colors in (a) correspond to the corresponding colors in (b). The anatomical labels are abbreviated in (b) according to the BrainInfo portal (<http://braininfo.rprc.washington.edu/>).

Figure 4.

Impulse response functions (IRFs). The average IRF ($n = 50$) is plotted for each of the 10 EEG group components (shown in Fig. 2) for a group fMRI component with a peak response over occipital cortical regions (a). The error bars represent the range of 97.5% of the values of the bootstrap resampled IRFs. Significant deviations are indicated by the diamonds (see the main text for details). The location of deviations overlaps well with the location of modulation expected based upon the canonical hemodynamic response function (HRF) (e.g. with a peak between 4–10 seconds). The occipital fMRI component is related to modulations in multiple EEG components (representing different frequencies and/or spatial locations). Increased responses within the “low alpha / high alpha” “high alpha” and “low beta” EEG components are related to *reduced* fMRI component responses, while increases in the “delta”, “theta”, “upper beta”, and “lower gamma” components are related to *increased* responses within the occipital fMRI component.

Figure 5.

Surface rendering of spatiotemporal networks. The BOLD fMRI components with negative relationships with the EEG components are rendered on the surface composite plots in a (blue). The components with positive relationships are rendered on the surface composite plots in b (red). The components were z-scored and thresholded at $z > 4$ within each plot. Different shades of each color within each plot were used to differentiate the different components. The peak response of the EEG component is indicated by the labels on top. The spatial topography and spectral characteristics of each EEG component is shown in Fig 2.

Table 1

Anatomic labels for each BOLD fMRI component that is negatively associated with EEG. An fMRI component is listed within a cell if it is associated with the corresponding EEG component (indicated by their peak frequency). The response (Z), volume (cc), and MNI coordinates are provided for the component with the largest peak response.

Anatomic Label	1 Hz	4.5 Hz	8 Hz	9.5 Hz	10 Hz	11 Hz	12.5 Hz	15 Hz	28.5 Hz	35 Hz	Max (Z)	Vol (cc)	max Z(x,y,z)
SuperiorFrontalGyrus	9	7 9		8	10			10 33	28	28	24.2	1.8	(3, 37, 51)
MedialFrontalGyrus	9	7 9		8	10			10 33			21.7	0.9	(3, 49, 42)
MiddleFrontalGyrus				8	10 12 14	12		10 12 14	28	28	13.7	5.9	(33, 61, 2)
InferiorFrontalGyrus				8	12 14 23	12 23		12 14			11.5	1.1	(-53, 17, -6)
PrecentralGyrus					10 14 17 18 23	23		10 14 17			7.7	1.5	(59, -18, 40)
ParacentralLobule					10			10			9.2	1.6	(3, -24, 51)
PostcentralGyrus					10 17 18			10 17			8.8	7.5	(53, -29, 51)
InferiorParietalLobule					17 18			17 20			10.2	7.2	(42, -68, 42)
SuperiorParietalLobule					39 40	39 40		20 39			10.2	1.1	(39, -68, 45)
AngularGyrus					39	39		20 39			8.3	2.2	(45, -65, 36)
SuperiorTemporalGyrus					14 18 23 24	23		14		29	15.2	6.3	(-53, 14, -8)
MiddleTemporalGyrus					23 24 30 39 40	23 30 39 40		39	28	28	9	0.5	(-59, 0, -3)
InferiorTemporalGyrus					24 30	30					7.6	2	(-56, -59, -12)
Insula					18						5	0.3	(-56, -31, 21)
ParahippocampalGyrus				32	32 46	46			28	28 29	13.2	2.9	(-18, -24, -11)
FusiformGyrus					30 42 46	30 42 46					11.9	2.3	(-50, -65, -14)
PosteriorCingulate				32 37	32 37	37					13.7	2.3	(3, -66, 12)
AnteriorCingulate	9 48	9 48						33	48	48	8.8	0.4	(3, 11, -3)
CingulateGyrus					10 36			10 33			10.7	4.5	(0, 22, 32)
Uncus										29	5.5	0.2	(-27, 2, -20)
Precuneus				32 37	10 32 36 37 38 39 40	37 39 40		10 20 39			13	8.9	(3, -76, 45)
Cuneus		53		32 37	32 36 37 38 39 40 42	37 39 40 42		39	28	28	14.8	1.8	(3, -69, 9)
SuperiorOccipitalGyrus					39 40	39 40		39			7.4	1.7	(-30, -86, 24)
MiddleOccipitalGyrus					30 39 40 42 46	30 39 40 42 46		39			8.4	1.7	(-50, -67, -9)
InferiorOccipitalGyrus					40 42	40 42				29	10.6	3.1	(-24, -94, -10)

Anatomic Label	1 Hz	4.5 Hz	8 Hz	9.5 Hz	10 Hz	11 Hz	12.5 Hz	15 Hz	28.5 Hz	35 Hz	Max (Z)	Vol (cc)	max Z(x,y,z)
Lingual Gyrus				32 37	23 32 37 40 42 46	23 37 40 42 46			28	28	13.3	1.2	(3, -76, 4)
Caudate	48	48							48	48	16.5	2.5	(6, 12, 8)
Thalamus	51	51 53							51	51	20.2	1.6	(3, -17, 12)
Culmen				32	32 46	46			28	28 29	11.4	0.5	(-18, -27, -16)
Declive					46	46					7.3	1.5	(-24, -53, -12)

Table 2

Anatomic labels for each BOLD fMRI component that is positively associated with EEG. An fMRI component is listed within a cell if it is associated with the corresponding EEG component (indicated by their peak frequency). The response (Z), volume (cc), and MNI coordinates are provided for the component with the largest peak response.

Anatomic Label	1 Hz	4.5 Hz	8 Hz	9.5 Hz	10 Hz	11 Hz	12.5 Hz	15 Hz	28.5 Hz	35 Hz	Max (Z)	Vol (cc)	max Z(x,y,z)
SuperiorFrontalGyrus	8 10 33	8 10 33			9		10		68 10 33	2 8	13.9	4.8	(30, 61, 2)
MedialFrontalGyrus	8 10 33	8 10 33			9		10		6 8 10 33	2 8	9.4	1.5	(0, -21, 51)
MiddleFrontalGyrus	8 10 12 14	8 10 12 14					10		6 8 10 12 14	2 8 12 14	13.7	5.9	(33, 61, 2)
InferiorFrontalGyrus	8 12 14 16 21 23	8 12 14 16 23	16						8 12 14 23	8 12 14 22	12.4	8.2	(-50, 20, -9)
PrecentralGyrus	10 14 16 17 18 21 23 26	10 14 16 17 18 23 26	16				10		10 14 17 18 23	2 14 17 18	10.6	9.5	(-56, -10, 31)
ParacentralLobule	10	10					10		10		9.2	1.6	(3, -24, 51)
PostcentralGyrus	10 16 17 18 26	10 16 17 18 26	16				10		10 17 18	17 18	10.4	2.1	(-59, -23, 15)
InferiorParietalLobule	17 18	17 18							17 18 19 20	17 18 19 20	10.2	7.2	(42, -68, 42)
SuperiorParietalLobule	39 40	39 40							20 39 40	20 39	10.2	1.1	(39, -68, 45)
AngularGyrus	39	39							19 20 39	19 20 39	9.1	2.2	(-50, -56, 36)
SuperiorTemporalGyrus	14 16 18 21 23 24 26	14 16 18 23 24 26	16						14 18 19 23	14 18 19 22	15.2	6.3	(-53, 14, -8)
MiddleTemporalGyrus	23 24 30 39 40	23 24 30 39 40 41							19 23 30 39 40	19 39	9	0.5	(-59, 0, -3)
InferiorTemporalGyrus	24 30	24 30 41							30		7.6	2	(-56, -59, -12)
Insula	18 21 26	18 26							18	18 22	9.4	4.4	(-48, -20, 15)
ParahippocampalGyrus	21 32 46	32 46									6.2	0.7	(21, -52, 5)
FusiformGyrus	30 46	30 41 42 46							30		11.9	2.3	(-50, -65, -14)
PosteriorCingulate	32 37	32 37							37	37	13.7	2.3	(3, -66, 12)
AnteriorCingulate	33	33			9			48	33		8.8	0.4	(3, 11, -3)
CingulateGyrus	10 33	10 33 36					10		10 33		10.7	4.5	(0, 22, 32)
Precuneus	10 32 37 38 39 40	10 32 36 37 38 39 40					10		10 19 20 37 39 40	19 20 37 39	13	1.6	(6, -82, 40)
Cuneus	32 37 38 39 40 43 44	32 36 37 38 39 40 41 42 43 44							37 39 40	37 39	16.3	1.4	(9, -99, 0)
SuperiorOccipitalGyrus	39 40	39 40							39 40	39	7.4	1.7	(-30, 86, 24)

Anatomic Label	1 Hz	4.5 Hz	8 Hz	9.5 Hz	10 Hz	11 Hz	12.5 Hz	15 Hz	28.5 Hz	35 Hz	Max (Z)	Vol (cc)	max Z(x,y,z)
MiddleOccipitalGyrus	30 39 40 44 46	30 39 40 41 42 44 46							30 39 40	39	8.4	1.7	(-50, -67, -9)
InferiorOccipitalGyrus	40 43	40 41 42 43							40		35.8	0.9	(21, -94, -8)
LingualGyrus	23 32 37 40 43 44 46	23 32 37 40 41 42 43 44 46							23 37 40	37	35.4	3.1	(21, -97, -8)
Caudate								48			16.5	2.5	(6, 12, 8)
Thalamus					51			51			18.7	0.8	(3, -6, 3)
Culmen	32 46	32 41 46									7	1.2	(-27, -50, -13)
Declive	46	41 46									8	0.4	(-42, -62, -15)