

UNIVERSITY OF BIRMINGHAM

Research at Birmingham

Cross-sensory modulation of alpha oscillatory activity: suppression, idling and default resource allocation

Van Diepen, Rosanne ; Mazaheri, Ali

DOI:

[10.1111/ejn.13570](https://doi.org/10.1111/ejn.13570)

License:

None: All rights reserved

Document Version

Peer reviewed version

Citation for published version (Harvard):

Van Diepen, R & Mazaheri, A 2017, 'Cross-sensory modulation of alpha oscillatory activity: suppression, idling and default resource allocation', *European Journal of Neuroscience*, vol. 45, no. 11, pp. 1431-1438.
<https://doi.org/10.1111/ejn.13570>

[Link to publication on Research at Birmingham portal](#)

Publisher Rights Statement:

Checked for eligibility: 25/04/2017

"This is the peer reviewed version of the following article: van Diepen, R. M. and Mazaheri, A. (2017), Cross-sensory modulation of alpha oscillatory activity: suppression, idling and default resource allocation. *Eur J Neurosci*, which has been published in final form at doi:10.1111/ejn.13570. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving."

General rights

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

Take down policy

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact UBIRA@lists.bham.ac.uk providing details and we will remove access to the work immediately and investigate.

MISS ROSANNE MARIA VAN DIEPEN (Orcid ID : 0000-0002-9635-1109)

Article type : Research Report

Cross-**sensory** modulation of alpha **oscillatory** activity: **suppression**, idling and default resource allocation

Rosanne Maria van Diepen¹ & Ali Mazaheri²

[Research Report]

¹ Department of Psychiatry, Academic Medical Center, University of Amsterdam, Meibergdreef 9, 1105 AZ, Amsterdam, The Netherlands.

² School of Psychology, University of Birmingham, Birmingham, B15 2TT, United Kingdom.

Corresponding author Ali Mazaheri, ali.mazah@gmail.com, Fax: +44 (0)121 414 4897.

running title: Default resource allocation in cross-**sensory** attention

Keywords: oscillations, attention, EEG, visual cortex

Abstract

Alpha oscillations (~10 Hz) have been suggested to have an inhibitory influence on stimulus processing within the context of attention being coordinated across space, with an increase in the power of alpha activity occurring in spatially irrelevant regions. However, with respect to

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/ejn.13570

This article is protected by copyright. All rights reserved.

Accepted Article

cross-**sensory** attention (distribution of attention to different sensory modalities) an increase in alpha activity from baseline has not yet been definitively linked to active inhibition of distraction.

In the current study, we examined the role of top-down alpha modulation in facilitating and suppressing stimulus processing between the visual and auditory domain. We utilized two cross-**sensory** paradigms, one containing distractors while the other paradigm only contained targets, in order to separate distractor related activity. We found a cue induced increase from baseline for the power of occipital alpha activity in posterior cortex when participants anticipated the occurrence of auditory targets combined with visual distractors. Interestingly there was no increase in alpha power observed in the condition where auditory targets occurred without distractors. These findings suggest that the increase in alpha activity from baseline reflects top-down drive processes serving to inhibit distracting input. However, we found that there was no significant difference in the absolute occipital alpha power between when participants were expecting a visual distractor, and the session where no visual distractors were present. We account for these findings by suggesting that an increase in alpha power in the anticipation of visual distractors, rather than being exclusively inhibitory, could also signal the re-allocation of resources in the sensory systems.

Introduction

The most predominant oscillatory activity in the EEG/MEG is at the frequency of 10 Hz and is commonly referred to as the alpha rhythm. The increase in amplitude of alpha activity over a sensory region of the cortex has been tied to the inhibition of that region (Hanslmayr *et al.*, 2007; Van Dijk *et al.*, 2008; Romei *et al.*, 2008; Lange *et al.*, 2013). This has led to the theoretical framework in which information is believed to be routed to relevant brain areas by inhibition of irrelevant brain regions through the increase of alpha activity (Foxe *et al.*, 1998; Klimesch *et al.*, 2007; Mazaheri & Jensen 2010).

The vast majority of studies finding evidence for the functional inhibitory role of alpha activity have used paradigms in which spatial attention shifts within one modality (i.e. Yamagishi *et al.*, 2003; Kelly *et al.*, 2006; Rihs *et al.*, 2007; Rihs *et al.*, 2009; Gerven *et al.*, 2009; Kelly *et al.*, 2009; Handel *et al.*, 2011; Snyder *et al.*, 2011). Comparatively fewer studies that have investigated alpha modulation in the context of suppressing information in a task irrelevant sensory modality (Foxe *et al.*, 1998; Fu *et al.*, 2001; Mazaheri *et al.*, 2014) in the scope of attentional cuing across different modalities (e.g. visual and auditory). These studies for the most part have examined the differences in alpha activity *between conditions* where attention was directed to a specific modality. In addition, while some studies have found an increase in alpha activity from a baseline in the sensory regions of the distracting modality (Fu *et al.* 2001), it is unclear if this increase is related to functional inhibition of a region or alternatively simply reflecting a sensory region not being engaged but rather 'idling' (Jensen *et al.*, 2002; Foxe & Snyder, 2011).

In the current EEG study we utilized two variants of a cross-**sensory** attention task where symbolic visual cues validly signaled the modality (visual or auditory) of an upcoming target to be discriminated. In one variant the target was presented alone, while in the other variant target stimuli were presented alongside distractors in a different modality. We focused our analysis on the cue induced changes in the power of occipital alpha activity in anticipation of targets/distractors. We were interested in how the attentional cues modulated the pretarget alpha oscillations and the consequences of this modulation on attentional performance, with regards to the facilitation of target processing as well as inhibition of distractors.

Materials and methods

Participants

Eighteen participants (16 female, age range 18-28 years) were recruited at the University of Amsterdam and Amsterdam University of Applied Sciences. All participants signed informed consent documents before the start of the experiment. Participants reported normal or corrected-to-normal vision, no hearing disabilities, and no history of psychiatric or neurological disorders. Participants were compensated with 10 per hour. This study was approved by The University of Amsterdam Department of Psychology Ethics Committee.

Apparatus and Procedure

The participants were seated 60 cm from the monitor in a dimly lit room. They practiced at least 90 trials before starting the experiment. The stimuli were presented using Presentation software (Neurobehavioral Systems Inc., Albany, CA, USA) on a 24 inch LCD monitor (BenQ XL2420T) with a refresh rate of 120 Hz.

Subjects performed two cross-**sensory** cuing experiments (counterbalanced) in which they had to attend to an auditory or visual stimulus (Figure 1). The visual stimuli, presented centrally for 25 ms (3 screen refreshes), consisted of Gabor patches having a visual angle of $\sim 6.2^\circ$ with 3 possible types of orientation: -5° , 0° , 5° clockwise. The auditory stimuli, presented for 25 ms via speakers, were pure tones with 3 possible frequencies: 500 Hz, 1000 Hz, 2000 Hz (including 5 ms rise and 5 ms fall shaped by a Blackman window). Participants judged the orientation of the visual stimulus or pitch of the auditory stimulus using a 3-button response device using their right hand. Prior to target presentation a 100 ms cue was presented, indicating whether participants had to respond to a visual ('V') or auditory ('inverted V' representing an A) stimulus. All target orientations and tone frequencies were presented an equal number of times.

During the ‘*Distractor absent*’ experiment a single target was presented without a distractor, while in the ‘*Distractor present*’ experiment the target was always accompanied by a distractor in the opposing modality (a visual distractor during an auditory target and vice versa). The difference with previous cross-sensory cuing paradigms (Fu *et al.*, 2001; Mazaheri *et al.*, 2014) is that trials with and without distractors are presented in different blocks. This means that activity related to distractor suppression can be separated because it is known when to expect a distractor and when not.

Visual and auditory stimuli were not presented exactly simultaneously with Presentation software: visual stimuli were presented 1219 ms ($\sigma = 5$ ms) after cue onset while auditory stimuli were presented at 1256 ms ($\sigma = 3$ ms) for the ‘distractor-present’ paradigm. For the ‘distractor-absent’ paradigm visual stimuli were presented ~1217 ms ($\sigma = 4$ ms) after cue onset, auditory stimuli 1260 ms ($\sigma = 3$ ms). Total trial duration was 2560 ms. Reported reaction times are in relation to the presentation of the target modality.

The ‘distractor-present’ session contained 168 auditory-cued trials and 168 visual cued trials. The ‘distractor-absent’ session contained 144 attend-auditory and 144 attend-visual trials. To verify if subjects were using the cue for preparation in the ‘distractor-absent’ condition, 60 trials containing an uninformative cue (diamond shape) were added. A comparison of reaction times for the uninformative and informative cues should result in a difference such that longer reaction times are present for the informative cues. The uninformatively cued trials were not analyzed in relation to preparatory alpha activity. Moreover, both paradigms contained twenty percent ‘catch’ trials containing no target to be able to look at phase angle modulations (Van Diepen *et al.*, 2015), which were not analyzed in the current manuscript.

EEG acquisition and processing

EEG data were acquired using a WaveGuard 10-5 cap system developed by ANT, with 64-Ag/AgCl electrodes, spanning from frontal, temporal, central and occipital scalp sites. The EEG was sampled at 1024 Hz with an online average reference and then subsequently imported into MATLAB for all further off-line analyses. The electro-oculogram (EOG) was recorded between supra- and infra- orbital sites around the right eye for vertical movement (blinks), and outer canthi of the left and right eyes for possible horizontal eye-movements. Impedance was maintained below 100 k Ω . Offline processing and analyses were performed using Matlab (Natick, MA), functions from EEGLAB (Delorme & Makeig, 2004) and the Fieldtrip software package (Oostenveld *et al.*, 2011). The EEG data were highpass-filtered at 0.5 Hz and epoched from -1 to +2.5 s, time-locked to cue onset. Reported times in the current manuscript are from here on however in relation to visual target presentation. Trials with substantial muscle artefacts were identified and removed through visual inspection (12.7% and 15.0% of trials for the **distractor-present** and **distractor-absent** experiment respectively). Bad electrodes were identified and interpolated using the spherical spline interpolation routine in EEGLAB (2 subjects with 2 channels, 2 subjects with 1 channel). Ocular artefacts were removed using Independent Component Analysis (ICA) (Jung *et al.*, 2000). We only analyzed correct trials. Trials with an RT < 100 ms were considered incorrect and excluded from further analysis.

Frequency analysis

In order to obtain time-intervals of interest Time-Frequency-Representations (TFRs) of power were estimated to allow the examination of the course of alpha activity after presentation of the cue. Per trial a sliding time window **with steps of 50 ms** was tapered with a Hann window having an adaptive time window of three cycles for each frequency of

interest ($\Delta T = 3/f$). Similar approaches were used by Osipova et al. (2006), Jokisch and Jensen (2007), Mazaheri et al. (2009). We calculated what time-point after cue presentation alpha power started to differ between the attend-auditory and attend-visual condition, irrespective of distractor presence. Therefore TFR data were averaged over the distractor-present and distractor-absent block. Changes in baseline-corrected alpha power (relative change = $(\text{Power} - \text{Power baseline} [-500 -100 \text{ ms precue}]) / \text{Power baseline}$) were statistically assessed for every time-point between cue and target presentation using a non-parametric cluster-based permutation test as described in Maris & Oostenveld (2007). Type I errors due to multiple comparisons were reduced by clustering neighboring channels and time-points that showed a similar effect. A probability value is obtained through the Monte Carlo estimate of the permutation p-value of the cluster of channels by randomly swapping the conditions in participants 1000 times and calculating the maximum cluster-level test statistic. Statistical analysis comparing conditions time-point by time-point revealed that alpha power started to differ significantly between the attend auditory and attend visual condition starting at 517 ms prior to target presentation (700 ms post cue). As such we chose to focus on alpha power in the interval -500 to 0 ms prior to the onset of the targets. In order to minimize spectral leakage from the stimulus evoked response of the targets the data was windowed using a Hanning taper from -500 to 0 ms prior to target presentation after which the Fast Fourier Transform was obtained. All our subsequent statistical analysis was done from the alpha power (8-12 Hz) obtained from this step.

Modality specific modulations

We hypothesized that an increase in alpha power from baseline in posterior channels would only be present during the presentation of a visual distractor (i.e. attend-auditory/Distractor-present condition) if alpha oscillations are used as a mechanism to actively inhibit distraction.

Accepted Article

First, baseline-corrected alpha activity (relative change) prior to visual distractor presentation was compared to zero using a cluster-based permutation test, to isolate preparatory activity related distractor inhibition.

Then, we examined whether the increase in alpha activity was absent when an auditory target was to be identified without simultaneous presentation of a visual distractor. This was done to make sure that the increase was specific for distractor suppression. Baseline differences could be present between the distractor-absent and distractor-present condition because they were measured during different blocks. Alpha power prior to cue presentation was therefore included in the analysis as baseline in addition to preparatory pretarget activity. Values were entered into a 2x2x2 repeated-measured ANOVA with the levels *time* (baseline/pretarget) *modality* (attend-auditory/attend-visual) and *distraction* (present/absent). Alpha power was averaged over trials and over occipital channels that showed a significant increase from baseline during the visual distractor condition as found using the aforementioned cluster-based permutation-test (Figure 3 right topography). The order of the distractor-present and distractor-absent blocks was included in the model as between-subject variable.

Relation between alpha power and behavior

Behavioral benefits associated with alpha power changes were examined using linear regression of posterior alpha power on reaction times (similar analysis is performed in Jones et al. (2010)). For every subject absolute alpha power was averaged over channels located over the posterior region showing a significant modulation from baseline during visual distractor expectation (Figure 3 right topography). Trials were then divided into 10 bins based on alpha power sorted from low to high. Alpha power and associated RT's were calculated per bin by averaging over trials and then over subjects. The regression analysis was performed separately for the different target and distractor conditions. The analysis for visual target trials was done to examine the benefit of alpha power

modulations in occipital cortex during processing of target information. **The same analysis was performed** for auditory target trials to infer the influence of alpha power modulations when the sensory region was irrelevant.

Results

Behavioral

In both experiments, visual targets were identified faster than auditory targets (*distractor present*: 639 ms vs. 728 ms, $t(17) = -4.26$, $p = 0.0004$, *distractor absent*: 606 ms vs. 697 ms, $t(17) = -7.12$, $p = 0.000002$). The percentage of correct trials was also higher for visual targets compared to auditory targets (*distractor present*: 96 % vs. 88 %, $t(17) = 7.20$, $p = 0.000001$, *distractor absent*: 98 % vs. 95 %, $t(17) = 3.24$, $p = 0.005$).

Given that cues were not essential to perform the task correctly in the distractor-absent session, reaction times of trials with informative cues were compared to trials with uninformative cues to verify whether participants showed benefits from them. RTs for auditory targets decreased from 748 ms for uninformative cues to 697 ms for informative cues ($t(17) = -5.10$, $p = 0.00008$). For visual targets the average RT decreased from 642 ms for uninformative cues to 606 ms for informative cues ($t(17) = -5.91$, $p = 0.00002$). The faster identification of trials with an informative cue suggest that top-down processes facilitated target processing. Response times are visualized on Figure 2.

The attentional cues did not influence task accuracy: auditory targets were identified in 93 % of trials with an uninformative cue and in 95 % with an informative cue ($t(17) = -1.48$, $p = 0.16$). Visual targets were identified in 98 % of trials with both informative as well as uninformative cues ($t(17) = -0.15$, $p = 0.917$). Given the high performance rates, we speculate that the absence of a difference is due to a ceiling effect.

To test whether participants were disturbed by the presentation of distractors in a different modality, RTs from the distractor-present blocks were compared to RTs from the distractor-absent experiment. Presentation of auditory distractors during visual targets slowed RTs on average by 24 ms ($t(17) = -3.29, p = 0.004$). Visual distractors during auditory targets slowed RTs on average by 31 ms ($t(17) = -3.77, p = 0.001$). Presentation of a distractor in a different modality is detrimental for task performance and a mechanism for active inhibition of distractors could be beneficial during this task.

Pre-stimulus Alpha power was relatively decreased during expectation of a Visual Target. Consistent with previous studies, alpha power was greater over occipital and frontal channels prior to expectation of an auditory target compared to the expectation of a visual target (Figure 3 left topography). Time-point - by - time-point analysis on Time-Frequency data shows that these cue-induced modulations started 700 ms after cue onset (i.e 500 ms prior to targets, $t = 164.499, p < 0.001$, Monte-Carlo corrected for multiple comparisons).

Posterior Alpha power increased when a Visual Distractor was expected

Simply contrasting activity prior to visual target expectation with activity prior to auditory target expectation does not distinguish processes related to **the suppression** of distraction from those related facilitation of target processing. As such alpha activity prior to visual distractor presentation (i.e alpha power in the -500ms to 0 interval prior to target onset) was therefore also compared to its precue baseline. Alpha power was increased in posterior channels when an auditory target was paired with a visual distractor, supporting the hypothesis that alpha power actively suppresses distraction in order to enhance target processing ($t = 32.62, p = 0.022$, Monte-Carlo corrected for multiple comparisons, Figure 3, right topography).

Expectation of visual distractor did not boost posterior alpha power above idling level

To establish whether the increase in alpha activity was exclusively related to **suppression** of distraction, the (absolute) amount of pretarget alpha power (i.e alpha power in the -500ms to 0 interval prior to target onset) was compared to alpha power during the block in which no distraction was expected (Figure 4). To be able to take possible baseline differences between the two blocks into account, average alpha power was entered into a mixed ANOVA with factors *time* (baseline/pretarget) *modality* (attend-auditory/attend-visual) and *distractor presence* (present/absent). *Counterbalancing order* was added as a between-subject variable. A three-way interaction would be expected when alpha power only increased from baseline during the expectation of a distractor. There was indeed a significant three-way interaction between the effects of *time*, *modality* and *distractor presence* $F(1,16) = 5.434$, $p = 0.033$, supporting the hypothesis that alpha power only increases during expectation of a visual distractor (Figure 5).

For further exploration of the hypothesis that alpha only increases prior to distractor expectation, the simple interaction between *time* (baseline/pretarget) and *distractor presence* (present/absent) was examined for auditory target trials. An interaction would be expected when alpha power increases during the distractor-present block but not during the distractor-absent block. A significant interaction effect was indeed found ($F(1,17) = 11.655$, $p = 0.003$). However, there was no difference in absolute alpha power prior to target presentation ($t(17) = 0.038$, $p = 0.970$). Instead, alpha power was different between the blocks at baseline ($t(17) = 2.256$, $p = 0.038$), with lower alpha power during the distractor-present block. For visual trials, the interaction between time and distractor presence was not significant ($F(1,17) = 1.0622$, $p = 0.317$). Only a main effect of distractor presence was found, indicating lower levels of alpha power during the block with distraction than the block without distraction ($F(1) = 1.6339$, $p = 0.022$). In summary, although alpha power was increased in posterior

channels in expectation of a visual distractor, the increase did not lead to higher levels of absolute alpha power compared to when no distraction was expected. Instead, participants showed differences in baseline alpha power between the block with and without distraction.

The four-way interaction between the effects of *time*, *modality*, *distractor presence* and *counterbalancing order* was significant, $F(1,16) = 4.687$, $p = 0.046$, indicating that the interaction was different for the two counterbalancing sequences. To examine how the three-way interactions differed from each other, we performed 4 separate mixed ANOVA's for the 4 task-conditions with *time* as within-subject and *counterbalancing order* as between-subject factor. Only a main effect for *time* was present during auditory target trials with distraction ($F(1) = 7.51$, $p = 0.015$) and a difference between *counterbalancing* groups was present for the auditory and visual targets during the block with distractors ($F(1,16) = 10.079$, $p = 0.006$ and $F(1,16) = 8.821$, $p = 0.009$, respectively) such that alpha power was lower for the group that performed the block with distraction first (Figure 5). No interactions were found, possibly due to the low number of subjects per group ($n = 9$). This means that we were not able to determine where the difference between the two counterbalancing groups is located.

The Alpha modulation was predictive of behavior during Target Detection, but not during Distractor Suppression.

The suppression of alpha activity in occipital channels prior to visual target presentation **significantly predicted reaction times during trials with distraction ($p = 0.019$, $R^2 = 0.516$) as well as during trials without distraction ($p = 0.0009$, $R^2 = 0.768$)**, such that lower alpha power lead to shorter reaction times (Figure 6). **Against expectation**, the increase in alpha power during visual distraction **did not predict shorter reaction times ($p = 0.838$,**

R²= 0.005). Also when no distraction was expected during auditory target presentation did the alpha power not predict target detection speed (p = 0.835, R² = 0.006).

Discussion

Using a cross-sensory attention task we found a post-cue increase in posterior alpha power prior to expectation of a visual distractor. This increase in alpha activity was absent when participants performed the same task - identification of an auditory target - without presentation of visual distractors. This finding is consistent with a functional inhibitory account of alpha power modulation in task-irrelevant cortices. However our additional findings do not unequivocally support the functional inhibitory frame work of alpha power increases. First, the post-cue increase in occipital alpha power did not have any significant behavioral benefits in terms of reactions times. Second, and more important, was our observation that there was no significant difference in the absolute occipital alpha power between when participants were expecting a visual distractor, and the sessions where no visual distractors were present. This observation would suggest that the level of alpha power present during the task where the visual cortex needed to be functionally inhibited (i.e .when distractors are present) was not significantly different from when the visual cortex was assumed to be idle (i.e . auditory target are presented alone).

In order to account for these observations we hypothesize that alpha power at the baseline period in the two tasks reflected the task-specific default allocation of resources to the sensory systems. An increase in alpha power from a baseline level of activity over task-irrelevant regions likely reflects inhibitory processes. However, high levels of alpha without any modulation from baseline reflect the default resource allocation of the task irrelevant sensory regions. Thus, here the functional inhibitory role of alpha comes into play only when

the power is increased relative to the default level set due to task demands. The increase in the suppression of alpha activity in anticipation of visual-targets in the distractor-present sessions could reflect the re-allocation of resources to the visual stream to accommodate the demand for visual target discrimination in presence of distracting auditory input.

Although the increase in alpha activity from baseline during expectation of distraction is a novel finding, the absence of an influence on performance is in line with previous research. Mazaheri *et al.* (2014) also examined alpha power in a cross-**sensory** paradigm and found both for the visual and the auditory domain that alpha activity in the region processing the target was correlated with reaction times. A correlation was absent when the alpha power was related to distractor processing. Moreover, Foxe *et al.* (2014) employed a cross-**sensory** paradigm with visual and auditory targets and distractors. Here trials in which the target modality was switched were compared to trials in which the target modality was similar to the previous trial. The increased effort during a switch trial was seen in decreased alpha power in occipital cortex for trials in which the target modality was switched to visual. However, no increase in alpha power was present when the target modality switched to auditory. The inhibitory effect of alpha power was however supported when fast switch trials were compared to slow switch trials: alpha power was higher for the former than for the later. Only when specific subgroups were utilized the influence of distractor related alpha activity was found beneficial for task performance. This could mean that the influence is specific for switch trials. An alternative explanation for the absence of a correlation is that the inhibitory influence of alpha activity in distractor processing is small or focal and therefore hard to detect. Only when the difference between subgroups is large enough, the power to detect differences in alpha activity is large enough. A different use of subgroups has been effective in showing a relation between behavior and distractor related alpha activity. Haegens *et al.* (2012) found that increased alpha power lead to increased performance when comparing

Accepted Article

correct and incorrect trials for a somatosensory cuing paradigm. Perhaps, as proposed above, the difference in alpha power is large enough to be detected when correct and incorrect trials are compared. Conversely, **suppression** through alpha oscillations is more relevant when competing information is presented within the same modality (similar to spatial attention) than when attention is shifted between modalities. While we focused on the processing of competing information, cross-**sensory** attention might be predisposed on the collaboration between different modalities (Banerjee *et al.* 2011).

To conclude, based on primarily studies of spatial attention, alpha oscillations are thought to have an inhibitory influence on stimulus processing. Our findings suggest that the role of alpha power in irrelevant regions during cross-**sensory** attention might be more complicated and intricate than serving an exclusively **suppressive** role.

Competing Interests

Authors declare no conflict of interest

Acknowledgements

We thank the anonymous reviewers for their suggestions on a previous version of this manuscript.

References

- Banerjee, S, Snyder, A C., Molholm, S., & Foxe, J. J. (2011). Oscillatory alpha-band mechanisms and the deployment of spatial attention to anticipated auditory and visual target locations: supramodal or sensory-specific control mechanisms?. *The Journal of Neuroscience*, 31(27), 9923-9932.
- Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods*, 134(1), 9-21.
- Driver, J., & Spence, C. (2000). Multisensory perception: Beyond modularity and convergence. *Current Biology*, 10(20), R731-R735.

- Foxe, J. J., Murphy, J. W., & De Sanctis, P. (2014). Throwing out the rules: anticipatory alpha-band oscillatory attention mechanisms during task-set reconfigurations. *European Journal of Neuroscience*, 39(11), 1960-1972.
- Foxe, J. J., Simpson, G. V., & Ahlfors, S. P. (1998). Parieto-occipital approximately 10 Hz activity reflects anticipatory state of visual attention mechanisms. *Neuroreport*, 9(17), 3929-3933.
- Foxe, J. J., & Snyder, A. C. (2011). The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention. *Front Psychol*, 2, 154.
- Fu, K. M., Foxe, J. J., Murray, M. M., Higgins, B. A., Javitt, D. C., & Schroeder, C. E. (2001). Attention-dependent suppression of distracter visual input can be cross-modally cued as indexed by anticipatory parieto-occipital alpha-band oscillations. *Brain Res Cogn Brain Res*, 12(1), 145-152.
- Haegens, S., Luther, L., & Jensen, O. (2012). Somatosensory Anticipatory Alpha Activity Increases to Suppress Distracting Input. *Journal of Cognitive Neuroscience*, 24(3), 677-685.
- Handel, B. F., Haarmeier, T., & Jensen, O. (2011). Alpha oscillations correlate with the successful inhibition of unattended stimuli. *J Cogn Neurosci*, 23(9), 2494-2502.
- Hanslmayr, S., Aslan, A., Staudigl, T., Klimesch, W., Herrmann, C. S., & Bauml, K. H. (2007). Prestimulus oscillations predict visual perception performance between and within subjects. *Neuroimage*, 37(4), 1465-1473.
- Jensen, O., & Mazaheri, A. (2010). Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front Hum Neurosci*, 4, 186.
- Jones, S. R., Kerr, C. E., Wan, Q., Pritchett, D. L., Hämäläinen, M., & Moore, C. I. (2010). Cued spatial attention drives functionally relevant modulation of the mu rhythm in primary somatosensory cortex. *Journal of Neuroscience*, 30(41), 13760-13765.**
- Jung, T. P., Makeig, S., Humphries, C., Lee, T. W., McKeown, M. J., Iragui, V., & Sejnowski, T. J. (2000). Removing electroencephalographic artifacts by blind source separation. *Psychophysiology*, 37(2), 163-178.
- Kelly, S. P., Gomez-Ramirez, M., & Foxe, J. J. (2009). The strength of anticipatory spatial biasing predicts target discrimination at attended locations: a high-density EEG study. *European Journal of Neuroscience*, 30(11), 2224-2234.
- Kelly, S. P., Lalor, E. C., Reilly, R. B., & Foxe, J. J. (2006). Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *J Neurophysiol*, 95(6), 3844-3851.
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev*, 53(1), 63-88.
- Lange, J., Oostenveld, R., & Fries, P. (2013). Reduced occipital alpha power indexes enhanced excitability rather than improved visual perception. *J Neurosci*, 33(7), 3212-3220.

- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *J Neurosci Methods*, 164(1), 177-190.
- Mazaheri, A., van Schouwenburg, M. R., Dimitrijevic, A., Denys, D., Cools, R., & Jensen, O. (2014). Region-specific modulations in oscillatory alpha activity serve to facilitate processing in the visual and auditory modalities. *Neuroimage*, 87, 356-362.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput Intell Neurosci*, 2011, 156869.
- Rihs, T. A., Michel, C. M., & Thut, G. (2007). Mechanisms of selective inhibition in visual spatial attention are indexed by alpha-band EEG synchronization. *European Journal of Neuroscience*, 25(2), 603-610.
- Rihs, T. A., Michel, C. M., & Thut, G. (2009). A bias for posterior alpha-band power suppression versus enhancement during shifting versus maintenance of spatial attention. *Neuroimage*, 44(1), 190-199.
- Romei, V., Brodbeck, V., Michel, C., Amedi, A., Pascual-Leone, A., & Thut, G. (2008). Spontaneous fluctuations in posterior alpha-band EEG activity reflect variability in excitability of human visual areas. *Cereb Cortex*, 18(9), 2010-2018. dSnyder, A. C., & Foxe, J. J. (2010). Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. *J Neurosci*, 30(11), 4024-4032.
- van Diepen, R. M., Cohen, M. X., Denys, D., & Mazaheri, A. (2015). Attention and temporal expectations modulate power, not phase, of ongoing alpha oscillations. *J Cogn Neurosci*, 27(8), 1573-1586.
- van Dijk, H., Schoffelen, J. M., Oostenveld, R., & Jensen, O. (2008). Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. *J Neurosci*, 28(8), 1816-1823.
- van Gerven, M., & Jensen, O. (2009). Attention modulations of posterior alpha as a control signal for two-dimensional brain-computer interfaces. *J Neurosci Methods*, 179(1), 78-84.
- Yamagishi, N., Callan, D. E., Goda, N., Anderson, S. J., Yoshida, Y., & Kawato, M. (2003). Attentional modulation of oscillatory activity in human visual cortex. *Neuroimage*, 20(1), 98-113.
- Zumer, J. M., Scheeringa, R., Schoffelen, J. M., Norris, D. G., & Jensen, O. (2014). Occipital Alpha Activity during Stimulus Processing Gates the Information Flow to Object-Selective Cortex. *Plos Biology*, 12(10).

Figure captions

Figure 1. Task design (not at scale). Participants identified the rotation of a Gabor patch on half of the trials and the pitch of a tone on the other half of the trials, using their right hand. A preceding cue denoted the modality of the upcoming target, enabling

participants to prepare and shift attention to the target modality. All participants performed two versions of this cross-modal cuing paradigm (order counterbalanced): in one version ('distractor-present') the target was accompanied by a distractor in the opposite modality, while in the other 'distractor absent' version the targets were presented alone. The 'distractor absent' paradigm also contained uninformative cues which did not inform the modality of the upcoming target.

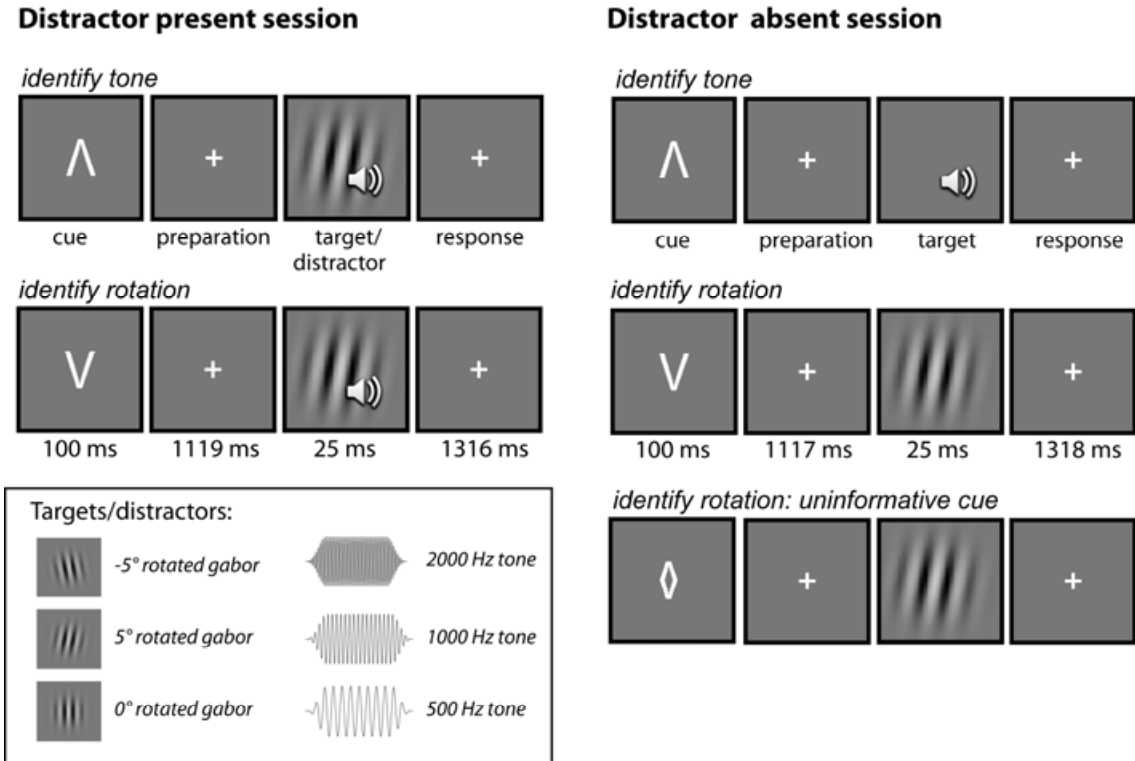
Figure 2. Average response time during auditory and visual target trials. Subjects responded faster to visual targets than to auditory targets. Response times increased for both type of targets when a distractor was presented in the opposing modality or when the modality of the target was not cued prior to presentation.

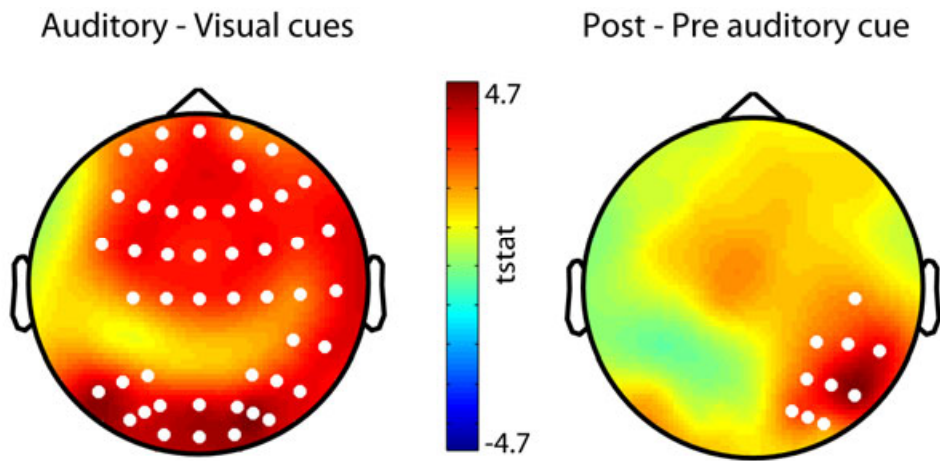
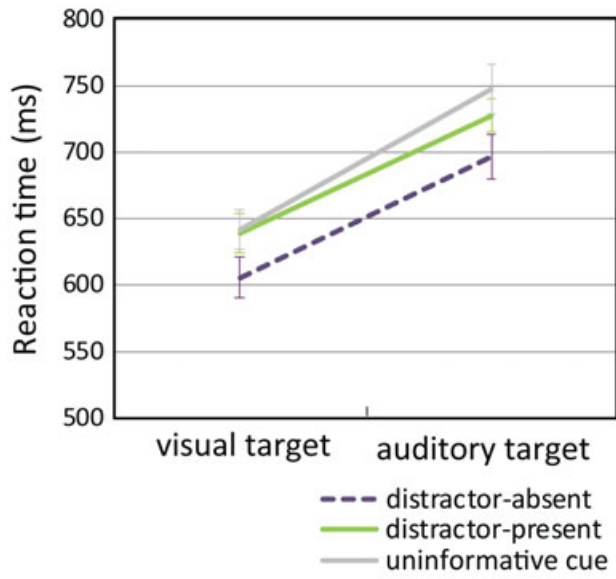
Figure 3. Modulation of alpha power induced by expectation of a visual distractor -500 to 0 ms prior to auditory target onset. Left topography: The difference between pre-target alpha power for cues signaling auditory versus cues for visual discrimination (in the presence of distractors of a different modality) revealed significantly more alpha activity in electrodes over the visual and frontal cortex. Right topography: -500 to 0 ms prior to the auditory targets, expectation of a visual distractor induced an increase in alpha power in posterior channels relative to the precue baseline.

Figure 4. Time-Frequency-Representations of power in posterior channels. The relative change from baseline (A) revealed that alpha power increased in occipital channels when a visual distractor was expected. Absolute values (B) show the difference in absolute alpha power between the distractor-present and distractor-absent block. **Data are smoothed for display purposes only.**

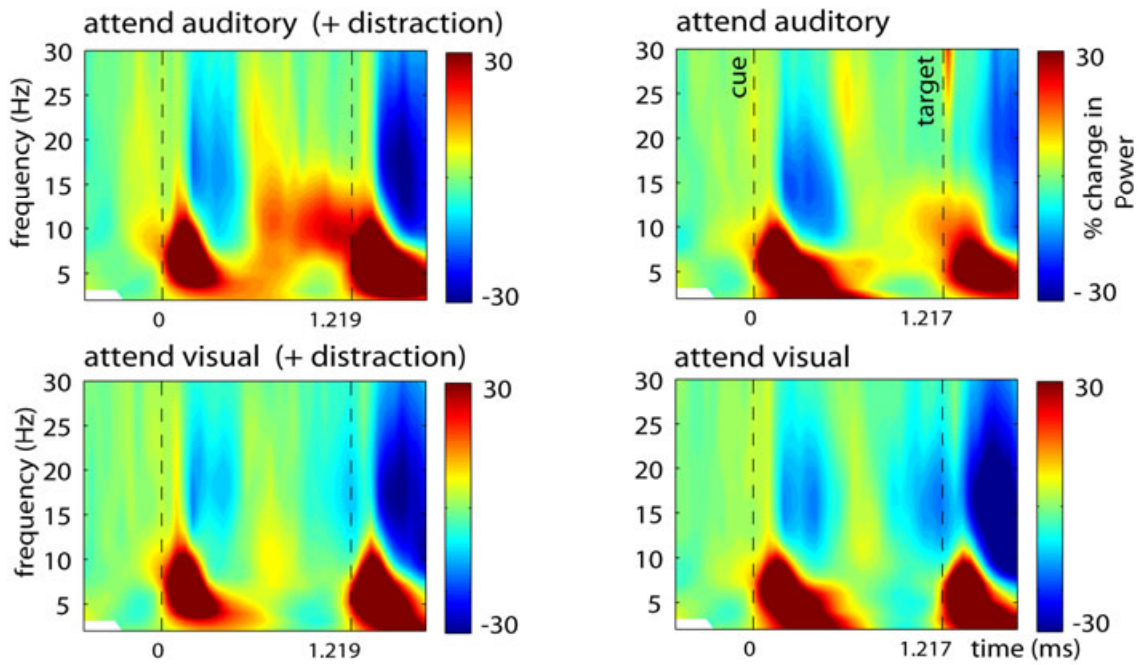
Figure 5. **Mean** absolute alpha power (+ **within subject SEM**) at baseline and prior to target presentation in posterior channels (see figure 3, right panel). **When all subjects were considered**, alpha power was lower prior to target presentation when a visual target was expected (low saturation lines) compared to when an auditory target was expected (high saturation lines). Alpha power at baseline was lower for trials with a distractor (red lines) than without a distractor (blue lines). **Statistical power was too low to examine differences between the subgroup of participants (n = 9) that performed the block without distraction first (left) and for the subgroup (n = 9) that performed the block with distraction first (right).**

Figure 6. Influence of prestimulus alpha on reaction times. RT's are shown as a function of absolute alpha power in posterior channels sorted into 10 bins from low to high power. The black line represents the average over subjects and the standard error across subject (n=18). Alpha power had a significant impact on reaction times for visual target trials, but not for auditory target trials.





A. Relative change from baseline



B. Absolute power

