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Role of white-matter pathways in coordinating alpha oscillations in resting visual cortex

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ABSTRACT

In the absence of cognitive tasks and external stimuli, strong rhythmic fluctuations with a frequency ≈ 10 Hz emerge from posterior regions of human neocortex. These *posterior α -oscillations* can be recorded throughout the visual cortex and are particularly strong in the calcarine sulcus, where the primary visual cortex is located. The mechanisms and anatomical pathways through which local α -oscillations are coordinated however, are not fully understood. In this study, we used a combination of magnetoencephalography (MEG), diffusion tensor imaging (DTI), and biophysical modeling to assess the role of white-matter pathways in coordinating cortical α -oscillations. Our findings suggest that primary visual cortex plays a special role in coordinating α -oscillations in higher-order visual regions. Specifically, the amplitudes of α -sources throughout visual cortex could be explained by propagation of α -oscillations from primary visual cortex through white-matter pathways. In particular, α -amplitudes within visual cortex correlated with both the anatomical and functional connection strengths to primary visual cortex. These findings reinforce the notion of posterior α -oscillations as intrinsic oscillations of the visual system. We speculate that they might reflect a default-mode of the visual system during which higher-order visual regions are rhythmically primed for expected visual stimuli by α -oscillations in primary visual cortex.

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Introduction

The most salient feature of electrical activity in human neocortex in the absence of explicit cognitive tasks is strong ≈ 10 Hz oscillations (Berger, 1875; Hari and Salmelin, 1997). These posterior α -oscillations are typically recorded over occipital and posterior-parietal regions and are particularly strong within and around the calcarine fissure—where the primary visual cortex (V1) is located—as well as in the occipito-parietal fissure (Hari and Salmelin, 1997; Ciulla et al., 1999). Although initially regarded as functionally irrelevant, evidence is now accumulating that posterior α -oscillations do not merely reflect passive idling of visual areas but correlate with allocation of visuo-spatial attention (Yamagishi et al., 2005; Jensen et al., 2010; Capilla et al., 2012). For example, during anticipatory cue-stimulus intervals, α decreases in those regions of V1 that correspond to attended locations in the visual field and increases in unattended or distractor regions (Kelly et al., 2006; Rihs et al., 2007). Moreover, these modulations do not only pertain to spatial attention tasks but extend to feature-based attentional processes

in higher-order visual areas including the dorsal and ventral projection systems (Jokisch and Jensen, 2007; Snyder and Foxe, 2010). Thus, power fluctuations in posterior α -oscillations seem to reflect modulations in cortical excitability, constituting a fundamental mechanism for flexible routing of visual attention (Jensen et al., 2002; Romei et al., 2008; Spaak et al., 2012). Research on the neuronal mechanisms underlying attention-driven α -modulation is expected to benefit from a characterization of the resting-state organization of posterior α -oscillations.

Magnetoencephalographic (MEG) recordings in human subjects and local field potential (LFP) recordings in dogs and macaques have shown that posterior α -oscillations can be recorded throughout the visual system (Lopes Da Silva and Storm van Leeuwen, 1977; Salmelin and Hari, 1994; Hari and Salmelin, 1997; Ciulla et al., 1999; Bollimunta et al., 2008, 2011; Spaak et al., 2012). In addition to cortical sources of α , recordings in behaving dogs and slice preparations of cat lateral geniculate nucleus (LGN) have observed α -sources in thalamic nuclei, particularly the LGN and pulvinar (Lopes da Silva et al., 1973; Hughes et al., 2004). Moreover, the time-courses of sources in LGN and in particular the pulvinar were correlated with various α -sources in occipital cortex (Lopes Da Silva et al., 1980). Furthermore, EEG-fMRI recordings in humans have found resting-state fluctuations in posterior α -power

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to be correlated with fluctuations in blood-level-oxygenation-level (BOLD) signal throughout the visual system and in several subcortical nuclei (Goldman et al., 2002; Moosmann et al., 2003; Feige et al., 2005). Thus, although posterior α -oscillations seem to involve large-scale thalamo-cortical networks, the nature of their involvement remains controversial (Silva et al., 1991; Karamah et al., 2006).

In particular, it is unclear if α -oscillations are generated at the source locations identified by MEG or if they are generated at other locations and propagate through white-matter pathways. For example, α -oscillations in V1 might be generated within V1 itself (Liley et al., 1999), reflect propagated oscillations that are generated in the LGN (Lopes da Silva et al., 1974; Hughes et al., 2004), which is densely connected to V1 via the optic radiation, or reflect reverberation within thalamo-cortical loops (Robinson et al., 2001; Rennie et al., 2002). Similarly, α -oscillations in different regions of the visual system might be generated locally or reflect propagated oscillations from distant cortical or thalamic regions. In this study, we assessed the contribution of white-matter pathways in the propagation and coordination of posterior α -oscillations. To this end, we combined MEG source-modeling (Woolrich et al., 2011), diffusion tensor imaging (DTI) based probabilistic fiber tracking (Behrens et al., 2003b), and biophysical modeling.

The kind of biophysical model we used in this study is referred to as a *neural mass model*. Neural mass models have a long tradition (Wilson and Cowan, 1973; Lopes da Silva et al., 1974; Freeman, 2004) and have been applied to several EEG phenomena, including α -oscillations (Lopes da Silva et al., 1974), event-related potentials (Jansen and Rit, 1995), and epileptic seizures (Suffczynski et al., 2004). Neural mass models describe the electrical behavior of a piece of neural tissue in terms of macroscopic quantities and ignore the spatial extendedness of the tissue (Deco et al., 2008). An extension of neural mass models are so-called *neural field models* which can be thought of as consisting of a sheet of neural masses and describe the electrical behavior of neocortex in a spatially continuous manner (Deco et al., 2008). Neural fields have a long tradition as well (Wilson and Cowan, 1973; Nunez, 1974; Wright and Liley, 1995) and also have been applied to several EEG phenomena including delta, alpha, beta, and gamma oscillations (Nunez et al., 2001; Liley and Cadusch, 2002; Rennie et al., 2000, 2002; Robinson et al., 2001), sleep (Robinson et al., 2002; Steyn-Ross et al., 2005), and general anesthesia (Bojak and Liley, 2005; Hutt and Longtin, 2010; Hindriks and van Putten, 2012). They provide a theoretical framework in which different EEG phenomena can be integrated and their relationships be investigated (Robinson et al., 2001; Breakspear et al., 2006).

The motivation for using a neural mass model in the present study is that they make more feasible an initial investigation into how posterior α -oscillations might emerge from the topology of white-matter pathways and provide a direction for more extended modeling studies. It is of interest to note though, that the combination of neural mass models with white-matter topological data has proven effective in modeling the emergence of resting-state networks (RSNs) in blood-oxygenation level-depend(BOLD) functional magnetic resonance imaging (fMRI) imaging (Ghosh et al., 2008; Deco et al., 2009, 2011, 2013; Honey et al., 2009; Cabral et al., 2011). Thus, the current study should be regarded as an initial orientation that provides a startingpoint for constructing more extended models of the spatio-temporal behavior of α -oscillations in human cortex.

We found that the assumption of a single α -source in the calcarine sulcus (V1) could explain the source-strengths of α -oscillations throughout the occipital lobe, medial posterior-parietal cortex and temporal lobes. Furthermore, the source-strengths of α -oscillations in these regions correlated with both the functional and anatomical connections to V1, consistent with the assumption of a generator in V1. Although this study does not rule out the possibility that α -oscillations are generated throughout the cortex (Robinson et al., 2001; Rennie et al., 2002; Nunez and Srinivasan, 2006), it establishes a central role of V1-connectivity in coordinating α -oscillations in the visual system at rest.

Materials and methods

MEG recordings

Ten subjects (3 males, 20–39 years old, mean 27.9) underwent an eyes-closed resting-state MEG scan lasting 5 min on an Elekta Neuromag (Elekta Neuromag Oy, Helsinki, Finland). Data preprocessing included signal space separation, de-noising with independent component analysis (ICA), source reconstruction and bandpass filtering of the MEG signal. External noise was removed using Signal-Space Separation (SSS) and the data was down-sampled to 200 Hz, using the MaxFilter software (Elekta-Neuromag). Signal space separation is a spatial filtering applied to the sensor space data that compensates for external interference and sensor artifacts. This works by projecting the MEG data onto a basis set of spherical harmonics, followed by the removal of the basis functions that correspond to sources originating from outside the sensor array, before reconstructing the data (Taula et al., 2005). Harmonics corresponding to sources originating from within the sensor array were preserved whilst interfering sources from outside the environment surrounding the sensor array were rejected. The sensor-space MEG data were de-noised using temporal ICA to remove cardiac, 50 Hz mains and, in some subjects, eye movement artifacts.

Specifically, the data were decomposed into 64 components using fastICA (Hyvarinen, 1999) (64 is the rank of the MEG data after signal space separation). Prior to the ICA decomposition, each sensor type was normalized by its smallest eigenvalue to give an unbiased noise estimate across sensor types. Eye-blink, cardiac and mains interference ICA components were manually identified by the combined inspection of spatial topography and time course, kurtosis of the time course, and frequency spectrum for all components. The artifact components are removed by subtracting them from the data (Mantini et al., 2011). This enabled simultaneous de-noising of the data and correction of the lead fields (via the montage function in SPM8).

Each dataset was then co-registered into the Montreal Neurological Institute (MNI) space by registering the canonical MNI template to the Polhemus head shape data. A local sphere forward model (Huang et al., 1999) was then estimated using the head shape and sensor geometry. Before acquisition of the MEG data, a three-dimensional digitizer (Polhemus Fastrack) was used to record each subject's head shape relative to the position of the head position indicator (HPI) coils, with respect to three anatomical landmarks, or fiducials, which could be registered on the MRI scan (the nasion, and the left and right preauricular points). A structural MRI was also acquired. Individual meshes (including scalp, inner skull and cortical surfaces) are generated from an individual subjects structural MRI by applying the inverse of the same deformation field needed to normalize the individual structural image to an MNI template, to the canonical meshes derived from the MNI template (Mattout et al., 2007). Coregistration of the MEG sensor positions with the structural MRI and the meshes is then carried out via an approximate matching of the fiducials in the two spaces, followed by a more accurate surface-matching routine that fits the head-shape function (measured by Polhemus) to the scalp mesh. This procedure was carried out using scripts in the SPM8 package. Lead fields were computed using a single-shell head model (Nolte, 2003) based on the inner skull mesh using scripts in the SPM8 package.

Subsequently, the MEG data were bandpass filtered between 1 and 80 Hz. A LCMV beamformer was used to transform the original sensor time-series into source-space time-series, that is, to reconstruct the activity at the 90 center locations defined by the AAL brain parcellation. The beamformer uses the forward model and sensor-space covariance matrix to calculate a set of weights which spatially filter the signal so that activity from outside the source is suppressed and the activity from the chosen sources is extracted (Woolrich et al., 2011). The magnetometers and gradiometers were combined during beamforming by normalizing the data and lead fields for each sensor type by its respective minimum eigenvalue; this effectively gives both classes of sensor

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