

Distractor Suppression Uniquely Contributes to the Lateralized Alpha Response in Spatial Attention

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Abstract:

In theory, selective attention results from target selection and distractor suppression. While neural oscillatory power in the alpha frequency band (~10 Hz) has been implicated in the selection of to-be-attended targets, there is lack of empirical evidence for its involvement in the suppression of to-be-ignored distractors. Here, we use electroencephalography (EEG) recordings of N = 33 human participants to test the pre-registered hypothesis that alpha power relates to distractor suppression (<https://osf.io/bv7zs>). In an auditory spatial pitch discrimination task, we manipulated the side (left vs right) of either a target or distractor tone sequence, while fixing the other in the front. Alpha power relatively increased contralateral to the target stream and decreased ipsilaterally. Critically, alpha lateralization reversed in direction for the suppression of distractors, which agrees with the hypothesized involvement of alpha power in distractor suppression. Source analysis revealed that suppression modulated lateralized alpha power in more anterior, frontal cortical regions than selection. Alpha lateralization bore functional significance in that it allowed us to predict single-trial behavioural accuracy. Findings support a model in which suppression is not a necessary by-product of selection but an independent neuro-cognitive process.

Keywords: spatial attention; target selection; distractor suppression; alpha oscillations; attentional filter

Introduction

Goal-oriented behaviour requires selective processing of relevant information but also suppression of irrelevant, distracting input. Evidence suggests that attentional selection is neurally implemented through enhanced gain (e.g., Motter, 1993) and selectivity (e.g.,

Spitzer, Desimone, & Moran, 1988) in neural processing of the attended stimulus. However, it is less clear at present how the suppression of distracting information (i.e., “filtering”) is implemented.

A large collection of empirical evidence suggests that decreasing power of alpha oscillations (~10 Hz) in cortical regions processing target stimuli indicates release from inhibition to enhance target processing. However, it has recently been questioned whether increasing alpha power in cortical regions processing distractors does indeed support the notion of distractor suppression (e.g., Foster & Awh, 2018).

Since partly opposing post-hoc interpretations of empirical data have further complicated the selection-versus-suppression debate in the past, we here test a set of clearly defined, pre-registered hypotheses (<https://osf.io/bv7zs>) to test whether there is evidence for a suppression account of neural alpha oscillations.

In previous spatial attention studies, spatial locations of target and distractor have often been perfectly confounded by design (e.g., Haegens, Handel, & Jensen, 2011; Wöstmann, Herrmann, Maess, & Obleser, 2016). That is, whenever the target stimulus was presented on the left, the distractor was on the right, and vice versa. This made it impossible to unambiguously assign observed neural processes to either target selection or distractor suppression.

Here, we decoupled the spatial arrangement of target and distractor tone sequences by keeping one of the two fixed in the front of the participant and varying the spatial position of the other between left and right. This allowed us to test the hypothesis that suppression of distractors on the left versus right side modulates lateralized alpha power.



Methods

The task was adapted from Dai and colleagues (2018). On each trial, two tone sequences were presented concurrently at two different locations and were separated in their fundamental frequency (i.e., pitch). Tone sequences were presented in the periphery (i.e., free field) using a pair of loudspeakers. The location of a loudspeaker could be either front or side (i.e., 0 or ± 90 degrees azimuth with no elevation, respectively; all relative to ear-nose-ear line).

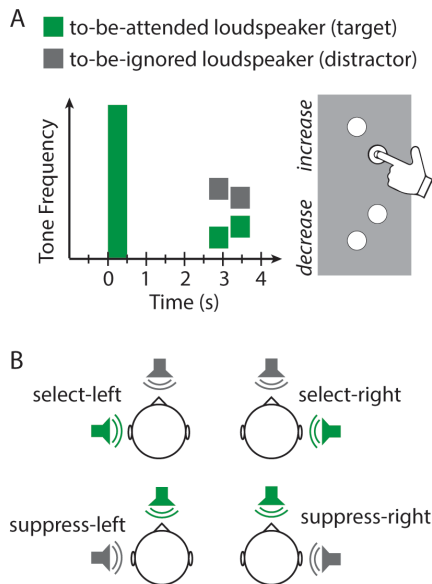


Figure 1. (A) Trial design. Presentation of a broadband auditory spatial cue (1–10 kHz) was followed by two tone sequences, each consisting of two brief (0.5 s) complex tones, at different locations. Participants had to indicate whether the tone sequence at the target location increased or decreased in pitch. (B) Competing tone sequences were presented in free field in four experimental conditions. To investigate target selection, the target loudspeaker could either be left or right (with the distractor fixed in the front; top row). To investigate distractor suppression, the distractor loudspeaker could either be left or right (with the target fixed in the front; bottom row).

At the start of each trial, an auditory cue was presented on one loudspeaker to inform the participant about the target location (front, left, or right). After a jittered period of ~ 2 sec (1.6–2.7 sec) relative to cue offset, two tone sequences were presented concurrently. Participants reported whether the target

tone sequence was increasing or decreasing in pitch. There were two response options for each possible direction (i.e., increasing or decreasing), indicating high/low confidence in the response. Every participant performed 576 trials, corresponding to 144 trials in four experimental conditions (see Fig. 1).

For behavioural data analysis, we calculated *confidence-weighted accuracy*, which is a composite measure of accuracy and confidence. In detail, we transformed binary accuracy on each trial into 1 and 1/3 for correct responses with respective high and low confidence, and into -1 and $-1/3$ for incorrect responses with respective high and low confidence.

The electroencephalogram of $N = 33$ participants was recorded at 64 active scalp electrodes. For EEG data analysis, we used the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) for Matlab (R2013b/R2018a) and custom scripts.

For each participant, two lateralization indices (LI) were calculated on absolute oscillatory power (Pow). The first index quantified the attentional selection of targets on the left versus right:

$$(1) LI_{\text{selection}} = (\text{Pow}_{\text{select-left}} - \text{Pow}_{\text{select-right}}) / (\text{Pow}_{\text{select-left}} + \text{Pow}_{\text{select-right}})$$

Going beyond previous spatial attention studies, the second index quantified the suppression of distractors on the left versus right:

$$(2) LI_{\text{suppression}} = (\text{Pow}_{\text{suppress-left}} - \text{Pow}_{\text{suppress-right}}) / (\text{Pow}_{\text{suppress-left}} + \text{Pow}_{\text{suppress-right}})$$

Results and Discussion

Distractor Suppression Uniquely Contributes to Alpha Lateralization

We found that selection of lateralized target stimuli under fixed distraction from the front induced pronounced hemispheric lateralization of oscillatory power in the alpha frequency band (Fig. 2A). This is in agreement with previous spatial attention studies that did not use distractors and found hemispheric lateralization of alpha power in response to targets on the left versus right side (e.g., van Ede, de Lange, Jensen, & Maris, 2011).

Alpha power relatively increased in the hemisphere ipsilateral to the target, and decreased contralaterally. Statistical comparison of the lateralization index ($LI_{\text{selection}}$) for occipito-parietal left- versus right-

hemispheric electrodes was statistically significant ($Z = 4.69$; $p < 0.001$). EEG source reconstruction revealed strongest lateralization of alpha power for target selection in bilateral parietal and occipital cortex regions (in line with Tune, Wöstmann, & Obleser, 2018).

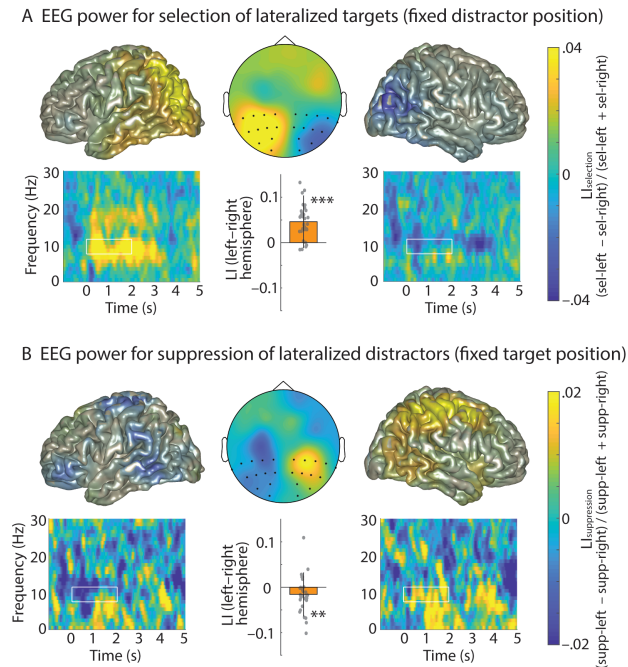


Figure 2. (A) Time-frequency representations on the left and right side show the grand-average lateralization index for selection of lateralized target stimuli ($LI_{\text{selection}}$) at 11 left- and 11 right-hemispheric electrodes (highlighted in topographic map), respectively. Topographic map and brain surfaces show LI for alpha oscillatory power in the time-frequency range marked by the white outline (8–12 Hz; 0–2 s). Bar graph, error bar, and dots show average, ± 1 between-subject SEM, and single-subject differences of alpha power lateralization for left- minus right-hemispheric electrodes, respectively. (B) Same as A, but for the lateralization index for suppression of lateralized distractors ($LI_{\text{suppression}}$). ** $p < 0.01$; *** $p < 0.001$.

The most important objective of the present study was to test whether the suppression of distractors on the left versus right side under fixed attention to the front induces lateralization of alpha power as well. This was the case (Fig. 2B). As predicted, suppression modulated alpha power orthogonally to selection: Alpha power relatively increased in the hemisphere contralateral to the distractor and decreased ipsilaterally. Thus, the lateralization index ($LI_{\text{suppression}}$)

was more negative at occipito-parietal left- versus right-hemispheric electrodes ($Z = -2.67$; $p = 0.008$).

The hemispheric difference in alpha lateralization (LI ; bar graphs in Fig. 2) was significantly more positive for $LI_{\text{selection}}$ than it was negative for $LI_{\text{suppression}}$ ($Z = 2.493$; $p = 0.013$). In other words, with the spatial position of the other sound source fixed in the front, spatial selection of the anticipated target induced stronger alpha lateralization than suppression of the distractor.

Although participants were instructed to keep central gaze during the entire experiment, it might be that systematic differences in saccadic eye movements for our spatial selection/suppression conditions confounded the results. To rule this out, we inspected the EEG for independent components tuned to vertical saccadic eye movements. In the event-related potential (ERP; not shown) on components tuned to vertical eye movements we found no significant differences between selection/suppression on the left versus right side (cluster-based permutation tests; all $ps > 0.15$). This suggests that EEG results were not confounded by systematic lateral eye movements.

More Frontal Sources for Distractor Suppression than for Target Selection

Although we had no hypothesis regarding differences of neural sources of alpha lateralization for selection versus suppression, we followed up on the apparently more anterior sources for suppression in Figure 2. Since this analysis focused on differences in spatial distribution but not strength or direction of alpha power modulation, we z-transformed each participant's lateralization index, followed by taking the magnitude (referred to as $LI_{\text{selection_norm}}$ and $LI_{\text{suppression_norm}}$).

Parieto-occipital cortex regions primarily in the left hemisphere exhibited relatively stronger alpha power modulation by target selection (pink regions in Fig. 3). Conversely, relatively stronger alpha modulation by suppression of distractors was evident in right superior and inferior parietal, right inferior temporal, left superior frontal, and bilateral superior and middle frontal cortex regions (blue regions in Fig. 3).

Alpha Lateralization Predicts Task Accuracy

Since thorough understanding of any neuro-cognitive process requires analysis of its relation to behaviour, we tested whether alpha lateralization would predict

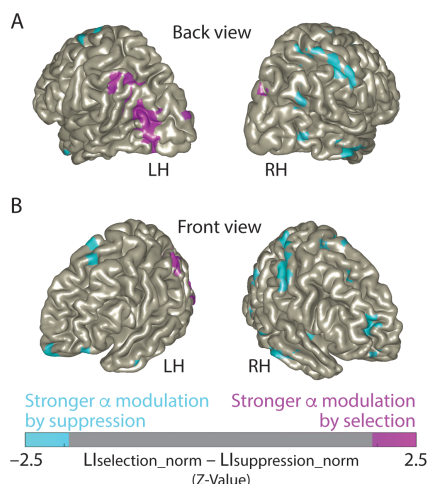


Figure 3. Brain surfaces show Z-values for the contrast of normalized lateralization indices: $Ll_{\text{selection_norm}}$ versus $Ll_{\text{suppression_norm}}$. Normalization of indices was accomplished by z-scoring single-subject indices, followed by taking the magnitude. Z-values on brain surfaces are masked in case $|Z| < 1.96$, corresponding to $p > 0.05$ for two-sided testing. **(A)** Back view of the brain; **(B)** Front view.

confidence-weighted accuracy. We used linear mixed-effects models to model the outcome variable single-trial confidence-weighted accuracy on the predictors titrated pitch difference (within both tone sequences), congruency of pitch direction across the two tone sequences (congruent versus incongruent), location of lateralized loudspeaker (left versus right), role of lateralized loudspeaker (select versus suppress), and single-trial alpha lateralization ($Ll_{\text{single-trial}}$), quantified as $(POW_{\text{left-electrodes}} - POW_{\text{right-electrodes}}) / (POW_{\text{left-electrodes}} + POW_{\text{right-electrodes}})$.

Importantly, the location \times role of lateralized loudspeaker \times $Ll_{\text{single-trial}}$ interaction significantly predicted task accuracy in the predicted direction ($F = 5.89$; $p = 0.015$): Relatively higher left-than-right hemispheric alpha power was beneficial in select-left and suppress-right trials but detrimental in select-right and suppress-left trials.

Conclusion

Although well-established models of attention rest on the assumption that irrelevant sensory information is filtered out (e.g., Broadbent, 1958), the neural implementation of such a filter mechanism is unclear.

Using a task design that decouples target selection from distractor suppression, we demonstrate that selection and suppression independently modulate lateralized alpha power, however, in opposite directions and in more frontal, executive cortical regions for suppression than selection. Furthermore, lateralized alpha power predicts participants' accuracy in the judgement of a pitch change in the target stimulus. These findings support so-called "active suppression" models of attention, in which suppression is not a necessary by-product of selection but an independent neuro-cognitive process.

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