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Dynamic spatiotemporal variability of alpha-BOLD relationships during the resting-state and task-evoked responses

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ABSTRACT

Accurate characterization of the spatiotemporal relationship between two of the most prominent neuroimaging measures of neuronal activity, the 8–13 Hz, occipito-parietal EEG alpha oscillation and the BOLD fMRI signal, must encompass the intrinsically dynamic nature of both alpha power and brain function. Here, during the eyes-open resting state, we use a 16 s sliding-window analysis and demonstrate that the mean spatial network of dynamic alpha-BOLD correlations is highly comparable to the static network calculated over six minutes. However, alpha-BOLD correlations showed substantial spatiotemporal variability within-subjects and passed through many different configurations such that the static network was fully represented in only ~10% of 16 s epochs, with visual and parietal regions (coherent on average) often opposingly correlated with each other or with alpha. We find that the common assumption of static-alpha BOLD correlations greatly oversimplifies temporal variation in brain network dynamics. Fluctuations in alpha-BOLD coupling significantly depended upon the instantaneous amplitude of alpha power, and primary and lateral visual areas were most strongly negatively correlated with alpha during different alpha power states, possibly suggesting the action of multiple alpha mechanisms. Dynamic alpha-BOLD correlations could not be explained by eye-blinks/movements, head motion or non-neuronal physiological variability. Individual's mean alpha power and frequency were found to contribute to between-subject variability in alpha-BOLD correlations. Additionally, application to a visual stimulation dataset showed that dynamic alpha-BOLD correlations provided functional information pertaining to the brain's response to stimulation by exhibiting spatiotemporal fluctuations related to variability in the trial-by-trial BOLD response magnitude. Significantly weaker visual alpha-BOLD correlations were found both preceding and following small amplitude BOLD response trials compared to large response trials.

Introduction

The intrinsic electromagnetic oscillations of the brain's neuronal populations are widely studied as functional correlates of cognitive systems. The 8–13 Hz alpha oscillation is the dominant characteristic of scalp EEG and the most readily measured electrophysiological signal of human brain activity. The alpha oscillation is a fundamental feature of both spontaneous and task-evoked brain activity and has been shown to play an important role in the perception of external stimuli (Babiloni et al., 2006; Haegens et al., 2011; Handel et al., 2011; Hanslmayr et al., 2007, 2013; Linkenkaer-Hansen et al., 2004) and many cognitive abilities (Basar et al., 2001, 1997; Jensen et al., 2002; Klimesch, 1999; Mazaheri and Jensen, 2010; Palva and Palva, 2011; Pfurtscheller and Lopes da Silva, 1999; Sauseng et al., 2005; Zumer et al., 2014). It is hypothesised that it provides a mechanism for gating and regulating the flow of information both within and between brain networks by selectively inhibiting task-irrelevant pathways (Jensen and Mazaheri, 2010; Klimesch et al., 2007; Zumer et al., 2014). Alpha is also a commonly used measure of a subject's level of arousal, attention and cortical excitability (Olbrich et al., 2009; Rihs et al., 2007, 2009; Romei et al., 2008; Roth, 1961; Strijkstra et al., 2003; Thut et al., 2006).

While alpha is therefore clearly an important neural oscillation with considerable behavioural and physiological implications, uncertainty still exists about how it is generated. Partly, this is a result of the difficulty in accurately localising the generators of scalp electromagnetic activity, and also a lack of sensitivity to crucial deep brain structures such as the thalamus. Consequently the relationship between the power of the occipito-parietal alpha oscillation and the amplitude of the blood oxygenation level dependent (BOLD) fMRI signal has long been of interest for localising the spatial origins of this neuronal activity and the cortical and subcortical regions whose activity is influenced by it. Commonly, this relationship has been assessed by computing the linear correlation between the two signal timeseries.

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However, the majority of previous studies only assess "static" alpha-BOLD correlations over at least several minutes, often as long as ten minutes (de Munck et al., 2008; de Munck et al., 2009; Goldman et al., 2002; Laufs et al., 2006, 2003). This neglects both the intrinsic, spontaneous nature of alpha oscillations as well as the dynamic information about temporal fluctuations in brain activity that they contain.

Static negative correlations between spontaneous fluctuations in resting-state alpha power and the BOLD signal have been observed in primary and lateral visual cortex (Ben-Simon et al., 2008; de Munck et al., 2008 2007, 2009; Feige et al., 2005; Goldman et al., 2002; Laufs et al., 2006, 2003; Liu et al., 2012; Mo et al., 2012; Moosmann et al., 2003; Wu et al., 2010; Zhan et al., 2014) as well as bilateral frontal and parietal regions resembling the dorsal attention network (DAN) (de Munck et al., 2007; Laufs et al., 2006; Mo et al., 2012; Zhan et al., 2014). In addition, positive correlations have been less frequently observed in the bilateral insula (Goldman et al., 2002), the thalamus (de Munck et al., 2007; Feige et al., 2005; Goldman et al., 2002; Liu et al., 2012; Wu et al., 2010) and the default mode network (DMN) (Mo et al., 2012; Wu et al., 2010).

Static alpha-BOLD correlations therefore encompass brain regions from multiple different intrinsic connectivity networks (ICNs) (de Munck et al., 2009; Feige et al., 2005; Goldman et al., 2002; Laufs et al., 2006; Mo et al., 2012). These ICNs are defined by strong static correlations in fMRI signal between their individual nodes, exhibiting high levels of within-network functional connectivity (Cole, 2010; Van Dijk et al., 2009), with distinct temporal patterns of activity compared to other ICNs, and hence low levels of between-network functional connectivity. By definition therefore different ICNs do not remain continually, coherently active with each other for periods of several minutes and beyond, otherwise they would be classed as the same ICN. Instead, the static alpha-BOLD network, which encompasses multiple ICNs (visual, saliency, DAN, DMN), is composed of dynamic networks that regularly come in and out of coherence with each other over long periods of time (Smith et al., 2012; Zalesky et al., 2014). On average this variable relationship with alpha approximates a common pattern of coupling, but to what extent this common pattern represents the actual regions involved in alpha fluctuations remains to be clarified.

Functional measures of dynamic neuronal interactions can be extracted by studying how the coherence in the activity of different brain regions fluctuates over time. In recent years, there has been an increase in studies implementing short time-windows to assess such temporally fluctuating, functional relationships both within- and between-ICNs (Allen et al., 2014; Chang and Glover, 2010; Gonzalez-Castillo et al., 2014; Handwerker et al., 2012; Hutchison et al., 2013b; Schaefer et al., 2014; Tagliazucchi et al., 2012; Wilson et al., 2015; Zalesky et al., 2014). These dynamic fMRI functional connectivity analyses have revealed that short-term correlations, on the order of tens of seconds, are closer to the dynamic temporal organization of brain activity and therefore more functionally informative, findings supported by recent MEG studies (Betti et al., 2013; de Pasquale et al., 2010).

An analogous dynamic analysis is well suited to studying resting-state alpha-BOLD coupling, due to the transient nature of alpha power fluctuations. A single, static measure of alpha-BOLD correlation can be considered an approximation of the average relationship over a period of ten minutes, but provides little useful functional information about brain dynamics. A dynamic approach would provide an informative tool to investigate the effect of transient alpha-BOLD correlations upon a subsequent task response or a transition between behavioural states. The central hypothesis of the current study is that the commonly reported static relationship between alpha power and visual/DAN/DMN/thalamic BOLD signal is an oversimplification and that these regions show temporal fluctuations in the strength of the alpha-BOLD correlation. It is acknowledged that the spatial location of alpha-BOLD correlation displays a large degree of between-subject variability (Goncalves et al., 2006; Laufs et al., 2006). More recent work has begun to show the potential of dynamic EEG-BOLD correlations to elucidate temporal patterns of resting-state brain connectivity (Chang et al., 2013; Tagliazucchi et al., 2012; Yu et al., 2016), but a basic understanding of the extent and functional significance of within-subject variability in alpha-BOLD coupling remains lacking.

In this study, we conduct a thorough investigation of the spatio-temporal dynamics of correlations between occipito-parietal alpha power and the BOLD signal during the eyes-open resting-state, before applying the method to study how the temporal profile of alpha-BOLD correlations fluctuates with variations in the trial-by-trial amplitude of the BOLD response to visual stimulation. We initially investigate how an individual's alpha power and alpha frequency contribute to the between-subject variability in the strength and spatial pattern of static resting-state alpha-BOLD correlations. We then employ a sliding window analysis to study the temporal dynamics of the resting-state alpha-BOLD relationship. Firstly, we compare dynamic to static correlations to investigate whether alpha-BOLD correlations can be accurately and meaningfully assessed at short timescales of 60, 32, 16 s or 8 s (30, 16, 8 or 4 MR samples).

We then investigate if alpha power is consistently correlated with the BOLD signal in the brains major ICNs. We assess how often brain regions that are correlated with alpha on average are actually un-coupled from alpha and from each other, addressing questions such as: whether the spatial pattern of alpha-BOLD coupling passes through different configurations, whether an alpha-BOLD network exists that temporally varies in strength, sometimes showing periods of no correlation at all, or whether it fractures into different components that show structured variations in regional correlations over time.

We use the extra information provided by this dynamic analysis to investigate differences in the spatial pattern and extent of alpha-BOLD correlations between periods of high and low alpha power. Finally, using an additional recording of EEG-fMRI responses to visual stimulation we investigate how the spatiotemporal pattern of dynamic alpha-BOLD correlations relates to the magnitude of the brain's response to stimulation and whether temporal differences in alpha-BOLD coupling are associated with differences in BOLD response amplitude.

Methods

Written informed consent was obtained from all participants and the protocol was approved by the Research Ethics Board of the University of Birmingham. Thirty-two right-handed subjects (age=26 ± 4 years, 16 females) took part in a resting-state EEG-fMRI study whereby they were instructed to lie-still and keep their eyes open for 6 min.

EEG-fMRI data acquisition

All experiments were conducted at the Birmingham University Imaging Centre (BUIC) using a 3T Philips Achieva MRI scanner. An eight-channel phased-array head coil was used to acquire a T1-weighted anatomical image (1 mm isotropic voxels) and whole-brain T2*-weighted, functional EPI data (180 volumes, 32 slices, 3×3×4 mm voxels, TR=2000 ms, TE=35 ms, SENSE factor=2, flip angle=80°). Subject's cardiac and respiratory cycles were continuously recorded throughout using the scanner's inbuilt pulse oximeter and respiratory belt. EEG data were simultaneously recorded from 62 scalp Ag/AgCl ring-type electrodes distributed according to the 10–20 system (EasyCap, Germany) with two additional channels used for recording the electrocardiogram and electrooculogram. The impedance at all recording electrodes was maintained below 20 kΩ. BrainAmp MR-plus EEG amplifiers (Brain Products, Munich) were used for recording data at 5 kHz with 0.016–250 Hz hardware filters. Subjects were positioned such that electrodes Fp1 and Fp2 were at the magnet isocentre in the

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