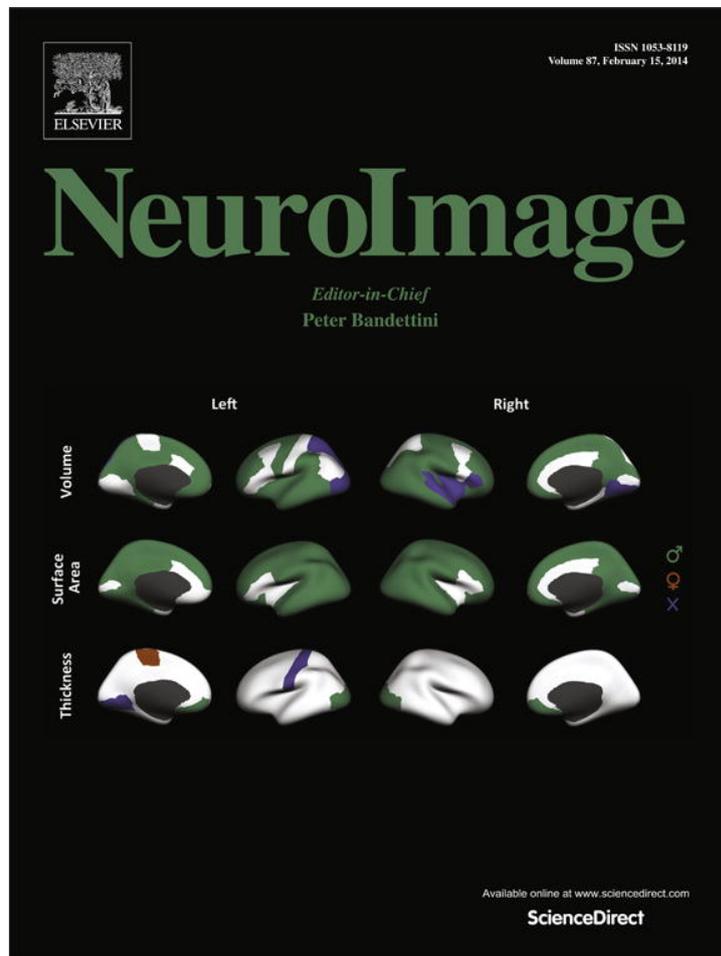


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Region-specific modulations in oscillatory alpha activity serve to facilitate processing in the visual and auditory modalities



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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.

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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 \wedge 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 mm³) 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.

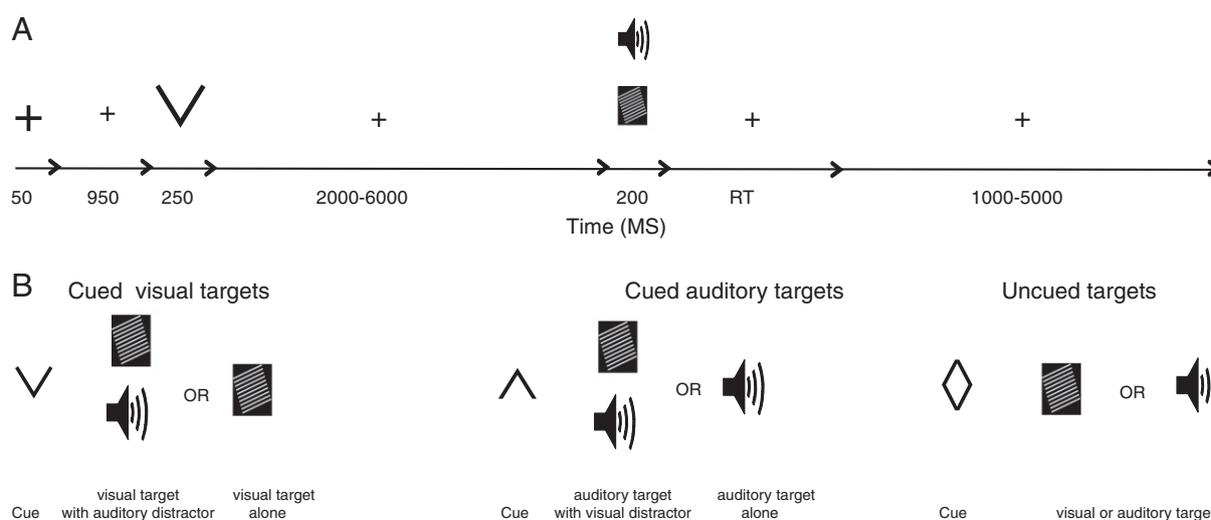


Fig. 1. The cross-modal paradigm. (A) An example trial sequence. A trial is initiated by brief change in a fixation cross followed by the attentional cue. A visual stimulus (in this case the target) and an auditory distractor are presented 2–6 s after the cue. The participants have to perform a discrimination 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; \wedge indicated an auditory discrimination; and a third type of cue, “ \diamond ”, dubbed as modality ‘ambiguous’ indicated only that a stimulus of a single modality would occur but giving no information about the modality itself.

Preprocessing

The data analysis was performed using FieldTrip, an open source Matlab toolbox developed at the Donders Centre for Cognitive Neuroimaging (<http://www.ru.nl/fcdonders/fieldtrip>). Trials containing movement, muscle, and superconducting quantum interference device (SQUID) artifacts were discarded by visual inspection and an automatic artifact removal routine rejected trials which had a mean field strength power 3 z-values above the mean. Infomax (standard, not extended) independent component analysis (Bell and Sejnowski, 1995) was used to remove any heart artifacts and eye movements not rejected by the semiautomatic routines (Jung et al., 2000). For all of our sensor level analyses, planar gradients from the MEG field distribution were calculated using a nearest-neighbor method described by Bastiaansen et al. (2001) and used in Haegens et al. (2010), Jokisch and Jensen (2007), Mazaheri et al. (2009), Nieuwenhuis et al. (2008), and Whitmarsh et al. (2011). The horizontal and vertical components of the planar gradients were estimated at each sensor location using the fields from the sensor and its neighboring sensors. The power values for the horizontal and vertical components after the spectral analysis were summed for each sensor location. For source reconstruction, we used the data from the true axial sensors and not the planar gradient estimate.

Pre-target oscillatory analysis

The oscillatory alpha activity was characterized by calculating the power spectra using the 1 second interval preceding the target. A 1 second Hanning taper was applied to the data prior to calculating the spectra to reduce any edge artifacts. The spectra were calculated for each individual trial. A similar approach was taken in Mazaheri et al. (2009) and (2010).

Statistical analysis

In order to assess the relationship between cue related changes in alpha power between the visual and auditory cue conditions we examined the difference in the power of frequencies in the alpha/lower beta band (8 to 16 Hz, using 1 Hz increments) between conditions (random effects analysis) across all sensors. We corrected for multiple-comparisons by means of the cluster (over sensors) level randomization (Maris and Oostenveld, 2007). This test controls the Type-1 error rate involving multiple comparisons (e.g. multiple sensors and/or time-frequency tiles). Next the Monte Carlo estimate of the permutation p-value of the cluster of sensors was obtained by comparing the cluster-level test statistic to a randomization null distribution assuming no difference between conditions. This distribution is obtained by randomly swapping the conditions in participants 1000 times and calculating the maximum cluster-level test statistic. A similar procedure has been used in a number of previous studies (Jokisch and Jensen, 2007; Mazaheri et al., 2009; Nieuwenhuis et al., 2008). In order to assess the relationship between cue related changes in alpha power and speed of target discrimination, we performed a trial-by-trial correlation (Spearman) in each participant between pre-target alpha power and subsequent target discrimination, across all sensors, to create topographies of the correlation. The correlation coefficients were subsequently converted to z-values using Fisher's r- to z-transformation to obtain a normally distributed variable. The statistical significance of the correlation topographies was assessed at the group level with a one-sample t-test of the correlations (alpha power vs. reaction time) at each sensor and then subjected to a cluster-level randomization test to correct for multiple comparisons.

Source reconstruction

Source reconstruction was performed using a frequency-domain beam-forming approach [dynamic imaging of coherent sources (DICS)].

The DICS technique uses adaptive spatial filters to localize power in the entire brain (Gross et al., 2001). A realistically shaped single-shell description of the brain–skull interface was constructed, based on the individual anatomical MRIs (Nolte, 2003). The brain volume of each individual subject was discretized to a grid with a 0.8 cm resolution and the lead field was calculated for each grid point. Using the cross-spectral density matrices and the lead-field, a spatial filter was constructed for each grid point (Gross et al., 2001), after which the power at each grid point was estimated in each trial for both conditions separately. A common filter was calculated for both visual and auditory cued conditions and then applied for the data separately for the individual conditions (see e.g. (Mazaheri et al., 2009; Whitmarsh et al., 2011)). The sources were estimated for the frequency bands pre-selected from the sensor level analysis. The source estimates of the individual participants' functional data along with the individual anatomical MRI images were spatially normalized to the MNI brain [Montreal Neurological Institute (MNI), <http://www.bic.mni.mcgill.ca/brainweb>] using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm>) prior to averaging. The source estimates were plotted on a standard MNI space single subject brain found in SPM8. The anatomical location of the sources was determined using the Anatomy toolbox in SPM8.

In order to assess the relationship between cue related changes in alpha power in source-space and speed of target discrimination, we performed a trial-by-trial correlation (Spearman) in each participant between pre-target alpha power at each grid point and subsequent target discrimination. The correlation coefficients were subsequently converted to z-values using Fisher's r- to z-transformation to obtain a normally distributed variable. The statistical significance of the correlations was assessed at the group level with a one-sample t-test of the correlations.

Results

Behavioral data

In the absence of distractors, participants showed significant benefit from attentional cueing. Informatively cued visual targets were discriminated significantly faster than the ambiguously cued visual targets (801 ms vs. 844 ms, $t(17) = 3.35$, $p < 0.01$) and informatively cued auditory targets were discriminated significantly faster than ambiguously cued auditory targets (903 ms vs. 972 ms, $t(17) = 4.8$, $p < 0.001$).

When the targets were presented together with distractors, participants demonstrated significant costs in response times. Reaction times to visual targets presented simultaneously with auditory distractors were significantly slower than those to visual targets presented alone (920 ms vs. 801 ms, $t(17) = 4.8$, $p < 0.001$). Likewise, reaction times to auditory targets that were presented with visual distractors were significantly slower than those to auditory targets presented alone (1142 ms vs. 903 ms, $t(17) = 10.5$, $p < 0.0001$).

Overall, the participants were significantly faster in the visual discrimination task, than the auditory (863 ms vs. 1009 ms, $t(17) = 7.8$, $p < 0.0001$).

Effects of the cross-modal cues on sensory regions

In order to investigate modality specific alpha modulation we contrasted pre-target alpha power after the visual vs. auditory discrimination cues. This contrast revealed a significant decrease in alpha activity (9–11 Hz) in sensors over the occipital cortex ($p < 0.05$; Fig. 2A, top-panel), but a relative increase in alpha/beta power (in the 14–16 Hz range) in clusters of sensors over the right temporal areas ($p < 0.05$, Fig. 2A, lower panel). Source analysis revealed the location of the maximal pre-target alpha power decrease to be in the primary visual cortex (lingual gyrus, Fig. 2B, top panel). Conversely, the location of the maximal increase in pre-target alpha power over the right sensors

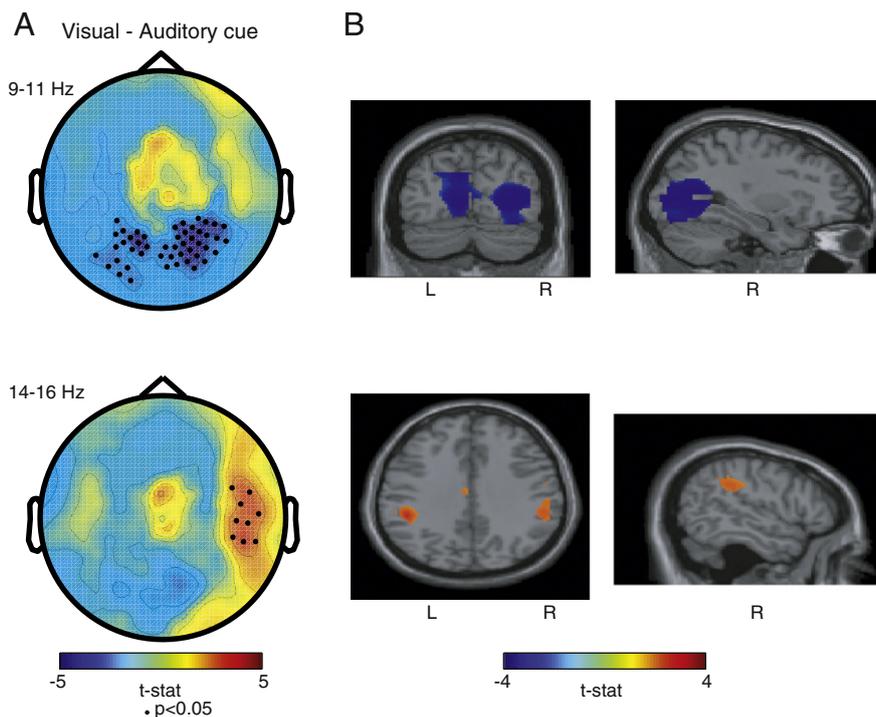


Fig. 2. Modality specific alpha/beta modulation as a result of cross-modal attentional cues. (A) The difference between pre-target power spectra for cues signaling visual versus cues for auditory (i.e. \wedge cue subtracted from \vee cue) discrimination revealed significantly less alpha activity (9–11 Hz) in sensors over the occipital cortex (upper panel) and greater alpha/beta activity (14–16 Hz) over the right temporal/parietal sensors (lower panel). The differences are expressed in terms of t-values. Sensors showing significant modulation ($p < 0.05$) corrected for multiple comparisons using cluster randomization routine (Maris and Oostenveld, 2007) are marked with large dots. (B) Top-panel: The pre-target alpha power decrease was maximal at the primary visual cortex. The source activations are plotted as t-values. The threshold for the display is set to t-values above 2.1 ($df = 16$, $p < 0.025$, one-tailed). Lower-panel: The increase in pre-target alpha/beta amplitude over the right sensors was maximal in the right supramarginal gyrus. The threshold for the display is set to t-values above 2.58 ($df = 16$, $p < 0.01$, one-tailed).

was found to be in right supramarginal gyrus (SMG). The MNI coordinates of the voxels with the maximal t-values can be found in Table 1.

Trial-by-trial modulation of pre-target alpha activity correlated with target discrimination time

We also investigated the functional relationship between alpha modulation and attentional performance. On a trial-by-trial basis, for each sensor we correlated the pre-target alpha power with the target discrimination response times. This resulted in correlation topographies for each participant. The statistical significance of these topographies on the group level was assessed with a cluster-level randomization test (see Methods). We found that when a visual target was presented with an auditory distractor, the power of the pre-target alpha activity (9–11 Hz) was significantly positively correlated with discrimination times ($p < 0.05$; Fig. 3A, top-panel) at a large cluster of the occipital, central and frontal sensors. When an auditory target was presented with a visual distractor, alpha/beta power (14–16 Hz) at a small cluster of the central–parietal sensors was positively correlated with discrimination times ($p < 0.05$; Fig. 3A, lower-panel). However, we did not

find any significant clusters of alpha power that correlated with either visual or auditory discrimination times when the targets were presented without distractors.

In source-space, the trial-by-trial correlations between alpha-power and visual discrimination times were maximal in the early visual cortices (Fig. 3B, top-panel). For the auditory targets, the correlation between alpha power and discrimination times was maximal at the precuneus and right superior temporal gyrus (STG, Fig. 3B, lower-panel). Please refer to Table 2 for MNI coordinates of the voxels showing the maximal correlation values.

Discussion

In the current study we found that cues signaling 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 right SMG. Thus, we were able to demonstrate the modulation of alpha activity by auditory attention that is distinct from the visual and sensory systems. On a trial-by-trial basis, alpha power over the visual areas was correlated with increased visual discrimination times whereas alpha power in the precuneus and right STG was correlated with increased pitch discrimination times. However, these correlations were only significant when the targets were presented alongside stimuli in a distracting modality. Taken together our findings support the view that the top-down modulation (i.e. attentionally controlled) of alpha power serves a functional role by suppressing processing in task-irrelevant regions. On the other hand, spontaneous increases of alpha power in task-relevant regions correspond to a reduction in processing capacity which can be detrimental to performance, especially in the presence of competing distracting input.

Table 1

MNI coordinates of the voxels showing maximal statistical difference between the visual and auditory cued pre-target alpha power.

MNI coordinates				
Region	X	Y	Z	t-Value
Supramarginal gyrus (R)	53	−38	33	2.3
Supramarginal gyrus (L)	−45	−38	33	2.5
Medial Frontal gyrus	−12	−11	70	3.0
Lingual gyrus, middle occipital (R)	27	−68	−2	−4.2

L, left hemisphere; R, right hemisphere.

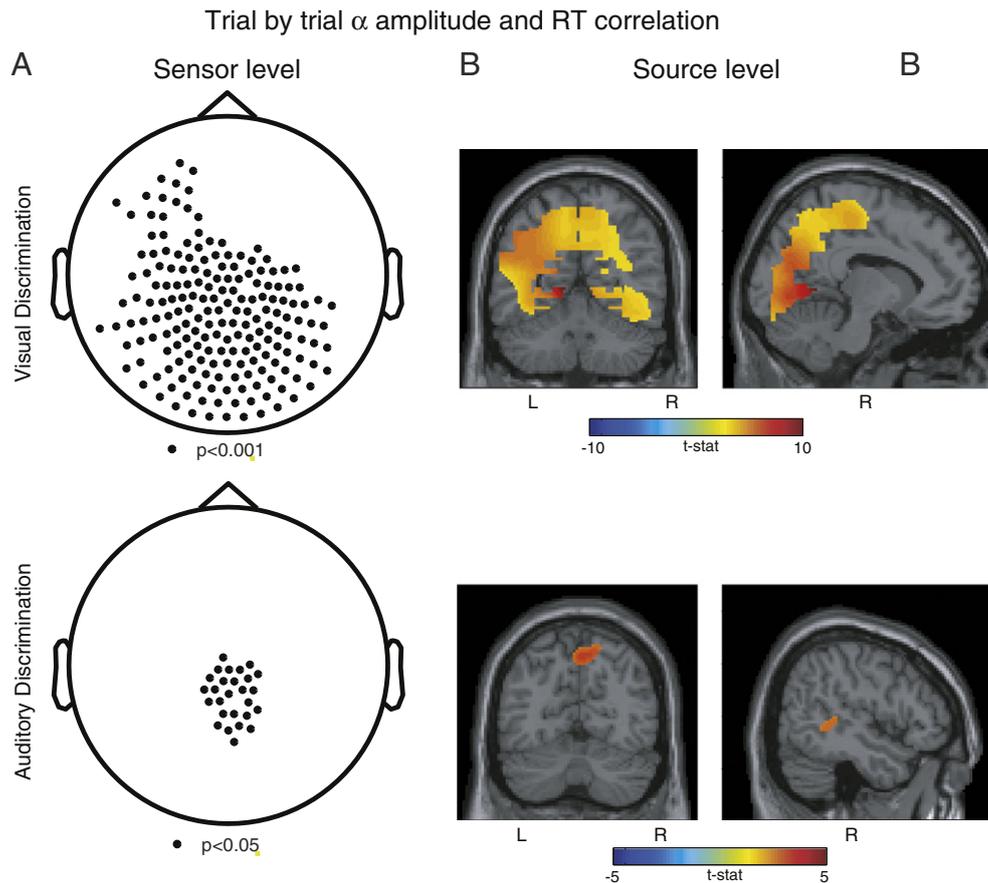


Fig. 3. Trial-by-trial correlation of pre-target alpha/beta amplitude and discrimination time in sensor and source space. (A) Top-panel: The amplitude of the pre-stimulus alpha activity across a wide range of the occipital and central parietal sensors was positively correlated with the time of visual discrimination. Sensors where a significant (one sided t -test, $p < 0.01$, corrected for multiple comparisons) correlation coefficient was found are marked with large dots. Bottom-panel: For the auditory discrimination alpha amplitude over a cluster of the central sensors showed a significant relationship (one sided t -test $p < 0.05$, corrected for multiple comparisons) between alpha amplitude and discrimination time in the presence of distractors. When distractors were not present, alpha power in these clusters was not significantly correlated with reaction times. (B) Top-panel: In source-space, alpha-power in the occipital cortex (lingual gyrus) had the strongest correlation with visual discrimination times. Lower-panel: The correlation between alpha/beta power and auditory discrimination times was largest in the precuneus and right superior/middle temporal gyrus. Notably, there were no significant voxels in the left temporal cortex. The threshold for the display is set to t -values above 2.58 ($p < 0.01$).

Top-down modulation of alpha power

Previous studies on spatial attention have found suppression of alpha activity in the visual stream contra-lateral to the focus of attention (Rihs et al., 2007; Romei et al., 2008b; Thut et al., 2003, 2006; Worden et al., 2000). The modulation of alpha activity over the occipital cortices appears to have a functional consequence for stimulus processing. Furthermore, previous work has demonstrated that visual discrimination abilities are reduced with an increase in posterior alpha activity (van Dijk et al., 2008; Zhang et al., 2008). Most recently, it has been found that the failure to lateralize the occipital alpha activity in response to an attention-directing arrow foreshadows imminent attentional failures (Bengson et al., 2012). These findings, in combination with our results, suggest that the occipital alpha serves to gate information in the early

Table 2
MNI coordinates of the voxels showing largest correlation between pre-target alpha power and target discrimination time.

Type of discrimination	Regions	X	Y	Z	t-Value
Visual	Lingual gyrus (L)	-10	-53	3	9.0
Auditory	Precuneus (R)	4	-66	52	3.2
	Superior/middle temporal gyrus (R)	50	-42	0	2.75

L, left hemisphere; R, right hemisphere.

visual system (Foxe et al., 1998; Jensen and Mazaheri, 2010; Klimesch et al., 2007).

We found that the informative cues modulated alpha activity in a cluster of sensors over the right temporal regions. The likely source of this activity was found to be in the right SMG. Previous fMRI studies have shown activity in the SMG to increase during attend auditory versus ignore auditory contrasts (Sabri et al., 2008) as well as pitch memory (Celsis et al., 1999). This has led to the speculation that this region may play a vital role in short-term storage of pitch information and pitch discrimination (Gaab et al., 2003). We speculate that the increase of alpha in the SMG might reflect the inhibition of a top-down region in regulating the processing of auditory information in the sensory cortices (i.e. the superior temporal cortex). Such an interpretation is consistent with “the interactivity thesis” used to account for the role of alpha activity with regard to spatial attention (Banerjee et al., 2011). In this framework a modality independent (i.e. supramodal) system interacts with a sensory system during the deployment of spatial attention. This suggests that the auditory alpha modulation does not serve an exclusively sensory gating role with respect to auditory attention, and that higher order regions related to the maintenance of auditory working memory such as the SMG are also affected.

To the best of our knowledge pre-stimulus modulation of alpha activity in anticipation of auditory targets has been reported in only two previous studies to date (Bastiaansen and Brunia, 2001) and (Muller and Weisz, 2012). Bastiaansen et al. found anticipatory alpha

modulation in the auditory cortex in only 2 of 5 participants. Muller and Weisz (2012) were able to demonstrate significant anticipatory alpha modulation in the auditory cortex, following visual cues signaling the location of the auditory stimuli. In our study we found alpha power over the right STG to be positively correlated with auditory discrimination times. This is in line with previous studies using PET (Zatorre and Belin, 2001), functional MRI (Lattner et al., 2005), MEG (Okamoto et al., 2009; Patel and Balaban, 2001) and EEG (Dimitrijevic et al., 2008; Shahin et al., 2006) that have found human pitch perception to rely on the right auditory cortex. Moreover, these neuroimaging studies are supported by lesion studies which have found the right auditory cortex to be essential for the retention of pitch in auditory short-term memory (reviewed in Zatorre et al., 2002).

Study caveats and considerations

One potential issue in cross-modal attentional studies is the sensory modality of the attentional cues. In our study visual stimuli informed the modality of both visual and auditory targets. The onset of the visual cues will result in stimulus-related evoked responses as well induced suppression of alpha activity in the visual cortices. We tried to minimize any potential sensory effect of the cues, by having relatively long cue to target intervals of 2–6 s. We also focused our analysis on the one second interval prior to target onset, which minimized the induction of any alpha activity in our analysis which was directly related to the onset of the cue stimuli. Nevertheless, to completely avoid the confounder introduced by the common visual cue, attentional cues in the somatosensory modality would have been the most appropriate.

Conclusion

Attention can be described as the focus of cognitive resources on relevant information while filtering or ignoring irrelevant information. We found that alpha modulation in the task relevant cortices plays a critical role in facilitating and suppressing information between modalities. Our work further adds to increasing evidence that the top-down modulation alpha power is a mechanism by which information is gated within the cortex. We were able to demonstrate that this phenomenon is not restricted to the domain of spatial attention and can be generalized to the auditory modality.

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Conflict of Interest Statement

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

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