



Top-down alpha oscillatory network interactions during visuospatial attention orienting



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ABSTRACT

Neuroimaging and lesion studies indicate that visual attention is controlled by a distributed network of brain areas. The covert control of visuospatial attention has also been associated with retinotopic modulation of alpha-band oscillations within early visual cortex, which are thought to underlie inhibition of ignored areas of visual space. The relation between distributed networks mediating attention control and more focal oscillatory mechanisms, however, remains unclear. The present study evaluated the hypothesis that alpha-band, directed, network interactions within the attention control network are systematically modulated by the locus of visuospatial attention. We localized brain areas involved in visuospatial attention orienting using magnetoencephalographic (MEG) imaging and investigated alpha-band Granger-causal interactions among activated regions using narrow-band transfer entropy. The deployment of attention to one side of visual space was indexed by lateralization of alpha power changes between about 400 ms and 700 ms post-cue onset. The changes in alpha power were associated, in the same time period, with lateralization of anterior-to-posterior information flow in the alpha-band from various brain areas involved in attention control, including the anterior cingulate cortex, left middle and inferior frontal gyri, left superior temporal gyrus, and right insula, and inferior parietal lobule, to early visual areas. We interpreted these results to indicate that distributed network interactions mediated by alpha oscillations exert top-down influences on early visual cortex to modulate inhibition of processing for ignored areas of visual space.

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Introduction

Converging evidence indicates that the control of visual attention involves a distributed network encompassing regions of occipital, parietal, temporal, and frontal cortex (Corbetta and Shulman, 2002). Electrophysiological imaging during attention control enables the localization and characterization of the dynamics of such network activity (Green and McDonald, 2008; Green et al., 2011). In particular, alpha-band (8–14 Hz) oscillations seem to play a critical role in the control of visual attention (Mazaheri et al., 2014; Rihs et al., 2007; Worden et al., 2000). Co-registered EEG-fMRI recordings have linked changes in alpha oscillatory power in sensory areas to BOLD signals in the attention network (Liu et al., 2014; Zumer et al., 2014) as well as to BOLD signals in the ventral visual pathway (Zumer et al., 2014). These studies allow the inference that top-down signals modulate alpha power in sensory cortices,

thus regulating information processing in those regions. Direct evidence for this causal link, however, is still lacking.

Characterizing directionality of oscillatory interactions in attention control networks is critical as increasing evidence indicates that alpha oscillations in early visual cortex play a mechanistic role in visual attention control. When attention is covertly deployed to one side of visual space, alpha-band oscillations are increased over ipsilateral visual areas (i.e., Rihs et al., 2007; Worden et al., 2000). These oscillations have been shown to originate in early visual regions (Yamagishi et al., 2003, 2005) and can be retinotopically modulated by selective visuospatial attention (Kelly et al., 2006). Such alpha oscillations are also relevant for cross-modal attention (Fu et al., 2001). As well, TMS investigations indicate that such alpha rhythms play a causal role in determining if information is selected for higher visual processing (Thut et al., 2006).

Granger causality (Granger, 1969) affords a potential means for investigating the direction of information flow within the attention control network. Granger causality is inferred via *post hoc ergo propter hoc* logic; a weak form of causality is implied if predictability of a time series is improved by the addition of a time-lagged second time series to the predictability inherent in the first. Recent advances in the imaging of

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network synchronization have provided new methods for investigating connectivity dynamics underlying cognitive processes (Palva and Palva, 2012), and methods have now been introduced to investigate Granger causality in a model-free way in specific frequency bands among brain regions during cognitive processing (Lobier et al., 2014; Wibral et al., 2011). Several studies have demonstrated changes in inter-regional oscillatory interactions during attention control (Siegel et al., 2008; Doesburg et al., 2008, 2009), but the directionality of information flow in distributed brain networks in this context remains unclear.

The present study evaluated the hypothesis that alpha-band, directed, network interactions within the attention control network are systematically modulated by the locus of visuospatial attention. Magnetoencephalography (MEG) was recorded while subjects performed a covert attention-orienting task. Beamformer analysis was used to localize areas activated during the control of visuospatial attention, and narrow-band transfer entropy (NBTE) was employed to investigate directional interactions among activated regions during attention control.

Methods

Participants and task

MEG was recorded inside a dimly lit magnetically shielded room at 600 Hz from 12 participants while they performed a covert visuospatial orienting task. All participants were neurologically normal and had normal or corrected to normal vision. MEG data were usable for 11 subjects, resulting in a group with a mean age of 21.3, range 21–37 (6 males, 9 right handed) for analysis. White visual stimuli were back-projected onto a dark screen 35 cm in front of subjects' eyes and responses were made via a response box placed under the right hand.

Participants were instructed to maintain fixation on a centrally positioned cross ($1.31^\circ \times 1.31^\circ$). Arrow cues ($1.64^\circ \times 1.64^\circ$) were briefly (100 ms) presented at fixation on each trial and instructed participants to covertly attend to a box ($1.97^\circ \times 1.97^\circ$) in either the lower left or lower right visual hemifield (6.2° below and 18.5° laterally from fixation). Left and right directional cues were equiprobable. Either a "+" or an "x" ($1.64^\circ \times 1.64^\circ$; 100 ms duration) would appear 1000–1200 ms following the onset of the directional cue in the box in the lower portion of either the left or the right visual field. The next trial began 2000 ms after the offset of the + or x. Both the type of stimulus and the location of appearance occurred with equal probability (the cue was not predictive). Participants were instructed to press a button if they detected a "+", but not an "x", at the cued location, and were instructed not to respond to any stimuli occurring at the non-cued location. This paradigm maximizes attention orienting to the cued location because, although stimuli occurred equally often in the uncued location, participants never had to respond to those stimuli. Thus, they had no reason to try to divide their attention between cued and uncued locations as they would have had they been required to respond to stimuli occurring in the uncued location. The behavioural profile associated with this paradigm and its relation to electrophysiology is more extensively discussed in Doesburg et al., 2008. Participants were asked to respond as quickly and accurately as possible and to minimize eye movements, blinks, and head movements. MEG was recorded in seven 5 min blocks. Head position was measured before and after each block, and blocks were rejected if more than 5 mm of motion was detected. Subjects were asked to perform an extra block when localization failed. This resulted in an average of 6.75 usable blocks, or an average of 933 trials (minimum 740, maximum 1269), per participant, about 510 (minimum 368, maximum 643) each to left and to right (varied slightly from participant to participant as cue side was randomly chosen). Cue-target interval data from all trials were analysed. Typical recording sessions lasted approximately 50 min.

MEG localization of the visuospatial attention control network

Distinct peaks in ERF/ERP time courses often reflect distinct stages of processing mediated by activity in different sets of brain regions, which collectively orchestrate complex cognitive processes such as visuospatial attention control. Thus, our approach was to identify times where such peak activations occurred during the control of visuospatial attention, and to use beamformer localization at those times to determine seed points for the study of directional interactions in the attention control network. The time series of MEG activity distributed across all 151 sensors in the cue-target interval was inspected for peak times of activation, which provided time points of interest for the beamformer source localization analysis. Using best fits based on fiducial information, an anatomical T1-weighted MRI scan was selected for each participant from a database of such scans, and this scan was used to create a unique multisphere head model for each participant (Lalancette et al., 2011). Event-related scalar beamformer (1–40 Hz) was used to identify sources of activity underlying each peak in the sensor-level waveform, considering both left cue and right cue trials together (Cheyne et al., 2006).

To evaluate the statistical significance of spatial peaks in the beamformer analysis, permutation statistics were employed. To this end, activation values were shuffled across voxel locations at each time point activation peak for each participant and the largest activation of the shuffled data across the entire beamformer space in the group average was recorded. This process was iterated to create a null distribution, and the ranking of "real" observed values in this surrogate distribution was used to evaluate their statistical significance. Since each instance of the surrogate distribution was the largest activation across all voxels, this effectively controls for false positives due to multiple comparisons (as activation at each voxel is compared against the largest activation that can occur by chance across all analyzed voxels). One issue with this type of statistical approach is that posterior cortical visual MEG responses tend to be quite large and "overwhelm" smaller but reliable frontal activations. Accordingly, more anterior and frontal areas were considered separately in the statistical analysis (dividing the source space around "zero" on the Y-axis of the X–Z Talairach plane). Activations were considered significant at $p < 0.01$.

In most of the significant beamformer-determined source voxels, a number of similar peak activations were observed across. In order to reduce redundancy and to derive seeds for the connectivity analysis, we identified all of the significant peak activations within a particular anatomically specified brain region and selected only one of them to represent that region, rather than averaging all of the significant voxels' activations. We felt that this would provide a more precise characterization of the region's activity for at least one computational role than would an average across peaks, as it was possible that somewhat spatially separated peak activations could be indexing different computations even if they occurred within the same anatomical region. Specifically, if multiple peaks occurred within the same brain region (i.e., left cuneus), the coordinates of the significant peak voxel in that region with the largest magnitude was selected as a seed location to represent that region. This procedure also helps to control experiment-wise error, at the cost of some generality, as the activations of only 11 voxels were ultimately selected for power and transfer entropy analysis. To enable subsequent analysis of inter-regional information flow, time series representing the activation of each seed voxel on each trial were reconstructed using beamformer analysis (Cheyne et al., 2006). All beamforming and statistical analysis on the beamformer images were performed using the BrainWave toolbox (<http://cheynelab.utoronto.ca/brainwave>).

Analysis of local alpha power changes

We computed the time course of relative power in the alpha-band in the left and right cuneus locations in order to verify that, as in previous investigations using attention-orienting paradigms similar to that of the

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