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Region-specific modulations in oscillatory alpha activity serve to facilitate processing in the visual and auditory modalities

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ABSTRACT

There have been a number of studies suggesting that oscillatory alpha activity (~10 Hz) plays a pivotal role in attention by gating information flow to relevant sensory regions. The vast majority of these studies have looked at shifts of attention in the spatial domain and only in a single modality (often visual or sensorimotor). In the current magnetoencephalography (MEG) study, we investigated the role of alpha activity in the suppression of a distracting modality stream. We used a cross-modal attention task where visual cues indicated whether participants had to judge a visual orientation or discriminate the auditory pitch of an upcoming target. The visual and auditory targets were presented either simultaneously or alone, allowing us to behaviorally gauge the "cost" of having a distractor present in each modality. We found that the preparation for visual discrimination (relative to pitch discrimination) resulted in a decrease of alpha power (9–11 Hz) in the early visual cortex, with a concomitant increase in alpha/beta power (14–16 Hz) in the supramarginal gyrus, a region suggested to play a vital role in short-term storage of pitch information (Gaab et al., 2003). On a trial-by-trial basis, alpha power over the visual areas was significantly correlated with increased visual discrimination times, whereas alpha power over the precuneus and right superior temporal gyrus was correlated with increased auditory discrimination times. However, these correlations were only significant when the targets were paired with distractors. Our work adds to increasing evidence that the top–down (i.e. attentional) modulation of alpha activity is a mechanism by which stimulus processing can be gated within the cortex. Here, we find that this phenomenon is not restricted to the domain of spatial attention and can be generalized to other sensory modalities than vision.

Introduction

Attention involves selective facilitation of relevant sensory input and suppression of irrelevant sensory input. Oscillatory activity in the alpha range (~10 Hz) has been proposed to play a pivotal mechanistic role in attention by gating information flow to relevant sensory regions through the inhibition of irrelevant regions (Foxe et al., 1998; Jensen and Mazaheri, 2010; Klimesch et al., 2007). Supporting this hypothesis are a number of studies reporting that oscillations in the alpha range are suppressed in brain regions processing attended information, but enhanced in regions processing unattended information (Bauer et al., 2012a,b; Haegens et al., 2011a, 2012; Jokisch and Jensen, 2007; Medendorp et al., 2007; Rihs et al., 2007; Romei et al., 2008a; Thut et al., 2003). Although the mechanism underlying alpha enhancement in directing functional inhibition is not fully understood some recent work demonstrates that alpha oscillations exercise a strong inhibitory influence on both spike timing and firing rate of neural activity (Haegens et al., 2011b; Mazaheri and Jensen, 2010).

The majority of studies that have examined the role of alpha oscillations and attention have used shifts of attention (often spatial) within one modality (often visual or sensory–motor). There have been comparatively fewer studies examining the influence of auditory spatial attention on alpha lateralization in the occipital parietal regions (e.g. Banerjee et al., 2011; Fu et al., 2001; Kerlin et al., 2010). This discrepancy can in part be attributed to skepticism about the existence of alpha power modulation by auditory attention that is distinct from the visual or sensory-motor systems (see (Weisz et al., 2011) for a review of this debate). Furthermore, previous research has suggested that the detection of an auditory alpha rhythm is difficult at the scalp level due to the

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relatively small spatial extent of auditory cortical areas (Bastiaansen and Knosche, 2000).

The aim of the current MEG study was to investigate if cortical specific modulation of alpha activity facilitates performance by suppressing information across the auditory and visual modalities. We utilized a cross-modal attention task in which symbolic visual cues signaled the modality (visual or auditory) of an upcoming target to be discriminated. The target was presented with or without the presence of a distractor in a different modality. Our investigation focused on how cues signaling whether to perform a visual or auditory judgment on upcoming targets modulated alpha activity across the scalp. We were also interested in the relationship of alpha power on performance on a trial-by-trial basis.

Methods

Participants

Eighteen healthy young adults (14 women; mean age, 23.5 years; range, 18–38) participated in the study. All participants were right handed with no history of psychiatric or neurological disorders. All had normal or corrected-to normal vision. Before the start of the experiment, written informed consent was obtained from each subject. The experiment was approved by a local ethical committee (CMO region Arnhem-Nijmegen, The Netherlands). The MEG data of one participant was excluded due to many artifacts.

Cross-modal attention paradigm

The start of a trial was indicated by a brief change in a fixation cross which was followed by the attentional cue one second later (Fig. 1). An 'informative' cue consisted of a symbol indicating what modality was to be discriminated: ∨ indicated that the discrimination was to be made on a visual stimulus whereas a ∧ indicated that the discrimination was to be made on an auditory stimulus. An informative cue was always followed by a stimulus of the cued modality presented either alone or together with a stimulus of the uncued modality (50/50). A third cue was modality-ambiguous, and indicated only that a stimulus of a single modality would occur but giving no information about the modality itself. The visual stimuli, presented centrally for 50 ms, consisted of circular gratings with 3 possible types of orientation: 80°, 90°, and 110° clockwise. The auditory stimuli were presented for 200 ms to both ears via ear-tubes and were pure tones with 3 possible frequencies: 250 Hz, 1000 Hz, and 4000 Hz. The visual discrimination of the targets involved judging the orientation of the gratings, while the auditory discrimination involved judging the pitch of the target. Fig. 1A illustrates an example trial sequence. There were 50 trials of each condition throughout the experiment. Participants responded by pressing one of three buttons using their right index finger, middle finger, or ring finger. In the current study, we focused exclusively on the changes in pre-target activity induced by the informative cues.

Behavioral analysis

We were interested in the distraction cost of having a target presented with a distractor of a different modality as well as the time it took to make the target discrimination (i.e. reaction times). Distraction cost was calculated as the reaction time difference between cued targets with distractors and cued targets without distractors. The first trial of each block and trials with incorrect responses were excluded from further analyses (less than 5%).

Data acquisition

The MEG data were acquired with a 275-sensor axial gradiometer system (CTF Systems Inc., Port Coquitlam, Canada) placed in a magnetically shielded room. Horizontal and vertical electrooculogram (EOG) activity was also recorded and later used to discard trials contaminated by eye movements and blinks. The MEG and EOG signals were digitized at 600 Hz, and later down-sampled to 300 Hz for offline analysis. The participants' head position relative to the gradiometer array was determined using coils positioned at the subject's nasion, and at the left and right ear canals prior to the start of data acquisition.

In addition to the MEG measurements, whole brain high-resolution anatomical images (voxel size = 1 mm^3) were acquired for each participant using a 1.5-T Siemens Sonata whole-body scanner (Erlangen, Germany). These images were used for reconstruction of individual head shapes to create forward models for the source reconstruction procedures described later.

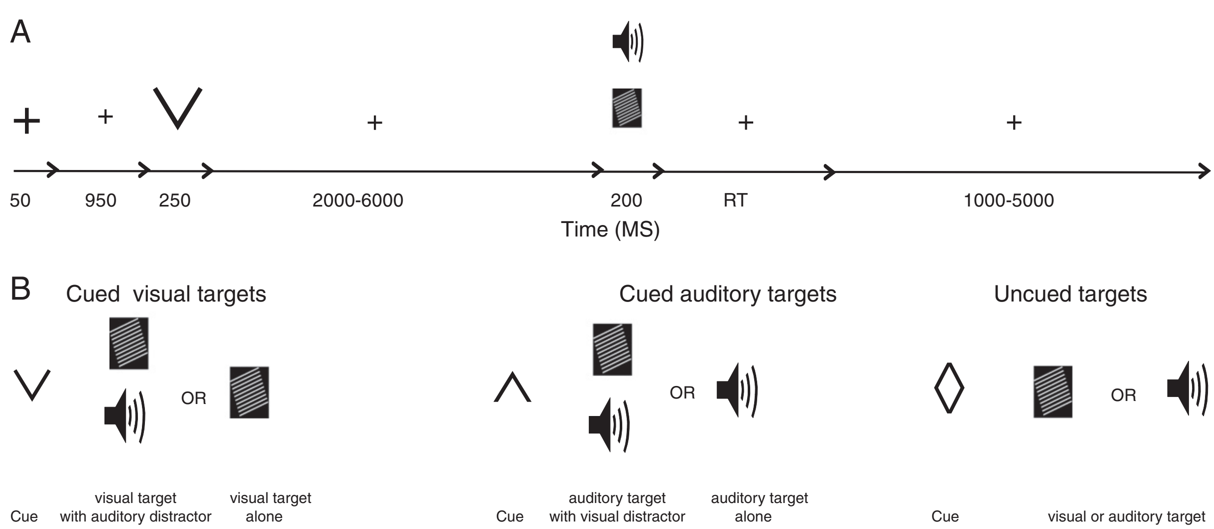

Fig. 1. The cross-modal paradigm. (A) An example trial sequence. A trial is initiated by brief change in a fixation cross followed by the attentional cue. A visual stimulus (in this case the target) and an auditory distractor are presented 2–6 s after the cue. The participants have to perform a discrimination on a physical feature of the modality (in this case orientation of grating) instructed by the cue by pressing one of three buttons. Stimuli could be presented alone or with a distractor of a different modality. (B) Cues and targets. A cue consisting of a symbol: ∨ indicated an visual discrimination; ∧ indicated an auditory discrimination; and a third type of cue," ", dubbed as modality 'ambiguous' indicated only that a stimulus of a single modality would occur but giving no information about the modality itself.