
Research Article: New Research | Sensory and Motor Systems

The role of alpha activity in spatial and featured-based attention

Alpha in spatial and featured-based attention

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DOI: 10.1523/ENEURO.0204-16.2016

Received: 14 July 2016

Revised: 14 September 2016

Accepted: 15 September 2016

Published: 27 September 2016

Author contributions: R.M.V.D., L.M., A.M., and J.J.G. designed research; R.M.V.D., L.M., A.M., and J.J.G. performed research; R.M.V.D., L.M., A.M., and J.J.G. analyzed data; R.M.V.D., L.M., A.M., and J.J.G. wrote the paper.

Funding: National Science Foundation
BCS-1230377-0

Funding: Netherlands Organization for Scientific Research

Conflict of Interest: The authors declare no conflict of interest.

This work was supported by the National Science Foundation (BCS-1230377-0) to JG and a Veni Grant from the Netherlands Organization for Scientific Research (NWO) to AM.

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Cite as: eNeuro 2016; 10.1523/ENEURO.0204-16.2016

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Accepted manuscripts are peer-reviewed but have not been through the copyediting, formatting, or proofreading process.

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1. **Manuscript Title:** The role of alpha activity in spatial and featured-based attention

1 2. **Abbreviated title:** Alpha in spatial and featured-based attention

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4. **Author contributions:** RD LM AM JG Designed research; RD LM JG Performed research; RD AM JG Analyzed data; RD LM AM JG Wrote the paper.

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6. **Number of figures:** 6

7. **Number of tables:** 0

8. **Number of multimedia:** 0

9. **Number of words for abstract:** 249

10. **Number of words for significance Statement:** 106

11. **Number of words for Introduction:** 746

12. **Number of words for Discussion:** 1112

2 13. **Acknowledgement:** We would like to thank Tony Shahin and Andrew Kessler for invaluable help with
3 running participants.

4
5 14. **Conflict of interest:** The authors declare no conflict of interest.

6
7 15. **Funding Sources:** This work was supported by the National Science Foundation (BCS-1230377-0) to
8 JG and a Veni Grant from the Netherlands Organization for Scientific Research (NWO) to AM.

9 **Abstract**

10 Modulations in alpha oscillations (~10 Hz) are typically studied in the context of anticipating upcoming
11 stimuli. Alpha power decreases in sensory regions processing upcoming targets compared to regions
12 associated with distracting input, hereby promoting processing of relevant information while
13 suppressing irrelevant information. In the current EEG study using healthy human volunteers we
14 examined whether modulations in alpha power also occur *after* the onset of a bi-laterally presented
15 target and distractor. Spatial attention was manipulated through spatial-cues and feature- based
16 attention through adjusting the color-similarity of distractors to the target. Consistent with previous
17 studies, we found that informative spatial cues induced a relative decrease of pre-target alpha power at
18 occipital electrodes contralateral to the expected target location. Interestingly, this pattern re-emerged
19 relatively late (300-750 ms) after stimulus onset, suggesting that lateralized alpha reflects not only
20 preparatory attention, but also ongoing attentive stimulus processing.

21 Uninformative cues (i.e., conveying no information about the spatial location of the target) resulted in
22 an interaction between spatial and feature-based attention in post-target alpha lateralization. When the
23 target was paired with a low-similarity distractor, post-target alpha was lateralized (500-900 ms).
24 Crucially, the lateralization was absent when target selection was ambiguous because the distractor was
25 highly similar to the target. Instead, during this condition mid-frontal theta was increased, indicative of
26 conflict processing. Behaviorally, the degree of alpha lateralization was negatively correlated with the RT
27 distraction cost induced by target-distractor similarity. These results suggest a pivotal role for post-
28 stimulus alpha lateralization in protecting sensory processing of target information.

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32 **Significance Statement**

33 A substantial amount of research has been dedicated to elucidating the role of alpha oscillations in
34 preparation for upcoming targets and distractors. Considerably less research has focused on alpha
35 activity *after* presentation of those stimuli. Using a novel paradigm, in which spatial attention was
36 manipulated using informative and uninformative spatial cues and feature-based attention using
37 distractors that were varied parametrically in color-similarity to the target, we show that post-stimulus
38 alpha hemispheric lateralization protects target processing after spatial and feature-based target
39 selection. Modulations in alpha power can therefore be regarded as a general mechanism for direction
40 of attention, not only for pro-active but also for reactive attention.

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57 1. Introduction

58 Attention allows us to selectively process information that is relevant to our current goals and
59 suppress irrelevant distractors. A number of studies have found a link between the allocation of
60 preparatory selective visuospatial attention and hemispheric modulations of oscillatory activity in the
61 alpha range (8 – 12 Hz) over occipital regions of the cortex. The power of alpha activity has been found
62 to decrease over occipital regions contralateral to target presentation compared to when the target was
63 expected ipsilaterally (Worden et al., 2000; Kelly et al., 2006; Thut et al., 2006; Kerlin et al. 2010). This
64 lateralization is believed to result in enhanced processing of targets (Osipova et al., 2008; Weisz et al.,
65 2011; Bauer et al., 2012; Lange et al., 2013) and decreased processing of distractors in downstream
66 areas (Zumer et al., 2014). In the current study alpha activity is examined pre- and post-stimulus
67 presentation, allowing the examination of alpha power changes during spatial and feature-based target
68 selection.

69 While there is clear evidence for the role of alpha in spatial attention, its involvement in
70 feature-based attention remains relatively unclear. Previous research has shown that mechanisms of
71 feature-based attention prioritize target-related features in a spatially non-specific way, even when the
72 location of the target is known (Saenz et al., 2002; Serences and Boynton, 2007; Andersen et al., 2008;
73 Zhang and Luck, 2009). However, none of these previous studies have examined whether alpha
74 oscillations in response to a spatially cued target can "protect" against attentional capture by a feature-
75 based distractor. In terms of hierarchical processing in the visual system, it is clear that spatial attention
76 operates through selection at lower (retinotopically mapped) levels of neuronal representations.
77 Conversely, attentional selection of specific features can only occur in functionally specialized cortical
78 regions (Snyder and Foxe, 2010). This raises the question of how higher-level featural attention depends
79 upon spatial attention and vice versa. It could be the case that both spatial and featural attentional
80 mechanisms operate together by boosting signals from the attended (retinotopic) location, or it may be

81 that each operates separately at the level of their specialized representations. Conversely, spatial
82 attention may itself be deployed in a way that is sensitive to feature-based attention, suggesting an
83 interaction between the two.

84 If mechanisms of feature-based selection recruit spatial attention once a target is identified,
85 then we might expect the presence of lateralized alpha even when a target can only be selected based
86 on color. Previous work has suggested that selection of an object based on features is followed by the
87 shift of spatial attention (Öğmen and Breitmeyer, 2006). Finding lateralized alpha during feature-based
88 selection would be novel evidence that spatial attention is recruited to suppress distractor processing in
89 order to shield target processing, once a target has been identified based on its non-spatial features. In
90 contrast, if the mechanisms of spatial and feature-based attention are largely independent, then we
91 would not expect effects of spatial attention associated with posterior alpha to impact feature-based
92 attentional capture, nor find changes in alpha activity when spatial cues are absent.

93 The purpose of the current experiment was to explore how spatial attention and featural
94 attention might interact. In what follows, we used spatial (hemispheric) lateralization of alpha
95 suppression to index the physiological correlates of spatial attention and asked whether this
96 neurophysiological signature depended upon attentional set for features. We employed a novel visual
97 cuing paradigm involving the presentation of a bilateral visual search array; spatial attention was
98 manipulated with a valid pre-cue and feature-based attention was manipulated by the degree of
99 distractor-to-target color similarity. Behavioral responses were collected simultaneously with ongoing
100 EEG that measured posterior alpha as an index of spatial attentional selection. While previous studies
101 have focused exclusively on the modulation of alpha power during the cue-target interval, we also
102 examined how post-target alpha activity was modulated as function of the distractibility of the target-
103 similar distractors.

104 In addition to alpha oscillations, we examined potential post-target differences in theta activity.
105 Increased theta band activity in midfrontal channels has been found in situations of conflict and
106 resolution processes (Cavanagh et al., 2012; Nigbur et al., 2012; Cohen and Donner, 2013; Cavanagh and
107 Frank, 2014; Cohen, 2014; Van Driel et al., 2015) and could therefore be an indication of the absence of
108 selective attention occurring in visual cortex.

109 In brief, we showed a profound interaction in alpha lateralization and a complementary
110 modulation in theta activity, suggesting that attentional gain at lower (retinotopic) levels of the visual
111 hierarchy is mediated by convergent spatial and feature attentional mechanisms.

112

113 2. Material and Methods

114 2.1 Participants

115 20 healthy participants (14 female) were recruited from the University of California Davis. The average
116 age of included participants (n = 16, see section Methods and Materials, Analyses, Behavioral) was 24.8
117 years and all were right-handed. Participants reported normal or corrected-to-normal vision, no color
118 blindness and no history of neurological or psychological illness. Before the start of the experiment
119 signed informed-consent was obtained in accordance with the University of California, Davis
120 Institutional Review Board.

121 2.2 Procedure

122 The stimuli were presented using Presentation software (Neurobehavioral Systems Inc., Albany, CA,
123 USA) on a 24 inch monitor with a refresh rate of 60 Hz. Before the start of the experiment participants
124 practiced at least 60 trials or more until they reached a threshold of 70 % correct. Participants were
125 seated approximately 100 cm from the monitor.

126 2.3 Task

127 Participants reported the identity of a letter (A, B or C) presented in a target stimulus by making a 3-
128 button alternative forced choice using their right hand. The target was a red diamond shaped box that
129 appeared on the left or right of a central fixation cross with equal probability. The distance from the
130 fixation cross to object center was 5.5 degrees of visual angle; and the width of the object from center
131 to edge was 1.1 degrees.

132 A distractor was presented in a square shaped box in the hemifield opposite to target. The distractor
133 also contained a letter (A, B or C), but the letter was never the same as the target. The color of the
134 distractor box was the same red as the target (D1, luminance cd/m² and CIE x,y= 48.8, .639, .343) or was
135 1 of 3 other colors ranging from orange to yellow (D2 = 52.7, .635, .343; D3= 73.4, .578, .385, D4 = 110,
136 .510, .385). The brightest object based on luminance values was the most yellow distractor. Thus,
137 luminance and target-similarity were opposite to each other and therefore the effect of one on
138 attention cannot explain the effect of the other. To ensure that participants did not become over-
139 trained on shape selection, the target and distractor shape were switched every block (e.g. square
140 became target and diamond became distractor). The target and distractor colors remained the same.
141 Thus, while it would be possible for the subject to select the target entirely based on shape, color was
142 never irrelevant. The target could be selected based on color on 75% of trials (D1 only occurred on 25%
143 of trials), and while the target color was consistent throughout the experiment, the target shape
144 changed from block-to-block (every 48 trials). This design increased the likelihood of subjects continuing
145 to use color as a criterion for target selection, despite shape also being indicative. The behavioral results
146 are evidence that mechanisms of feature-based attention for color led to greater selection of distractors
147 as a function of target-color similarity.

148 In 50 % of the trials a spatial cue (< or >) indicated the location (left or right) of the upcoming target
149 1200-1500 ms prior to visual search display with 100% validity (i.e., "cued trials"). On these trials, it was
150 possible for participants to anticipate the target location. In the other 50% of trials, the cue (\diamond) was
151 uninformative about the location of the target (i.e., "uncued" trials). On uncued trials, participants
152 identified the target based on shape and color. Participants were asked not to make an eye-movement
153 towards the target but to shift their attention covertly. Fixation was monitored using an EyeLink 1000
154 Desktop Mount (SR Research) eye-tracker acquiring data at 500 Hz from the right eye.

155 An example sequence of a trial is illustrated in Figure 1. First the cue (left, right, uninformative) was
156 shown for 200 ms. A variable cue-target interval lasting 1200 - 1500 ms followed the cue to reduce
157 temporal expectancies for the onset of the search screen. The target and distractor were shown for 150
158 ms followed by another variable target-cue interval, during which participants responded to the target.
159 Every condition (2 cue x 4 distractor-similarity) included 108 trials for a total of 864 trials, lasting about
160 48 minutes. Trials were pseudo-randomized such that all possible trial types (distractor-type x cue-
161 presence x lateralization x target letter) were presented before repeating trials. Breaks occurred every
162 48 trials.

163

164 2.4 EEG acquisition and processing

165 EEG were acquired using a 64-channel cap system with a 10/20 layout developed by Biosemi
166 (Amsterdam, The Netherlands). The EEG was sampled at 1024 Hz and re-referenced to Cz during
167 importation into Matlab (Natick, MA) using EEGLAB 11 (Delorme and Makeig, 2004).

168 Using EEGLAB the EEG data were re-referenced to average reference, highpass-filtered at 0.5 Hz and
169 epoched from -2.4 to +1.9 s, time-locked to target onset. Epochs were baseline-corrected using -0.2 s to
170 0 s pre-target. Incorrect trials and trials with an eye movement during the cue-target interval were

171 removed from further analyses (see section Methods and Materials, Analyses, Behavioral). Remaining
172 ocular artefacts were removed using Independent Component Analysis (ICA, infomax algorithm)
173 incorporated as the default 'runica' function in EEGLAB. A principle component analysis (PCA) was used
174 to reduce dimensionality of the data prior to performing the ICA. Then data were transported into
175 Fieldtrip 13_1_1b (Oostenveld et al., 2011) format. A semi-automatic routine (using the ft_rejectvisual
176 function of Fieldtrip) was applied to the EEG data to remove epochs with noise.

177 2.5 Time Frequency Representation

178 Time frequency representations (TFRs) of power were estimated per trial, using sliding time windows
179 tapered with a Hann window having an adaptive time window of three cycles for each frequency of
180 interest ($\Delta T = 3/f$). Similar approaches were used by Osipova et al. (2006), Jokisch and Jensen (2007),
181 Mazaheri et al. (2009) and Van Diepen et al. (2015). Although this approach uses a smaller number of
182 cycles in comparison to Morlet wavelet approaches of time frequency decompositions (i.e. 5-7 cycles); it
183 does afford the maximum temporal resolution for pre and post fluctuations in alpha power. A baseline
184 correction was applied such that every time point represents the relative change in power from the
185 average power at baseline ($(\text{Power timepoint} - \text{Power baseline})/\text{Power baseline}$). A 400 ms interval prior
186 to cue presentation was used as the baseline interval, ending 100 ms before the possible onset of a cue
187 with the largest cue to target interval.

188 2.5 Analyses

189 2.5.1 Behavioral

190 Trials were rejected when the target was not identified or when participants moved their eyes towards
191 the target or distractor. An eye movement was identified as a horizontal eye movement exceeding 1.5°
192 from central fixation during the interval from cue presentation to the response. The quality of eye-
193 tracker data of five participants was not sufficient to detect eye movements. For three of those

194 participants an electro-oculogram (EOG) was recorded at the outer canthi of the left and right eyes and
195 eye movements were identified by visual inspection of the data. On average $7.1 \% \pm 1.5$ of trials were
196 removed due to eye movements. Eye movements were only removed using ICA for the two participants
197 without eye data. (Results were similar when the analyses were repeated without these two
198 participants.)

199 Participants scoring two standard deviations below average accuracy were excluded from analyses (two
200 participants). In addition, the presence of a distractor-similarity-effect was assessed for every participant
201 by applying an independent samples t-test between the reaction times (RTs) for trials with the most
202 similar distractor (D1) and from the least similar distractor (D4), using correct trials only. Data of two
203 participants were removed because they did not show a basic feature-based distractor similarity effect
204 ($p < 0.05$) (i.e., the target-colored distractor did not interfere more with target processing than a
205 distractor from a different color category). This was surprising and suggested these subjects were
206 atypical given that the effect was expected from decades of psychological research (e.g., Treisman and
207 Gelade, 1980; Duncan and Humphreys, 1989; Wolfe, 2004). Note, however, that this exclusion criterion
208 was entirely based on the main effect of feature-based attention and was orthogonal to our analyses of
209 interest on the interaction between spatial cueing and feature-based attention. A second independent
210 samples t-test confirmed that all remaining participants showed a significant reduction in RT in trials
211 with an informative cue (see section Results, Behavioral), hence no data had to be excluded based on
212 the absence of a spatial cuing effect.

213 The effect of condition on reaction times and percentage of correct responses was calculated using a 2-
214 way repeated-measures ANOVA with 2 factors: cue-presence (cued/uncued) and distractor-color (D1 -
215 D4). Furthermore, we examined for every condition whether participants scored above chance level, by

216 comparing the score against chance level (33.3 %), using an independent samples t-test (two-tailed,
217 Bonferroni correction for multiple comparisons).

218

219 2.5.2 EEG

220 In order to increase signal-to-noise ratio, data were pooled over hemispheres by flipping the sources
221 with respect to experimental condition, according to the procedures outlined in Buchholz et al. (2013,
222 2014). Data from trials with left targets were mirrored and pooled with data from right trials. This
223 created a dataset in which the right hemisphere denotes activity ipsilateral to target presentation and
224 the left hemisphere represents contralateral activity.

225 2.5.3 Statistics

226 Changes in alpha power (averaged across 8 – 12 Hz) between conditions were statistically assessed by
227 means of the cluster (channels and time-points) level randomization (Maris and Oostenveld, 2007)
228 procedure. This test controls the Type-1 error rate involving multiple comparisons (e.g. multiple
229 channels and/or time-frequency tiles). A probability value here is obtained through the Monte Carlo
230 estimate of the permutation p-value of the cluster of channels was by randomly swapping the
231 conditions in participants 1000 times and calculating the maximum cluster-level test statistic. A similar
232 procedure has been used in a number of previous studies (Jokisch and Jensen, 2007; Mazaheri et al.,
233 2009).

234 2.5.4 Feature based attention

235 Trials with distractor similarity levels of D1 and D2 were pooled into a ‘high distraction’ condition while
236 trials with distractors D3 and D4 were pooled to create a ‘low distraction’ condition. The decision for
237 these groupings was driven by the reaction time performance of the participants (see Figure 2). The
238 resulting conditions were tested individually for alpha lateralization *after* presentation of the visual

239 search display. As described above, a cluster-based permutation test was performed for every condition,
240 contrasting ipsilateral to contralateral activity for all time points between 0 and 1500 ms. Reported
241 results show topographies and statistics after averaging time-points containing a cluster of electrodes
242 with a $p < 0.05$ (Monte-Carlo corrected for multiple comparisons).

243 [2.5.5 Behavioral consequence of lateralization during feature-based attention](#)

244 The relationship between the alpha lateralization and task performance was assessed by correlating the
245 difference in reaction times between targets with low similarity distractors and those with high
246 similarity distractors, with the posterior alpha lateralization across the participants.

247 The obtained 'distractor cost' represents the behavioral consequence of increased distraction. Only
248 uncued trials were used so that cue-related spatial attention did not affect the analysis. Alpha
249 lateralization was calculated by subtracting the average alpha power contralateral to target presentation
250 from alpha activity ipsilateral to target presentation. Therefore oscillatory power was averaged over
251 channels and time-points showing a significant difference in lateralization between trials with low and
252 high target-distractor-similarity. The difference in lateralization between low and high similarity
253 distraction for every participant was correlated with the individual distractor cost using a Spearman rank
254 correlation.

255 [2.5.6 Frontal Theta](#)

256 A difference in theta activity (averaged across 4 - 6 Hz) between the low and high distraction condition
257 was also examined for every time point between 0 and 1500 ms. Theta activity was averaged over time-
258 points containing a cluster with $p < 0.05$. Trials with left and right targets were pooled without
259 transposing the data to an ipsilateral and contralateral set. Note that we are assuming here that featural
260 attention does not show any (spatial) lateralization, enabling us to pool data from both hemispheres.
261 The length of the sliding time-window used to calculate the power of a theta oscillation is wider than for

262 an alpha oscillation (3/f). The baseline was therefore changed to the pre-target period (-700 to -300), to
263 avoid spurious results due to temporal leakage from the cue or post-target activity. Because only trials
264 with uninformative cues were contrasted and left and right target trials were grouped, this pre-target
265 period should not show any differences between conditions.

266

267 3. Results

268 3.1 Behavioral

269 The mean reaction time (RT) for correct trials was 847.4 ± 21.6 ms. The RT data were entered into a 2
270 cue-presence (cued, uncued) x 4 distractor-similarity (1, 2, 3, 4) repeated measures ANOVA. A main
271 effect of cue ($F(1, 15) = 85.4, p < .0001$) was found such that RT was shorter for informative cue $799.3 \pm$
272 21.7 ms than for uninformative cue trials 895.5 ± 22.6 ms. Participants were thus able to use the cue to
273 select the target faster (Figure 2). When distractor conditions were examined separately, all distractor
274 conditions showed a benefit from cue presence ($p < 0.001$ for cued vs uncued trials, two-tailed,
275 Bonferroni corrected for multiple comparisons).

276 A main effect of distractor-similarity was also present ($F(3, 45) = 67.9, p < .0001$). Distractors induced
277 more distraction when the color was more similar to the target color. Trials with the highest target-
278 distractor-similarity (D1) showed the longest reaction times 910.2 ± 24.6 ms. Reaction times decreased
279 when distractor colors became less similar to the color of the target (D2) 875.2 ± 22.5 ms, (D3) $803.6 \pm$
280 21.0 ms, (D4) 798.8 ± 21.2 ms. Post-hoc tests were significant ($p < .0001$, Bonferroni corrected for
281 multiple comparisons) for all possible pairs except distractors 3 and 4.

282 Most importantly, the interaction between the spatial cue and distractor-similarity was significant (F
283 $(3,45) = 34.8, p < .0001$), suggesting that the spatial cue facilitated target selection to a different extent
284 for the different distractor colors. The difference in reaction times for cued and uncued trials was largest

285 for the most similar colors (D1) $159.8,1 \pm 16.5$ ms and decreased as distractors became less similar in
286 color (D2) $126.3 \pm 17,3$ ms (D3) $51.5 \pm 7,5$ ms (D4) 46.9 ± 8.5 ms. Pairwise comparisons using a
287 Bonferonni correction show that the amount of cue related benefit (RT uncued – RT cued) was
288 significantly different between all distractor conditions ($p < 0.049$), except for D3 and D4 ($p = 1.000$).

289 The presence of a valid cue facilitated target detection when the distractor was highly target-similar, but
290 the usefulness of the spatial cue was reduced when the target was highly distinct from the distractor
291 and competition for attention during visual search was low. Thus, the spatial cue mainly facilitated
292 behavior when feature-based competition for attention during visual search was high. Based on these
293 RT results the distractor conditions that were most distracting (D1 & D2) and the least distracting (D3 &
294 D4) were collapsed together in subsequent analyses, and labeled as 'high-similarity' distractors and 'low-
295 similarity' distractors, respectively.

296 Average accuracy was 87.9 ± 9.7 %. Performance decreased when distractors were more similar to the
297 target (main effect of distractor-type $F(3,45) = 3.249$, $p = 0.016$). No difference in performance was
298 present between cued and uncued trials (no main effect cue-presence $F(1,15) = 1.274$, $p = 0.277$).
299 However, an interaction was present in accuracy scores between cue-presence and distractor-type (F
300 $(3,45) = 3.175$, $p = 0.033$), indicating that cues only increased accuracy for trials with high target-
301 distractor similarity. Furthermore, all participants scored above chance for every condition (33.4 %
302 based on 3 target letter identities, or 50 % based on guessing after knowing what letter is in the target
303 and distractor). T-tests show that scores for all conditions significantly differ from chance ($p < 0.0001$ for
304 all comparisons, corrected for multiple comparisons).

305 Together, these data demonstrate that the effect of distractor similarity was attenuated when a valid
306 spatial cue was presented, especially when the distractor was very target-similar. This suggests that
307 participants used the spatial cue to pre-select the target location and that doing so "protected" them

308 against attentional capture by the feature-similar distractor. The spatial cue affected behavioral
309 performance to a lesser extent when the distractor color was dissimilar, mostly likely because feature-
310 based competition was low and performance was already at, or near, ceiling.

311 3.2 EEG

312 *3.2.1 Informative spatial cues induce alpha lateralization in posterior channels*

313 We first conducted an analysis on the main effect of cue-presence in order to replicate previous studies
314 demonstrating alpha lateralization in response to a spatial cue. As expected, we found that after
315 presentation of a cue signaling an upcoming left or right target, alpha activity in channels located
316 contralateral to the distractor increased compared to channels contralateral to target location (Figure 3
317 A & C, -1500 to 0 ms pre-target, $t = 27.23$, $p < 0.001$, Monte Carlo P-value, corrected for multiple
318 comparisons). The modulation was absent when left and right target trials with uninformative cues were
319 contrasted (Figure 3 B & D, no clusters to report). A significant interaction in alpha lateralization was
320 present between cued and uncued trials from -1050 to 0 ms prior to target onset (Figure 3 E, $t = 19.94$, p
321 $= 0.008$, Monte Carlo P-value, corrected for multiple comparisons). This demonstrates that participants
322 did indeed attend to the cued location in this study and that doing so produced a difference in
323 lateralized alpha.

324

325 *3.2.2 Cue-induced alpha lateralization reduces feature-based distractor competition*

326 In addition to preparatory changes in alpha activity, we also examined alpha activity after the visual
327 search display was presented. In all conditions *except* when the cue was uninformative and target-
328 distractor similarity was high, alpha activity was significantly lateralized such that it was lower over
329 regions contra-lateral than ipsilateral to the target (Figure 4). Spatially cued trials with low-similarity
330 distractors demonstrated this lateralization from 350 to 500 ms after target onset ($t = 23.68$, $p = 0.003$,

331 Monte Carlo P value, corrected for multiple comparisons); cued trials with high-similarity distractors
332 from 0 to 150 ms and re-appearing again at 450 to 750 ms after target onset ($t = 21.85$, $p = 0.002$, Monte
333 Carlo P value, corrected for multiple comparisons); and uncued trials with low-similarity distractors from
334 500 to 900 ms post target ($t = 22.71$, $p = 0.004$, Monte Carlo P value, corrected for multiple
335 comparisons). Although there was significant alpha lateralization in these three conditions, note that the
336 onset of alpha lateralization in all conditions was relatively late after stimulus onset; moreover, the
337 onset in the cued conditions occurred earlier than the uncued condition. This suggests that alpha
338 lateralization may reflect spatially lateralized attentive processing, rather than the initial selection of a
339 particular object. Additionally, the fact that this process was later in the uncued condition is consistent
340 with the idea that spatially selective processing of the target (and suppression of the distractor) was
341 preceded by the selection of the target based on its color.

342 It should be noted eye-movements were eliminated and therefore the target and distractor were clearly
343 lateralized with respect to fixation throughout the trial. Therefore lateralized alpha reflected the degree
344 to which attention was consistently oriented towards the target and away from the distractor during
345 visual search. Clear lateralization suggested that the target was consistently selected with little attention
346 to the distractor whereas a lack of alpha lateralization suggested that the distractor competed
347 successfully to capture attention as frequently as it did not, on average.

348 These results are consistent with the RT data and provide further evidence that the spatial cue was used
349 to successfully select the target and suppress the distractor, even in the presence of strong competition
350 from a high-similarity distractor. Similarly, alpha lateralization in the uncued low-similarity condition
351 confirms that spatial attention was easily drawn to the target because competition for attention based
352 on feature-similarity was low. However, trials with an uninformative cue and a high-similarity distractor
353 did not show any lateralization. This was even true when the statistical threshold was decreased, when a

354 pre-target instead of pre-cue baseline was used, and when activity was averaged over time (same time
355 interval as lateralization was found for uncued low distraction trials) to increase the signal-to-noise ratio.
356 This result is consistent with the RT data in indicating that the only condition in which the distractor
357 competed successfully against the target for attention was when there was no spatial cue and
358 distractor-similarity was high.

359 *3.2.3 Individual variability in post-target alpha lateralization correlates with RT distractor cost on uncued trials*

360 Together the previous RT and EEG results suggested that greater alpha lateralization during visual search
361 was associated with less distractor interference. Next, we tested whether this relationship predicted
362 individual differences in behavioral RT due to distractor-similarity in the uncued conditions. To do so, we
363 created an index of distractor cost (RT high-similarity minus RT low similarity) and an index of difference
364 in alpha lateralization (lateralization in high-similarity minus low-similarity). Note that less lateralization
365 in the high-similarity condition relative to the low-similarity condition produces larger negative values.
366 Inspection of the data indicated a single outlier (see Figure 5, green data point). Removal of the outlier
367 resulted in a significant correlation of $r = -0.53$, with $p = 0.047$, indicating that participants with greater
368 RT costs in the high-similarity condition also had less alpha lateralization in the high-similarity condition
369 relative to the low-similarity condition (Figure 5). To be conservative, we also ran the correlation with
370 the outlier, which produced marginally significant correlation, $r = -0.45$, $p = 0.082$. This result is
371 consistent with the group data in showing that alpha lateralization was indicative of less distractor
372 interference; and moreover, that the magnitude of the RT cost within an individual was correlated with
373 the degree of alpha lateralization in the high-similarity compared to low-similarity conditions. This
374 suggests a direct relationship between post-stimulus alpha lateralization and the degree of distraction
375 produced by a highly-similarity distractor.

376 *3.2.4 Post-target Midfrontal theta increase for highest distraction*

377 Our previous results suggest that a greater alpha lateralization translates to a better target selection and
378 this was found at the group level between conditions as well as at the individual level for uncued trials.
379 These results indicate that alpha lateralization is a reliable index of target selection and distractor
380 suppression. Only one condition did not show significant alpha lateralization and this condition also
381 produced the longest RTs indicating a failure to consistently suppress attention to the high-similarity
382 distractor. However, inference regarding the presence of distractor competition in that condition was
383 based on a null result: that is non-significant alpha lateralization. To further examine the hypothesis of
384 increased attentional competition in this condition, we compared theta activity between the two
385 uncued conditions (low-similarity vs. high-similarity distractors). If the lack of alpha lateralization in the
386 high-similarity condition is due to greater distractor competition, we would expect a concomitant
387 increase in midfrontal theta as a reflection of greater reactive attention control. Consistent with our
388 expectations, the uncued trials with high-similarity distractors did indeed show an increase in average
389 theta activity (4-6 Hz) in midfrontal channels in the time window 700 - 1250 ms after target onset
390 compared to the low-similarity condition ($t = 24.40$, $p = 0.013$, Monte Carlo P value, corrected for
391 multiple comparisons). No such difference was present between the cued conditions (Figure 6, no
392 cluster to report). This is the opposite of the alpha lateralization contrast found between these same
393 conditions in the previous analysis. The result is consistent with the conclusion that the lack of posterior
394 alpha in the uncued high-similarity condition was due to increased distractor competition.

395

396 **4. Discussion**

397 Shifting attention to a particular location in space allows observers to detect objects in the
398 attended location better than in unattended locations (Helmholtz, 1867; Posner, 1980). This effect is

399 supported by increases in the gain of sensory neurons with receptive fields over the attended location
400 (Hillyard et al., 1994; Hopfinger et al., 2000; O'Connor et al., 2002). In contrast, attentional capture by
401 task relevant features is spatially non-specific. For example, target-colored objects capture attention
402 even if they appear in unattended, or even task-irrelevant, locations (Serences and Boynton, 2007;
403 Zhang and Luck, 2009; Andersen et al., 2009) . Thus, feature-based attention is thought to operate in
404 parallel across the visual field leading to attentional capture by target-similar distractors (Folk et al.,
405 1992), but it remains unclear if feature-based attentional capture interacts with spatial attention.

406 In the current visual search task, we explored the relationship between the mechanisms of
407 spatial and feature-based attention. We manipulated spatial attention using a pre-cue, and feature-
408 based attention through distractor-to-target similarity on a trial-by-trial basis. Reaction times verified
409 that the spatial cue interacted with feature-based attention such that when present, interference from
410 highly target-similar distractors was attenuated. The EEG results showed that the RT data reflected the
411 degree of alpha activity lateralization in posterior channels *after* target presentation. Post-stimulus
412 alpha power was higher contralateral to distractors compared to targets for all cued trials irrespective of
413 distractor similarity, but occurred on uncued trials only with low-similarity distractors. That is, significant
414 post-stimulus alpha lateralization occurred when there was a valid spatial cue irrespective of distractor
415 competition, but also when distractor competition was weak and there was no spatial cue. This indicates
416 that alpha lateralization indexes successful target processing (and distractor suppression) similarly when
417 success is due to spatial cueing or low distractor competition. Moreover, the strength of alpha
418 lateralization correlated with individual differences in the degree of distractor interference, suggesting
419 that alpha activity is a general index for the strength of attentional competition between lateralized
420 stimuli.

421 A lateralization of alpha activity arises due to the fact that different spatial locations are
422 processed by different hemispheres. In other words, the modulations in alpha activity work as a spatial

423 filter on incoming information. When a target can only be detected based on color during the current
424 experiment, the presence of lateralized alpha activity indicates that the same mechanism used during
425 spatial selection is recruited to enhance target processing after feature-based selection. Finding
426 lateralized alpha during feature-based selection is novel evidence that spatial attention is recruited to
427 protect target processing.

428 If alpha lateralization reflects attentional processing, one might expect its onset to coincide with
429 the latency of Event-Related-Potential components known to reflect attentional selection (Luck and
430 Hillyard, 1994). For example, the N2pc is an ERP component related to lateralized attention that usually
431 occurs between 200 to 300 ms after target presentation. Alpha lateralization in this study was found to
432 begin 350 ms after target presentation for cued trials, and 500 ms for uncued trials. This suggests that
433 the alpha modulation in our task occurred after initial attentional selection of the target. The slower
434 onset of lateralized alpha in the uncued compared to cued conditions is also consistent with ERP findings
435 that measurements of spatial attention are observed earlier (70 - 100 ms post-target onset, Gonzalez et
436 al., 1994) than changes due to feature-based attention (150 ms post-target onset, Anllo-Vento et al.,
437 1998). One hypothesis for this difference in latency is that the effect of feature-based attention seen at
438 150 ms may actually reflect processes that guide spatial attention to the target location after the target
439 had been selected based on its color (Öğmen and Breitmeyer, 2006). The slower onset of alpha
440 lateralization in the uncued condition in our study is consistent with this hypothesis and suggests that
441 targets were selected based on feature-based attentional processes that were followed by a shift in
442 spatial attention.

443 The fact that post-stimulus alpha lateralization started after stimulus offset in our experiment
444 implies that the inhibitory effect of alpha acted upon lingering visual representations in working
445 memory and not just on initial stimulus processing as would be present in the pre-target cue-induced
446 changes in alpha. Our results are consistent with a previous study that related post-stimulus alpha

447 lateralization to the efficient suppression of irrelevant information in short-term memory (Sauseng et
448 al., 2009). During their experiment a spatial cue was used to indicate which hemifield contained to-be-
449 remembered items and which contained distractors. They found that alpha activity contralateral to the
450 to-be-ignored stimuli correlated with the successful suppression of distractors and better recall of items
451 in the cued visual field. Our findings extend this result in showing that post-target alpha lateralization is
452 related to distractor suppression both in response to spatial cues and feature-based selection. In
453 addition, it is possible that in the uncued and high-similarity condition, subjects were forced to rely more
454 heavily on the shape information to distinguish the target from the distractor and that this may have
455 contributed to the delay in ability to select the correct target. Although we cannot know if subjects
456 sometimes used both shape information in combination with color when color discrimination was
457 difficult, the current results suggest that irrespective of what featural information was used to select the
458 target, alpha lateralization reflected the continued attentional processing of the target, once it was
459 identified and its location selected. It therefore seems that alpha power modulations reflect the gating
460 of relevant information by inhibition of neuronal spiking (Haegens et al., 2011) in response to task-
461 irrelevant information (Jensen and Mazaheri, 2010).

462 Interestingly, midfrontal theta showed the opposite pattern to alpha lateralization in the uncued
463 conditions: the uncued high-similarity condition showed no significant alpha lateralization, but did show
464 significant midfrontal theta in a later time period; and the low-similarity condition showed the opposite
465 pattern. Midfrontal theta was present when alpha lateralization was absent and distractor competition
466 was strong, suggesting that midfrontal theta reflected late reactive attentional control mechanisms to
467 reject highly similar distractors that compete for attention when earlier posterior alpha did not
468 successfully suppress the distractor. This suggests that posterior alpha and midfrontal theta reflect
469 mechanisms of earlier and later control of attention, respectively. It should be noted that the time
470 period of increased theta-band activity was late compared to typically found in other tasks (Cavanagh et

471 al., 2012; Nigbur et al., 2012; Cohen and Donner, 2013; Cavanagh and Frank, 2014; Van Driel et al.,
472 2015), however, reaction times in our experiment were also slower.

473 In sum, our results demonstrate that the modulation of alpha activity is not only a preparatory
474 mechanism for predicted target information and distraction, but also serves to protect processing of
475 relevant information after its selection based on spatial or feature-based information.

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478

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577

578

579 *Figure captions*

580 Figure 1. Task procedure (not at scale). The trial started with a 200 ms spatial cue. An informative cue
581 indicated whether the target would appear on the right or left of the fixation box with 100 %
582 validity. An uninformative cue indicated that the target could appear at either side with 50 %
583 chance. Then participants had 1200 to 1500 ms to prepare for the upcoming target. A target
584 and distractor were shown for 150 ms after which participants made a 3-forced choice
585 response based on whether the target object contained the letter 'A', 'B', or 'C'. After 1700 -
586 2000 ms the cue for the next trial was presented. The distractor box also contained a letter,
587 but never the same letter as the target (importantly, because there were three possible
588 letters, guessing the target identity based on the distractor letter would produce 33 % correct
589 performance).

590 Figure 2. Mean reaction times (+ SEM) as a function of distractor-type for cued and uncued. Uncued
591 trials show that increased target-distractor-similarity (D1) slows down RTs. This effect was
592 reduced when a spatial cue indicated target location prior to presentation.

593 Figure 3. Scalp topography of pretarget lateralization in alpha activity (averaged across 8-12 Hz, and time
594 -1050 to 0 ms). (A,B) The grand average power of alpha activity for left minus right targets.
595 (C,D) Data combined across hemispheres and compared for differences between channels

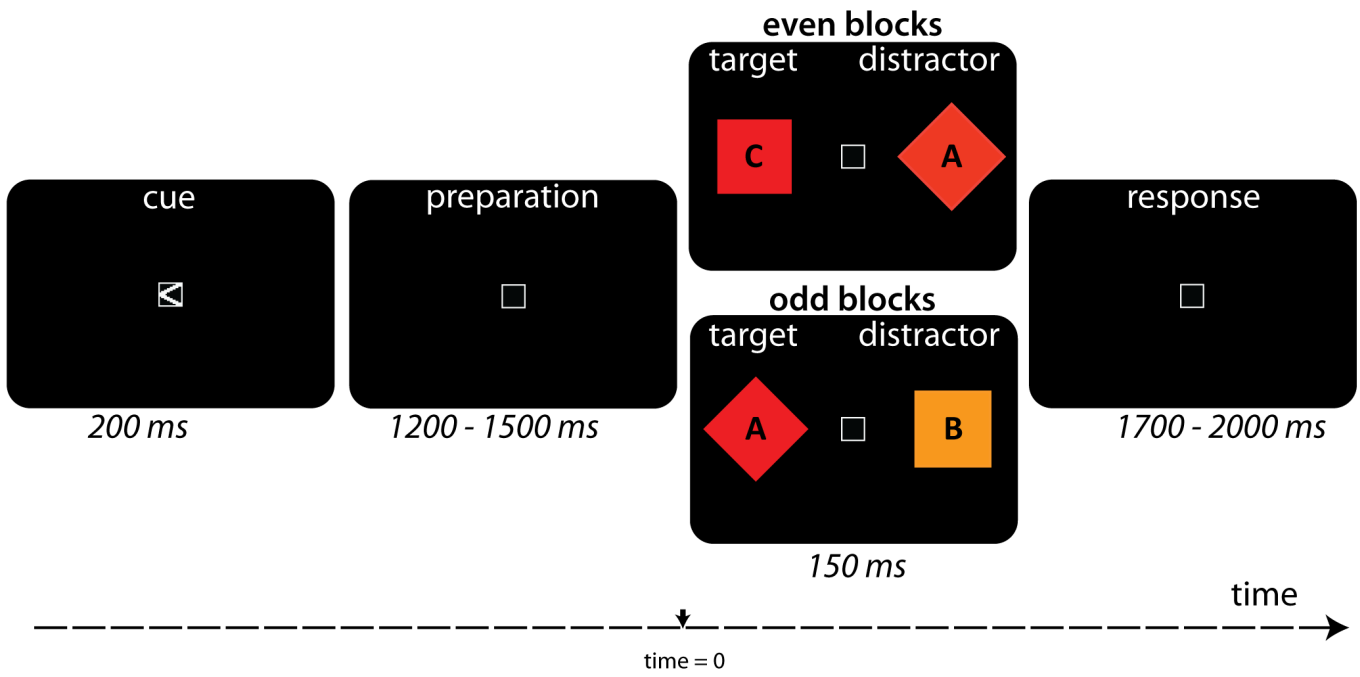
596 located contralateral and ipsilateral to target presentation. Warm colors indicate that alpha
597 power was higher contralateral to distractor presentation (i.e. ipsilateral to target
598 presentation). (E) The lateralization was significantly different between cued and uncued trials
599 for all time points between -1050 to 0 ms prior to target presentation. White dots represent
600 channels that showed a significant difference ($p < 0.05$) using the cluster-based permutation
601 test.

602 Figure 4. Scalp topographies and time course of alpha activity (averaged over 8 – 12 Hz) showing
603 lateralization in alpha activity after presentation of the target and distractor. (A) Data
604 combined across hemispheres and compared for differences between channels located
605 contralateral and ipsilateral to target presentation. Warm colors indicate that alpha power was
606 higher contralateral to distractor presentation (i.e. ipsilateral to target presentation). White
607 dots represent channels that showed a significant difference ($p < 0.05$) using the cluster-based
608 permutation test. (B) Time courses of alpha activity for ipsilateral (blue) and contralateral (red)
609 to target presentation. Grey shaded areas represent time-intervals where a significant
610 lateralization was present as found by the cluster-based permutation test. Trials with an
611 uninformative cue and high distraction were the only condition in which no lateralization of
612 post-target alpha activity was present.




613 Figure 5. Correlation between the difference in post-target alpha lateralization and the cost in RT for
614 uncued trials. Participants with a larger difference in lateralization between the high and low
615 distraction showed more RT cost for high distraction trials. An outlier is shown in pink.

616 Figure 6. Scalp topographies showing a relative increase in post-target theta-activity (averaged across 4
617 – 6 Hz, and time 700 to 1250 ms) for trials with high target-distractor-similarity when no
618 preceding cue was presented (left). White dots represent channels that showed a significant

619 difference ($p < 0.05$) using the cluster-based permutation test. When a spatial cue was
620 presented prior to target presentation (right), no difference in theta was found between the
621 low and high target-distractor-similarity conditions.



cues:

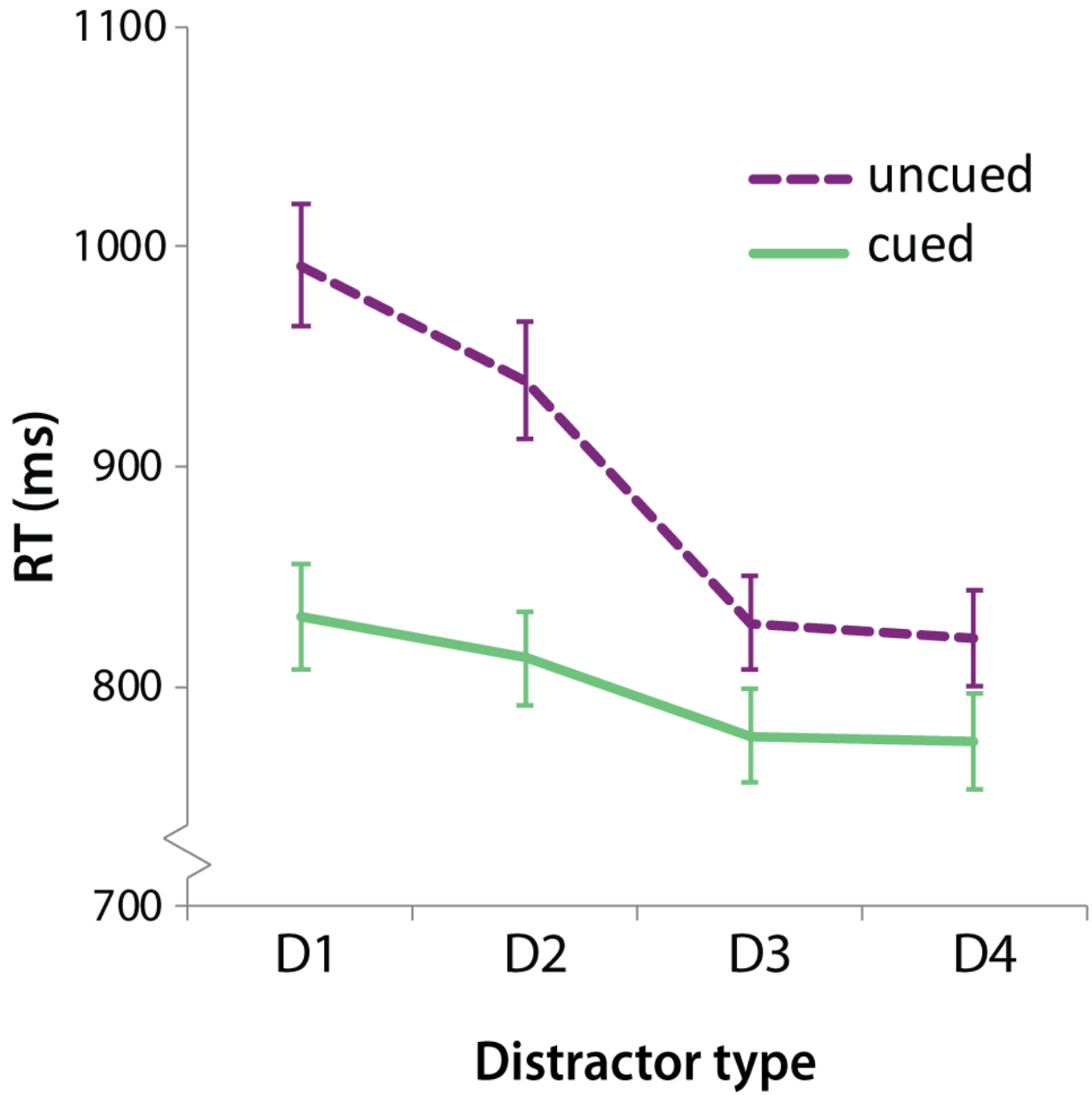
-  left cue
-  right cue
-  uninformative cue

targets:

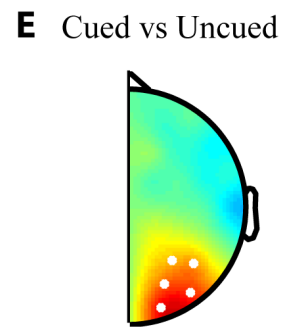
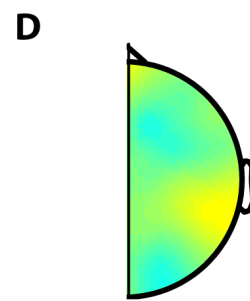
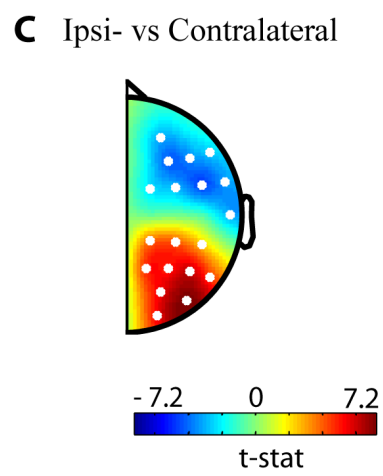
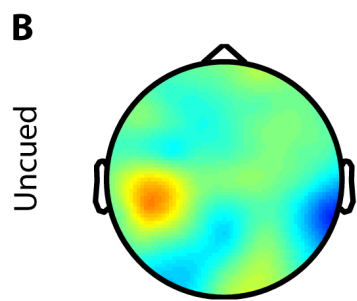
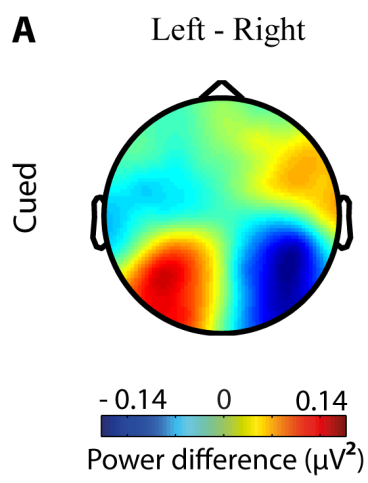
-  A
-  B
-  C

distractor colors:

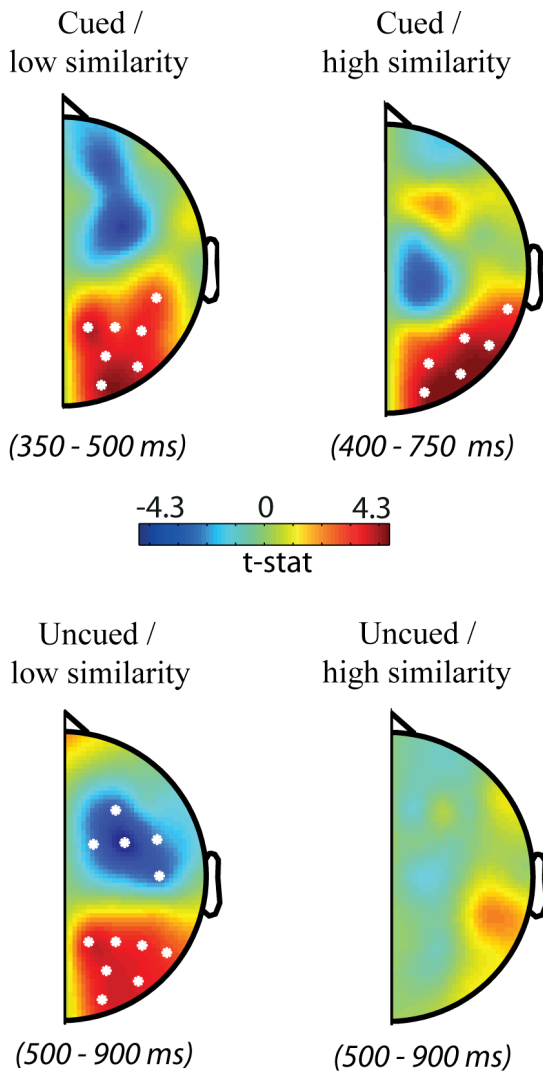
-  D1
-  D2
-  D3
-  D4



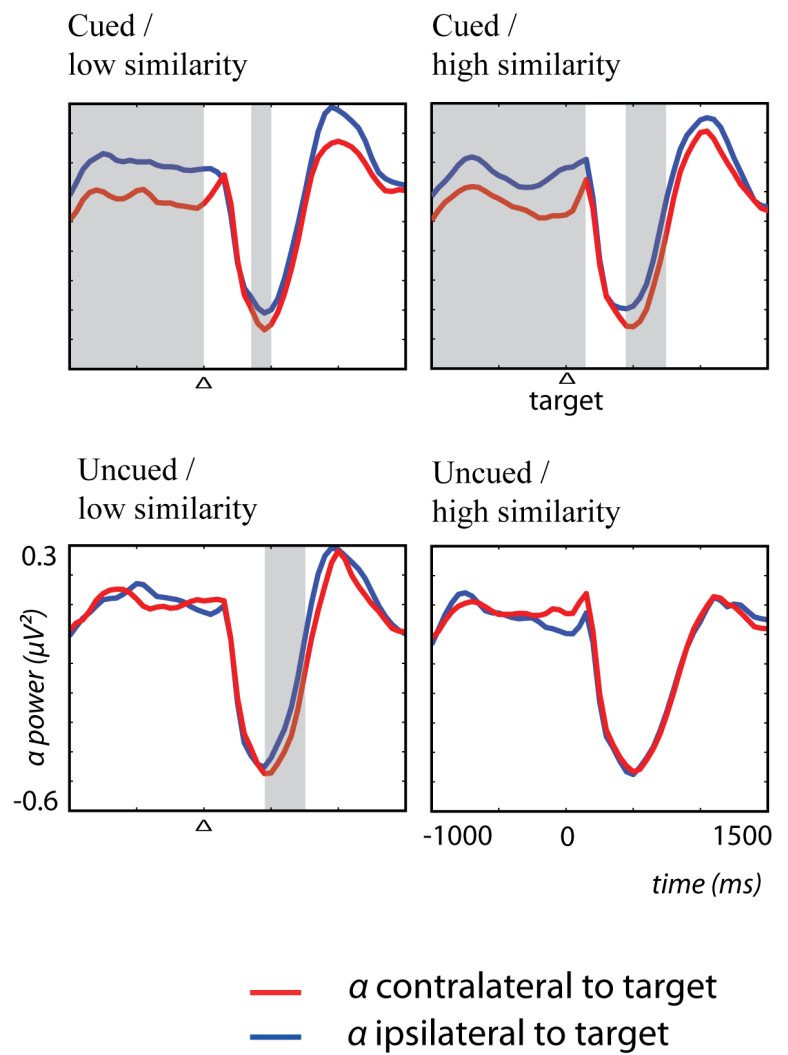
Alpha [8 - 12 Hz] pre-target

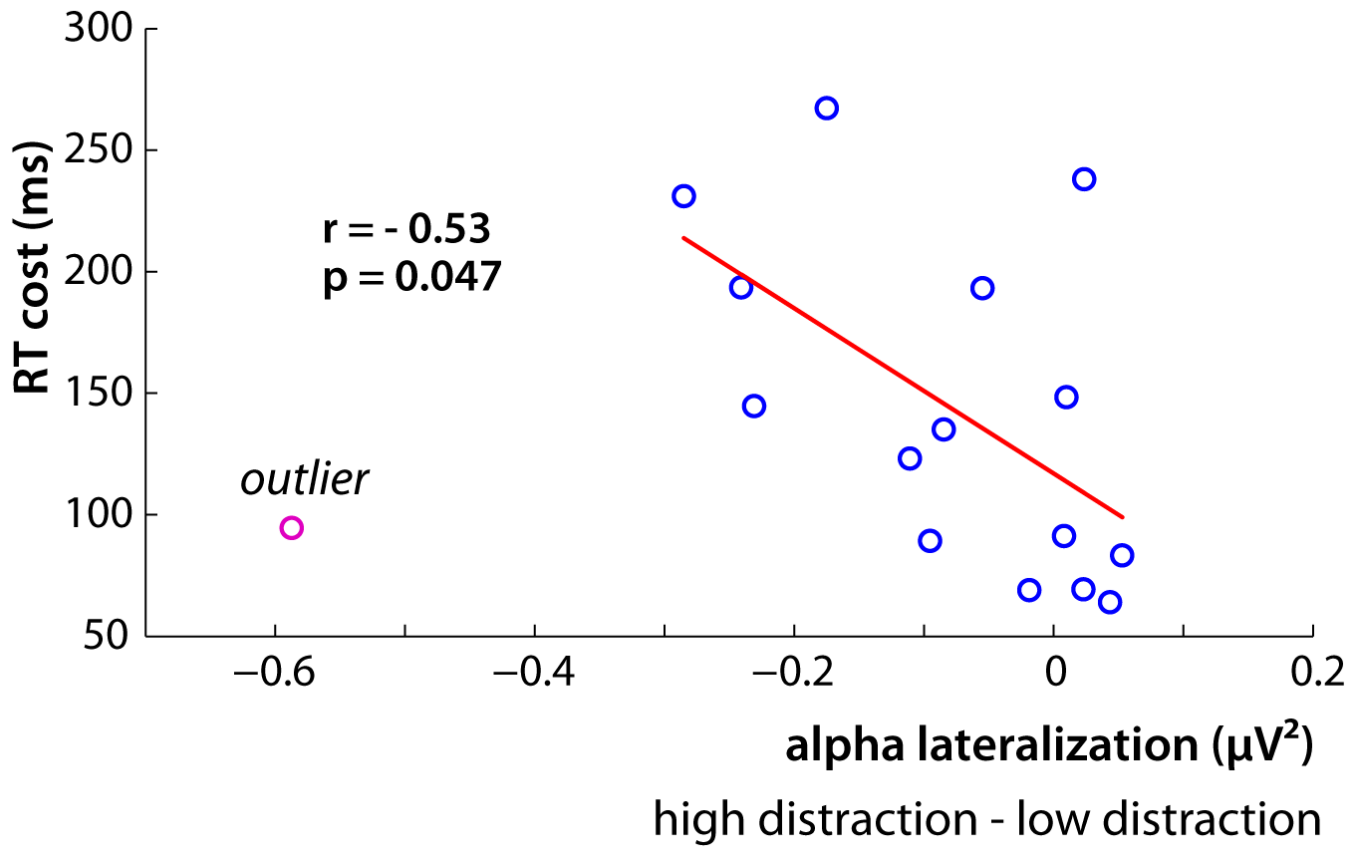


A Alpha [8 - 12 Hz] post-target



B Alpha time-course





Theta [4 - 6 Hz]
High distraction vs Low distraction

