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Distinct roles of theta and alpha oscillations in the involuntary capture of goal-directed attention

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Abstract

Mechanisms of attention assign priority to sensory inputs on the basis of current task goals. Previous studies have shown that lateralized neural oscillations within the alpha (8-14 Hz) range are associated with the voluntary allocation of attention to the contralateral visual field. It is currently unknown, however, whether similar oscillatory signatures instantiate the involuntary capture of spatial attention by goal-relevant stimulus properties. Here we investigated the roles of theta (4-8 Hz), alpha, and beta (14-30 Hz) oscillations in human goal-directed visual attention. Across two experiments, we had participants respond to a brief target of a particular color among heterogeneously colored distractors. Prior to target

onset, we cued one location with a lateralized, non-predictive cue that was either target- or non-target-colored. During the behavioral task, we recorded brain activity using electroencephalography (EEG), with the aim of analyzing cue-elicited oscillatory activity. We found that theta oscillations lateralized in response to all cues, and this lateralization was stronger if the cue matched the target color. Alpha oscillations lateralized relatively later, and only in response to target-colored cues, consistent with the capture of spatial attention. Our findings suggest that stimulus induced changes in theta and alpha amplitude reflect task-based modulation of signals by feature-based and spatial attention, respectively.

Keywords:
Goal-directed attention, attentional capture, neural oscillations, alpha, theta.

Active search of the visual environment is characterized by spatio-temporal uncertainty. Under such conditions, goal-directed attention allows flexible orienting to potential target stimuli based upon their locations or features. Despite advances in understanding the neural mechanisms of attention (e.g., Corbetta & Shulman 2002), it remains unclear how goal-directed selection is instantiated in the local circuits that process visual information. Here we examined the role of cortical oscillations (Buzsáki & Draguhn 2004) in the involuntary capture of goal-directed visual attention, focusing on the theta (4-8 Hz), alpha (8-14 Hz), and beta (14-30 Hz) frequency bands.

To date, there has been no work on the association between cortical oscillations and involuntary capture of goal-directed attention. Previous electroencephalography (EEG) studies of attentional guidance and capture have typically focused on a negativity in the event-related potential (ERP) over occipito-parietal electrodes, at around 200ms after the onset of a stimulus – the N2pc (Luck & Hillyard 1994). This component is observed following the presentation of lateralized stimuli possessing a goal-relevant feature, but is attenuated if the stimulus features are not task relevant (e.g., Eimer & Kiss 2008; Lien et al. 2008; Noesen et al. 2014). This link to goal relevance has led many authors to conclude that the N2pc reflects the

allocation of goal-directed attention (e.g., Eimer, 1996; Eimer & Grubert, 2014; Hickey et al. 2009). However, conflicting empirical results have led to suggestions that the N2pc may reflect other processes, such as the identification of goal relevant features prior to attentional allocation or object individuation (Eimer & Grubert 2014; Naughtin et al. 2016). Thus, it is currently unclear when goal-directed attention is allocated to a stimulus, and in what part of the EEG signal it is reflected. One promising candidate that has been identified in studies of voluntary attention is the occipito-parietal alpha oscillation.

There is extensive evidence for the involvement of alpha oscillations in voluntary attentional allocation (Foxe & Snyder 2011). In tasks in which centralized cues direct observers to attend to a location in the left or right hemifield, alpha oscillations measured over occipito-parietal cortex become lateralized such that alpha amplitude is decreased contralateral to the attended side of space (Sauseng et al. 2005; Worden et al. 2000). This alpha lateralization is maintained as long as attention is directed to one side of space (Kelly et al. 2006), the magnitude of lateralization tracks the likelihood of targets appearing at the cued location (Bauer et al. 2014; Gould et al. 2011), and predicts subsequent perceptual outcomes (e.g., Händel et al. 2011; Thut et al. 2006). The frequency of lateralized activity

can spread up to ~25 Hz (the beta range) in visual attention tasks (e.g., Bauer et al. 2014), but it is currently unclear whether this is simply an extension of the alpha range (Michalareas et al. 2016), or whether this beta activity reflects distinct processes (e.g., Sedley et al. 2016).

Evidence for the involvement of theta oscillations in goal-directed attention is also sparse. Dowdall et al. (2012) had participants perform visual search where targets did or did not "pop out". Theta power was greater contralateral than ipsilateral to the target location, and this effect was larger for "popout" than for "non-popout" displays. However, as ERPs are strongly represented in the theta range (Klimesch et al. 2004), it is unclear whether this increase in theta amplitude was an indication of theta's involvement in task-related processing, or simply reflects a spectral representation of the ERP.

Here we examined how oscillations in distinct frequency bands are impacted by the interaction of goal-directed attention with physical characteristics of the environment that elicit involuntary shifts of attention. Across two independent datasets, we show that theta and alpha oscillations are involved in different aspects of goal-directed attention. In contrast, beta oscillations, while showing stimulus induced amplitude

changes, were not associated with the goal-directed allocation of spatial attention.

Materials and Methods

Overview

We used a well-studied paradigm that provides a precise characterization of the locus of spatial attention (Folk et al. 1992) to investigate the roles of theta, alpha, and beta oscillations in goal-directed attention. Specifically, participants searched for a target of a particular color among heterogeneously colored distractors. Prior to the appearance of the target display we cued one location with a non-predictive cue that was either target- or non-target-colored (Folk & Remington 1998). Under such conditions, cues possessing behaviorally-relevant stimulus properties – such as the target color – are known to exert a strong and involuntary 'capturing' influence on the locus of spatial attention (e.g., Eimer & Kiss 2008; Folk et al. 1992, 2002; Zivony & Lamy 2014), even when they occur outside of awareness (Ansorge et al. 2009; Lamy et al. 2014). We recorded brain activity using EEG, with the aim of analyzing oscillatory activity elicited by these task-irrelevant cues.

Participants

Twenty-five individuals participated in Experiment 1 (aged 18-28 years, mean = 22.12, SD = 2.49, 16 females). A separate group of twenty-four individuals participated in Experiment 2 (aged 18-31years, mean = 22.33, SD = 2.92, 10 females). All participants were right-handed, had normal or corrected-to-normal vision, and provided written informed consent prior to participating. One participant was excluded from Experiment 1 due to a technical error that resulted in no EEG data being recorded for that individual. Participants were compensated for their time at a rate of $10 per hour. The study was approved by The University of Queensland Human Research Ethics Committee.

Behavioral Task

We employed a modified spatial cueing paradigm (**Figure 1a**; Folk et al. 1992) in which participants were required to identify the orientation of a target letter T of a particular color (red in Experiment 1, counterbalanced across individuals in Experiment 2). Participants fixated a central cross (0.3° x 0.3°, 1 pixel thick), surrounded by four placeholder circles (2.2° diameter, 2 pixels thick) placed 7.5° from fixation at the corners of an imaginary square. The placeholder circles and fixation cross were gray (RGB: 160, 160, 160) and were presented on a black background (RGB: 0, 0, 0). The fixation period lasted between 500 and 900ms (randomly determined) and was

followed by a cue period, during which the placeholder circles thickened to 4 pixels and one placeholder changed color for 67ms (except on no-cue trials, in which the circles thickened, but none changed color; **Figure 1A**). *Cues were non-predictive of the target location* (25% likelihood at each location), and could be red (RGB: 255, 0, 0), green (RGB: 0, 255, 0), blue (RGB: 0, 0, 255), yellow (RGB: 255, 255, 0), or gray (no-cue trials), with equal probability (20% of trials each). The cue display was followed by the fixation display for 133ms (the inter-stimulus interval [ISI]). Following this, the target display was presented for 100ms. The target display consisted of the fixation display, with the addition of four "Ts" (0.8° x 0.8°, 4 pixels thick) rotated by 90 degrees clockwise ("rightward") or counterclockwise ("leftward"), one placed centrally in each placeholder location. There were always two leftward and two rightward oriented "Ts" on every trial, each allocated a unique color from the set {red, green, blue, yellow}. In Experiment 1, all participants responded to the orientation of the red "T". In Experiment 2, target color was counterbalanced such that each participant was randomly allocated a target color from the set {red, green, blue, yellow}. The target display was followed by the fixation display for 1500ms, during which time participants could make their response to the orientation of the target-colored "T", pressing the left or right arrow key on the keyboard if the target was rotated to the left or right, respectively.

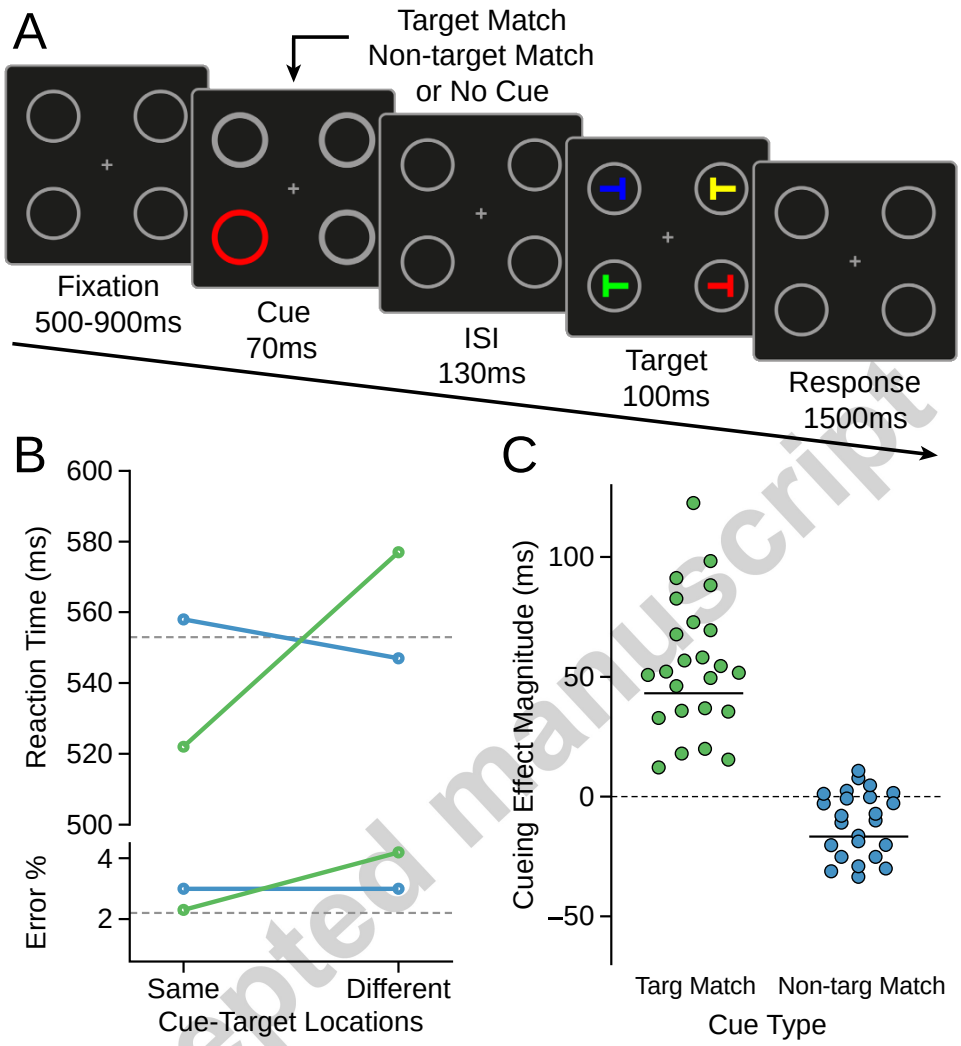

Figure 1. Paradigm and behavioral results for Experiment 1. ***A*** Schematic of the spatial cueing paradigm. Participants fixated centrally and reported whether the target "T" was rotated to the right or left. In Experiment 1 participants responded to the red "T". In Experiment 2 the color of the target "T" was counterbalanced across participants. Prior to target onset, a cue was presented that matched either the target color or a non-target color (or no cue was presented). This cue was equally likely at all locations, and so was not predictive of the subsequent target location. ***B*** Reaction time and error data for each condition in Experiment 1. Gray dashed lines represent the mean reaction time and error rate for the no-cue condition, which did not have a specific location in

relation to the target (see Methods). ***C*** The difference in reaction time between each cue condition when the cue appeared at the target location versus a different location. Positive cueing effects indicate that participants were faster when the cue and target appeared at the same location, and suggest that goal-directed attention was captured by the cue. Dots represent individual participants' cueing effect magnitudes. Horizontal lines represent the mean for the group.

Stimuli were presented on an NEC Accusync 120 CRT monitor with a resolution of 1024 x 768 and a refresh rate of 60 Hz. Stimulus presentation was controlled using the Psychophysics Toolbox extension (Brainard 1997; Kleiner et al. 2007) for MATLAB (MathWorks), running under Windows 7. Viewing distance was maintained at 57cm with the use of a chinrest. Participants made their responses by pressing either the left or right arrow key on a standard USB keyboard with their right hand.

Each block of the task contained a full factorial crossing of the five cue conditions (red, green, blue, yellow, no-cue), four cue positions (dummy coded for no-cue trials), and four target positions, to give a total of 80 trials per block. All participants completed one block of practice, during which they received feedback at the end of every trial. Feedback consisted of the word "CORRECT" or "WRONG!" presented centrally in white (RGB: 255, 255, 255) 14 point Arial font (3.5° x 0.5°) for 300ms. Incorrect

responses were also met with a 1000 Hz tone for 500ms. During the experiment there was no trial-by-trial feedback, but participants were informed of their accuracy (%) during the self-paced break at the end of every block. Excluding practice, participants completed a total of 1040 trials (13 blocks) each.

EEG recording

Continuous EEG data were recorded using a BioSemi Active Two system (BioSemi), digitized at a rate of 1024 Hz with 24-bit A/D conversion. The 64 active Ag/AgCl scalp electrodes were arranged according to the international standard 10–10 system for electrode placement (Chatrian et al. 1985), using a nylon head cap. As per BioSemi system design, the Common Mode Sense and Driven Right Leg electrodes served as the ground, and all scalp electrodes were referenced to the Common Mode Sense during recording. Eye movements were monitored online using bipolar horizontal electro-oculographic (EOG) electrodes placed at the outer canthi of each eye, and bipolar vertical EOG electrodes placed above and below the left eye.

EEG analysis

Offline EEG preprocessing was performed with the EEGLAB Toolbox (Delorme & Makeig 2004) for MATLAB, and analyses were performed with custom-written MATLAB scripts (some adapted from Cohen 2014). Data were high-pass filtered at 0.3 Hz and re-referenced to the average of all 64 scalp electrodes. Trial epochs were extracted from 800ms before cue onset to 2000ms after cue onset. Trials containing large muscle artifacts or eye movements were rejected by manual inspection of scalp and EOG electrodes. This resulted in an average loss of <1% of trials per participant. The data were then subjected to infomax Independent Components Analysis (ICA; Makeig et al. 1996). Blink artifacts, line noise, and other remaining artifacts, were identified and corrected using a combination of visual inspection of ICA components and the SASICA plugin for EEGLAB (Chaumon et al. 2015), which incorporates methods from the ADJUST (Mognon et al. 2011) and FASTER (Nolan et al. 2010) plugins.

All EEG analyses were performed at symmetrical left and right regions of interest (ROIs). These were P7, P9, and PO7 on the left, and P8, P10, and PO8 on the right. Event-related potentials (ERPs) were analyzed to validate our results in light of previous electrophysiological research using analogous spatial cueing paradigms. As mentioned in the Introduction, this research has largely focused on the N2pc component (e.g., Eimer et al.

2009; Lien et al. 2008), characterized by a greater negativity contralateral versus ipsilateral to a stimulus of interest, around 200ms post stimulus onset. Here we were interested in analyzing ERPs elicited by cue onset. These were computed for each of the six electrodes and then combined to form average ERPs for the left and right ROIs, classified as either ipsilateral or contralateral to the cue on each trial (collapsed across target location). The N2pc time window of interest was taken from 160-260ms, which is similar to that used to examine the N2pc in other studies using this type of paradigm (e.g., Noesen et al. 2014). Statistical analyses were performed by comparing the mean amplitude over the analysis period for the ipsilateral and contralateral ROIs for each condition.

Time-Frequency Analyses

Visual evoked ERPs are known to be strongly represented in the theta and alpha frequency ranges (Klimesch et al. 2004), but are not necessarily caused by amplitude changes in these frequency bands (Sauseng et al. 2007). To ensure that our results reflected fluctuations in endogenous oscillatory amplitude and were not spuriously influenced by ERP differences between conditions, our time-frequency analyses were all performed on non-phase-locked data. This was computed by subtracting the ERP of each condition from the single-trial EEG data making up that

condition, before performing the relevant time-frequency decompositions (described below) on the remaining data (Cohen 2014). This has the effect of removing any phase-locked components from the data, forcing the ERP to zero at all time points. Thus, any remaining effects cannot be spuriously influenced by the ERP.

Non-phase locked time-frequency spectra (averaged across all conditions and both ROIs) were produced using Morlet wavelets (Tallon-Baudry & Bertrand 1999) at 30 logarithmically spaced frequencies from 2 to 80Hz, with the number of wavelet cycles logarithmically spaced from 3 to 10 cycles. To test for non-phase-locked changes in oscillatory power produced by the task we then computed decibel change from the mean activity of a baseline period from -500 to -200 for each time and frequency. These changes from baseline were assessed for significance by downsampling to 128 Hz and performing *t*-tests at each frequency and each time from 0-1000ms, controlling for multiple comparisons by controlling the false discovery rate (FDR; Benjamini & Hochberg 1995).

To examine lateralization in broad-band frequency representations of non-phase-locked theta, alpha, and beta oscillations, these signals were extracted from the ERP-subtracted EEG signals by means of bandpass FIR

filters with transition widths of 25% of their respective maximum and minimum frequencies and filter orders equivalent to three cycles of the lowest frequencies in their respective passbands. The passbands used were: 4–7 Hz (theta), 9–12 Hz (alpha), and 16–26 Hz (beta). With their respective transition widths, this gave full width at half-maximum responses of: 3.5–8 Hz (theta), 7.6–13.7 Hz (alpha), and 14–29.9 Hz (beta). The filtered data were then Hilbert transformed, and the absolute value of the resulting signal was computed to extract the analytic amplitude. This was computed for each of the six electrodes of interest and averaged across electrodes to produce amplitude estimates for the left and right ROIs. Our hypotheses related to the time-course of oscillatory activity in these regions in response to lateralized stimuli under conditions of goal-directed attention. Lateralized stimuli are known to produce lateralization in both the alpha (e.g., Sauseng et al. 2005; Thut et al. 2006; Worden et al. 2000) and theta (Dowdall et al. 2012) bands. To quantify the magnitude of this lateralization we employed a *Lateralization Index* (Belyusar et al. 2013; Haegens et al 2011; Händel et al. 2011; Kerlin et al. 2010; Thut et al. 2006). The Lateralization Index (LI) was calculated for each participant at each time-point as:

$$LI_{Freq} = ROI_{Left}\left(\frac{LeftTarg - RightTarg}{LeftTarg + RightTarg}\right) - ROI_{Right}\left(\frac{LeftTarg - RightTarg}{LeftTarg + RightTarg}\right)$$

As shown in the formula above, we calculated the lateralization index relative to the location of the *target*. Furthermore, we calculated the lateralization index separately for trials in which the cue was in the same visual hemifield as the target (*same-side cues*), and for trials in which the cue and target appeared in opposite hemifields (*opposite-side cues*). This approach has the benefit of loading the target-related lateralization in the same direction, effectively cancelling out target-related activity in the comparison of lateralization produced by same- and opposite-side cues. This is a key feature of our analytic approach, as the temporal smearing caused by oscillatory analyses would otherwise blend the activity produced by the cues and targets (necessarily separated only by 200ms to avoid inhibition of return; Klein 2000), and would prevent us from drawing conclusions about cue-related activity specifically. For statistical analyses, lateralization for each frequency was downsampled to 128 Hz and compared between relevant conditions with FDR controlled *t*-tests at each time-point from 0-1000ms. We also conducted analyses on lateralization of *total-power* data in the theta, alpha, and beta bands, without removal of phase-locked components of the data. The results were qualitatively identical to those yielded by the analyses of non-phase-locked data (see supplementary material).

Results

Experiment 1 – Oscillatory Correlates of Goal Directed Attention

Behavioral Performance

For all behavioral and EEG analyses, excepting the analysis of error rates, only trials with correct responses were analyzed. As can be seen from **Figure 1B**, reaction times (RTs) in the cued-attention task were strongly modulated by the interaction between cue color and cue-target location. To confirm this statistically, RT data were analyzed using within-participant ANOVA with cue color (target matching, non-target matching) and cue-target location (same, different) as factors. There was no significant RT difference between trials containing target matching and non-target matching cues, $F(1,23) = 1.74$, $p = .201$, $\eta^2 = .07$. Responses were significantly faster when the cue and target were presented at the same location than when they were presented at different locations, $F(1,23) = 39.98$, $p < .001$, $\eta^2 = .64$. Critically, these were qualified by a significant interaction between cue color and cue-target location, $F(1,23) = 136.88$, $p < .001$, $\eta^2 = .86$ (**Figure 1B**). Follow-up, paired samples *t*-tests showed that RTs were significantly faster when target matching cues were presented at the same location as the target ($M = 522$ms, $SD = 59$ms), than when the

cue and target were at different locations (M = 577ms, SD = 63ms), $t(23)$ = 9.63, $p < .001$. By contrast, when the cue was non-target matching, RTs were significantly slower when the cue and target were presented at the same location (M = 558ms, SD = 59ms) than when they were presented at different locations (M = 547ms, SD = 58ms), $t(23) = 3.97$, $p < .001$.

The difference between same- versus different-location RTs for each cue type is the *cueing effect* (**Figure 1C**). The large positive cueing effect observed here for target matching cues has been reported in behavioral studies numerous times (e.g., Folk & Remington 1998; Folk et al. 1992, 1994; Harris et al. 2013; Lamy et al. 2004; etc.) and is generally interpreted as indicating the capture of spatial attention by cues possessing a goal-relevant property. Target colored cues are thought to capture spatial attention to their location, facilitating responses to a subsequent target when it appears at the attended location, but slowing responses when the target appears elsewhere. The small negative cueing effect observed for non-target matching cues has also been reported previously (see Carmel & Lamy 2015, for review) and has been shown to reflect processes other than goal-directed attention (Carmel & Lamy 2014, 2015). As such, we would not expect it to be reflected in reversed attention-related brain activity compared with that elicited by the target matching cues.

The pattern of error results qualitatively matched those present in the RT data (**Figure 1B**, lower axes). These were analyzed using within-participant ANOVA with cue color (target matching, non-target matching) and cue-target location (same, different) as factors. The main effect of cue color was not significant, $F(1,23) = 0.40$, $p = .533$, $\eta^2 = .02$. There was a significant main effect of cue-target location, $F(1,23) = 11.27$, $p = .003$, $\eta^2 = .33$, and a significant cue color by cue-target location interaction, $F(1,23) = 5.07$, $p = .034$, $\eta^2 = .18$. Follow-up tests revealed that when the cue matched the target color, responses were more accurate when the cue and target were at the same location ($M = 2.26\%$, $SD = 3.08$) than when the cue and target locations differed ($M = 4.15\%$, $SD = 3.33$), $t(23) = 3.01$, $p = .006$. When the cue matched a non-target color there was no difference in accuracy between same cue-target locations ($M = 2.98\%$, $SD = 2.42$) and different cue-target locations ($M = 3.04\%$, $SD = 2.26$), $t(23) = 0.18$, $p = .859$. Thus, the error data are broadly consistent with the RT data, and allow us to rule out any speed accuracy trade-off between conditions of interest.

ERP Analysis

Average EEG responses revealed increased negativity contralateral to target matching cues around 160ms post cue onset, which was absent following non-target matching cues (**Figure 2**). This was confirmed by analyzing mean ERP amplitudes during the relevant N2pc time window (160–260ms), using within-participant ANOVA with cue color (target matching, non-target matching) and ROI (ipsilateral, contralateral) as factors. This analysis revealed a significant cue color by ROI interaction, $F(1,23) = 15.86$, $p < .001$, $\eta^2 = .41$ (**Figure 2C**). Follow-up paired-samples *t*-tests revealed that EEG responses were significantly more negative contralateral than ipsilateral to the cued location following target matching cues (mean N2pc magnitude = -0.40 μV), $t(23) = 2.96$, $p = .007$ (**Figure 2C**, green line). Responses to non-target matching cues were no different between contralateral and ipsilateral electrodes ($M = -.03$ μV), $t(23) = 0.33$, $p = .745$ (**Figure 2C**, blue line). N2pc magnitude was significantly larger following target matching cues than following non-target matching cues, $t(23) = 3.98$, $p < .001$.

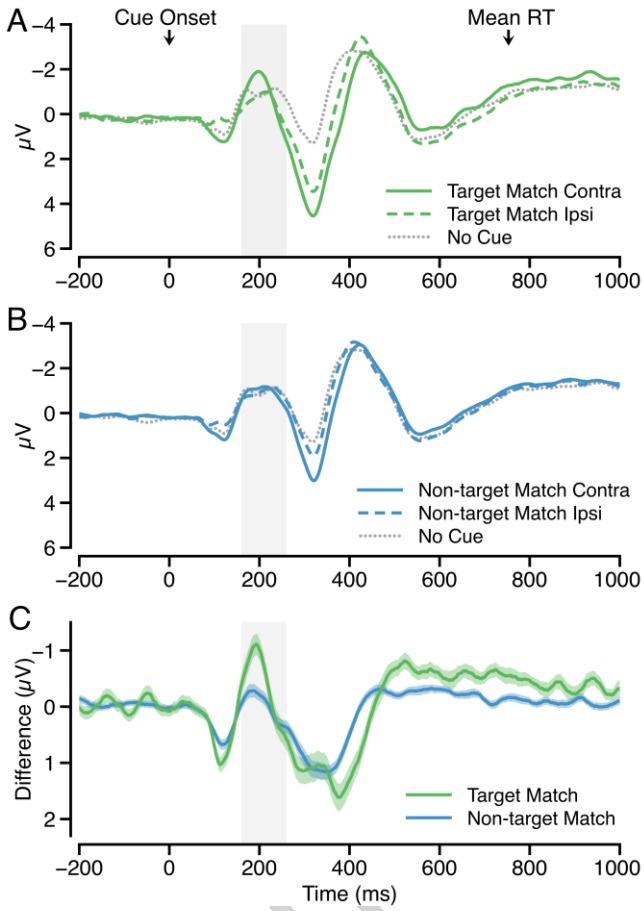

Figure 2. ERP results for Experiment 1. ***A***, Average ERP waveforms recorded at ROIs contralateral and ipsilateral to the target matching cues. The gray line shows the ERP averaged across both left and right ROIs for the no-cue trials. The shaded region shows the period for analysis. ***B***, As above, but for non-target matching cues. ***C***, Waveforms showing the magnitude of the difference between contralateral and ipsilateral electrodes for each cue condition. Error shading reflects one within-participant SEM (Cousineau 2005; Morey 2008) of the difference between contralateral and ipsilateral responses.

Time-Frequency Analyses

As a preliminary analysis to examine frequencies involved in this task we computed non-phase-locked spectral power change from baseline for

frequencies from 2-80 Hz (**Figure 3**). Power change from baseline was compared to zero using FDR corrected *t*-tests (Benjamini & Hochberg 1995). This revealed significant power increases across the theta range (3-7 Hz) from 94ms post-cue onset. There was also a significant decrease in power across the alpha and beta bands from 8-32 Hz from 141-679ms post-cue onset, extending out to 760ms for the alpha frequencies around 10Hz. Finally, there was a significant power increase in the 13-17Hz range from 828ms until the end of the analysis window.

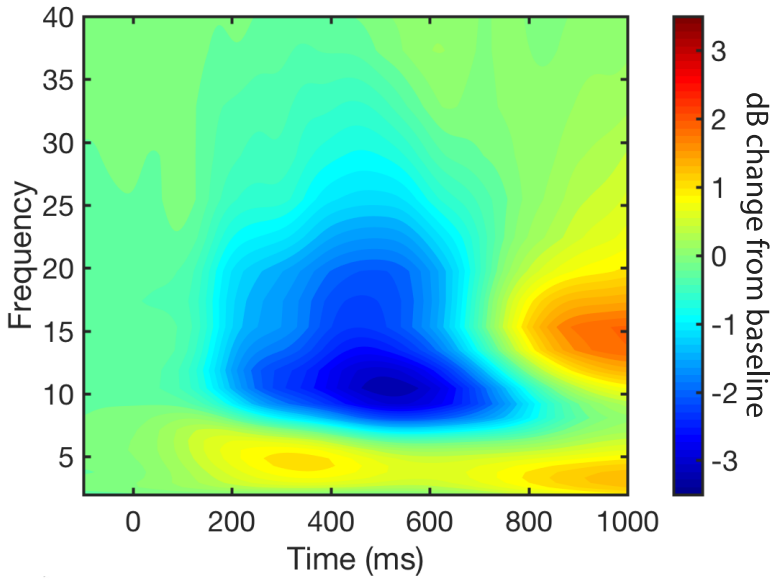

Figure 3. Change in non-phase-locked power relative to baseline (-500 to -200ms) for Experiment 1, averaged across left and right ROIs and averaged across all conditions. Frequency scale is limited to 40 Hz to show low frequency detail. There were no significant effects above 40 Hz.

Lateralization of responses in the non-phase-locked theta, alpha, and beta bands was analyzed using a series of FDR corrected *t*-tests (Benjamini & Hochberg 1995), which compared the LI for cue-locked responses when the cue and target were in the same visual hemifield with those on trials in which the cue and target were in different hemifields. These responses were computed relative to the target side, to cancel out differences that may be caused by temporal smearing of the target-induced response. Negative scores in this analysis indicate higher amplitude contralateral than ipsilateral to the target location, and positive scores indicate higher amplitude ipsilateral than contralateral to the target location.

Analysis of lateralization in the theta band revealed significant LI differences between trials in which the cue was on the target side and when it was opposite the target side, following both target matching and non-target matching cues (**Figure 4**). These differences were present from 125-328ms after the onset of target matching cues (**Figure 4B**), and from 109-375ms after the onset of non-target matching (**Figure 4C**). For both of these cue types, LI values were negative when the cue and target appeared on the same side, indicating greater theta amplitude contralateral to the target side (i.e., contralateral to the cue). LI was positive when the cue was

presented opposite the subsequent target, indicating greater theta amplitude ipsilateral to the target side (contralateral to the cue).

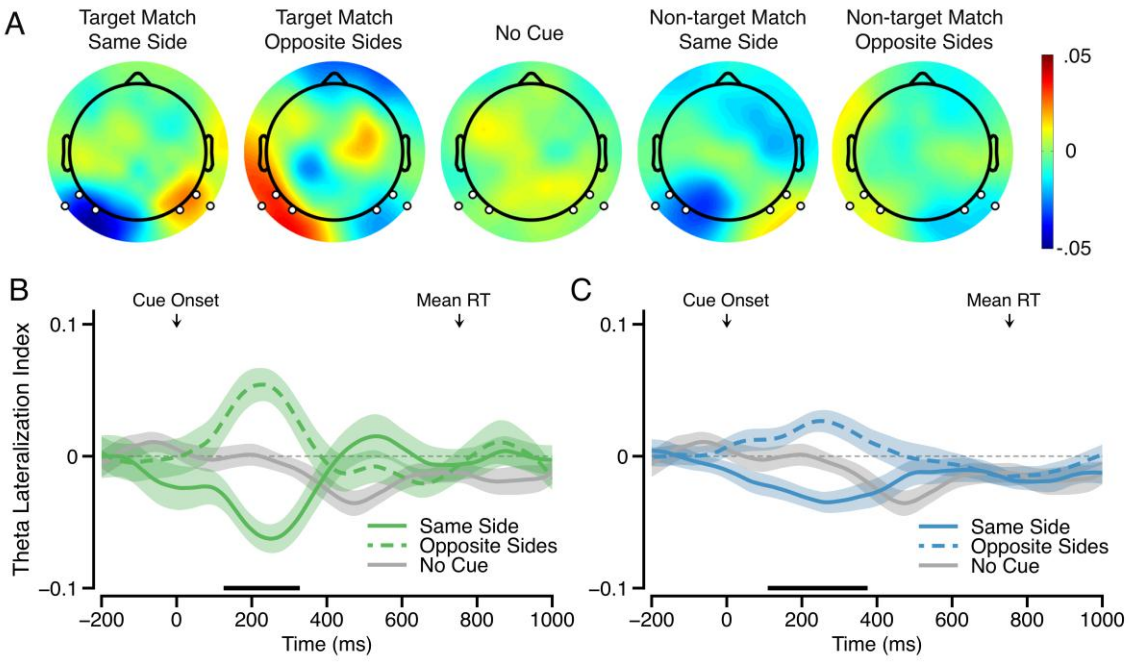

Figure 4. Lateralization of non-phase-locked theta amplitude for Experiment 1. ***A.*** Scalp topographies showing the distribution of non-phase-locked theta amplitude averaged over the period from 125ms to 328ms post-cue onset. Topographies are presented relative to a target on the left (right-side target trials have had their topography flipped). Thus, in these topographies, 'same side' refers to a cue on the left, and 'opposite sides' refers to a cue on the right. White dots represent analyzed electrodes. ***B&C,*** Non-phase-locked theta lateralization index for trials in which the cue and target appeared in the same visual hemifield (solid colored lines) or in opposite hemifields (dashed colored lines), and for no-cue trials (solid gray lines). Positive numbers indicate greater theta amplitude ipsilateral to the target side. Negative values indicate greater theta amplitude contralateral to the target side. Solid black lines along the x-axis represent significant lateralization differences between Same Side and Opposite

Side cue responses ($p < .05$), adjusted to control the false discovery rate (Benjamini & Hochberg 1995). Error shading represents one within-participant SEM (Cousineau 2005; Morey 2008).

To compare the magnitude of theta lateralization for target matching versus non-target matching cues, we computed the average LI difference between same- and opposite-side cues during the period of overlap of their effects (125-328ms), and then compared these between target matching and non-target matching cues. This revealed that the magnitude of theta lateralization was significantly greater following target matching cues ($M = 0.10$, $SD = 0.08$) than following non-target matching cues ($M = 0.05$, $SD = 0.04$), $t(23) = 2.82$, $p = .010$. The topographies (**Figure 4A**) show that the amplitude response sometimes spreads beyond the ROIs we selected a-priori, most commonly to electrodes O1/2. Reanalysis with these electrodes included in the ROIs produced qualitatively identical results for all analyses.

Alpha lateralization analysis revealed significant LI differences between trials in which the cue was on the target side and trials in which it was opposite the target side, only following target matching cues (**Figure 5**). These differences were present from 406-469ms after the onset of target matching cues (**Figure 5B**). There were no significant lateralization

differences in the alpha response to non-target matching cues (**Figure 5C**). Following target matching cues, alpha LI values were positive when the cue and target appeared on the same side, indicating decreased alpha amplitude contralateral to the target side (contralateral to the cue). LI was negative when the cue was presented opposite to the subsequent target location, indicating decreased alpha amplitude ipsilateral to the target side (contralateral to the cue). Alpha lateralization averaged over the period of significant lateralization following target-matching cues (406-469ms) was significantly greater following target matching cues (M = -0.06, SD = 0.08) than following non-target matching cues (M = -0.01, SD = 0.07), $t(23)$ = 3.03, p = .006.

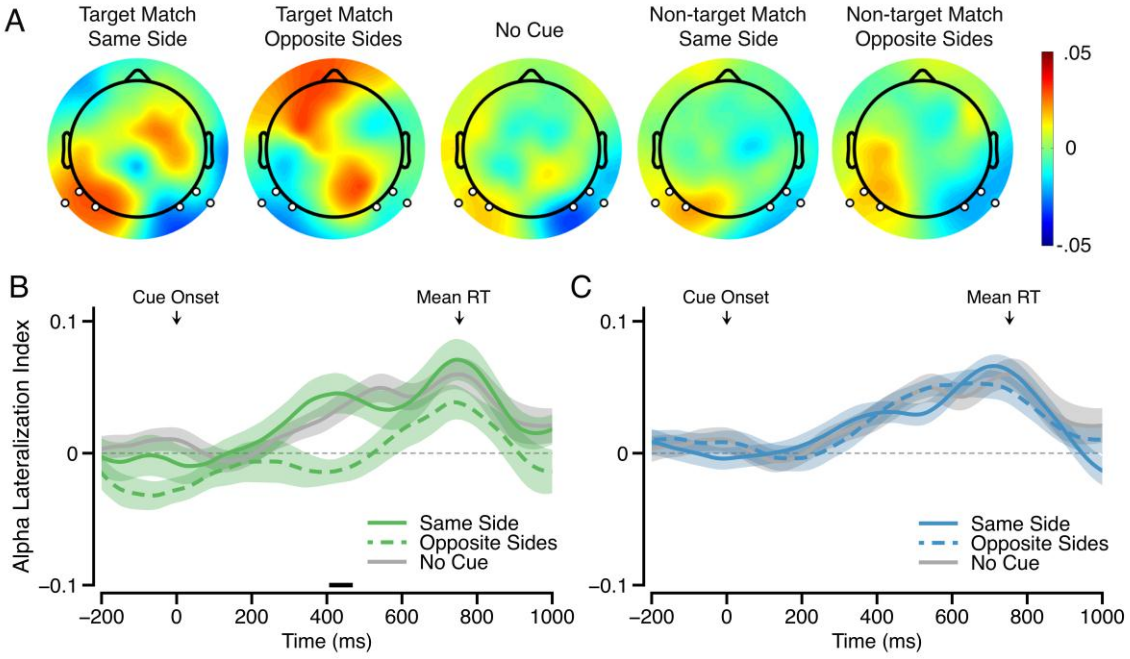

Figure 5. Lateralization of non-phase-locked alpha amplitude for Experiment 1. ***A.*** Scalp topographies showing the distribution of non-phase-locked alpha amplitude averaged over the period from 406ms to 469ms post-cue onset. Topographies are presented relative to a target on the left (right-side target trials have had their topography flipped). Thus, in these topographies, 'same side' refers to a cue on the left, and 'opposite sides' refers to a cue on the right. White dots represent analyzed electrodes. ***B&C,*** Non-phase-locked alpha lateralization index data for trials in which the cue and target appeared in the same visual hemifield (solid colored lines) or in opposite hemifields (dashed colored lines), and for no-cue trials (solid gray lines). Green lines indicate target matching cue trials. Blue lines indicate non-target matching cue trials. No-cue responses are identical in both plots. Positive numbers indicate greater alpha amplitude ipsilateral the target side. Negative values indicate greater alpha amplitude contralateral the target side. Solid black lines along the x-axis represent significant lateralization differences between Same Side and Opposite Side cue responses ($p < .05$), adjusted to control the false discovery rate (Benjamini & Hochberg 1995). Error shading represents one within-participant SEM (Cousineau 2005; Morey 2008).

Analysis of the beta band produced no significant differences in beta lateralization between cues appearing on the same side as the target compared with cues appearing on the opposite side to the target, for either target matching cues or non-target matching cues (**Figure 6**).

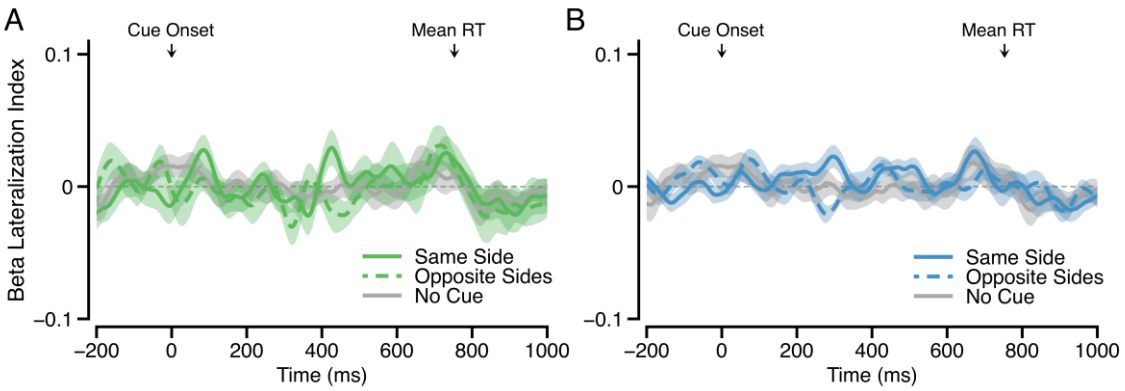

Figure 6. Lateralization of non-phase-locked beta amplitude for Experiment 1. ***A&B,*** Non-phase-locked beta lateralization index for trials in which the cue and target appeared in the same visual hemifield (solid colored lines) or in opposite hemifields (dashed colored lines), and for no-cue trials (solid gray lines). Green lines indicate target matching cue trials. Blue lines indicate non-target matching cue trials. No-cue responses are identical in both plots. Positive numbers indicate greater beta amplitude ipsilateral the target side. Negative values indicate greater beta amplitude contralateral the target side. Error shading represents one within-participant SEM (Cousineau 2005; Morey 2008). Same Side and Opposite Side cues did not produce significant differences in Beta lateralization in either condition.

Experiment 2 – Independent Replication Controlling Target Color

The results of Experiment 1 suggest active and dissociable involvement of theta and alpha frequencies in goal-directed stimulus processing and attentional allocation. It is important to note, however, that in Experiment 1, all participants responded to a red target, so that a single target color was always goal relevant throughout the task. It has been demonstrated numerous times that the particular feature of the target does not change

the pattern of behavioral results in paradigms like the one employed here (e.g., Folk & Remington 1998, and many others). Nonetheless, to rule this out as a potential confound, we replicated the experiment with a complete counterbalancing of target colors across participants. Experiment 2 also provided an opportunity to obtain an independent dataset, allowing us to examine the reliability of our results across experiments and participants. In light of recent reports on the low rates of replication of experimental results in several scientific fields, including cognitive science (Open Science Collaboration 2015; Szucs & Ioannidis 2016), economics (Camerer et al. 2016), and medicine (Begley & Ellis, 2012; Prinz et al. 2011), this replication provided additional confidence in the veracity of our conclusions.

Behavioral Performance

As can be seen from **Figure 7A**, the behavioral results of Experiment 2 closely replicated those of Experiment 1. Indeed, including Experiment as a between-group factor in the ANOVA below yielded a nonsignificant three-way interaction, $F(1,46) = 0.63$, $p = .430$, $\eta^2 < .01$. A Bayes factor analysis of the same ANOVA (Rouder et al. 2012) found the most likely model excluded the three-way interaction, and was preferred over a model including the three-way interaction by a factor of 14.7-to-1, suggesting no

difference in the interaction of cue color and cue-target location between the experiments (Dienes 2014).

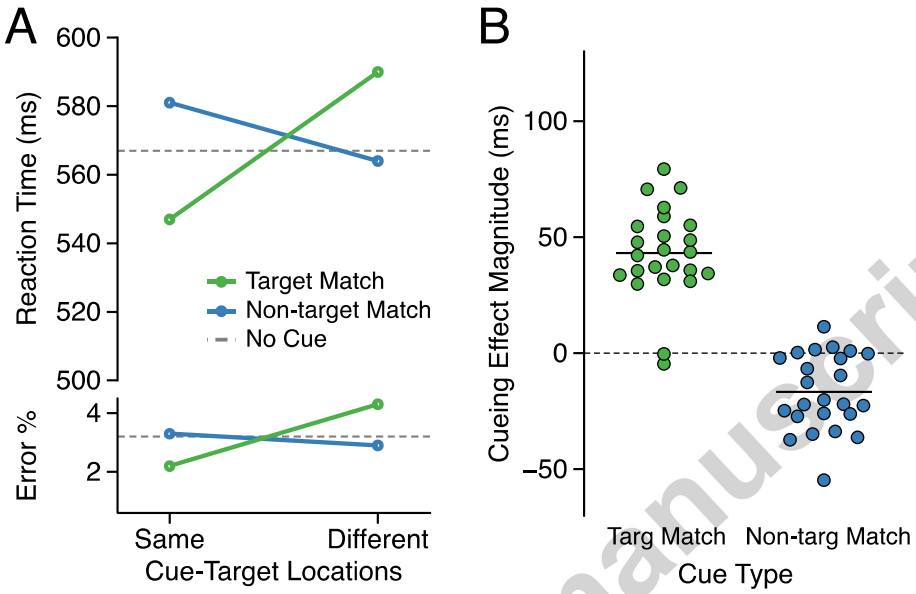

Figure 7. Behavioral results for Experiment 2. ***A*** Reaction time and error data for each condition. Gray dashed lines represent the mean reaction time and error rate for the no-cue condition, which did not have a specific location in relation to the target (see Methods). ***B*** The difference in reaction time between each cue condition when the cue appeared at the target location versus a different location. Positive cueing effects indicate that participants were faster when the cue and target appeared at the same location, and suggest that goal-directed attention was captured by the cue. Dots represent individual participants' cueing effect magnitudes. Horizontal lines represent the mean for the group.

As in Experiment 1, RT data were analyzed using within-participant ANOVA with cue color (target matching, non-target matching) and cue-target location (same, different) as factors for each experiment. There was no

significant RT difference between trials containing target matching and non-target matching cues, $F(1,23) = 2.85$, $p = .105$, $\eta^2 = .11$, but responses were significantly faster when the cue and target were presented at the same location than when they were presented at different locations, $F(1,23) = 25.89$, $p < .001$, $\eta^2 = .53$. There was also a significant interaction between cue color and cue-target location, $F(1,23) = 128.50$, $p < .001$, $\eta^2 = .85$ (**Figure 7A**). Follow-up, paired samples *t*-tests showed that RTs were significantly faster when target matching cues were presented at the same location as the target ($M = 547$ms, $SD = 49$ms), than when the cue and target were at different locations ($M = 590$ms, $SD = 49$ms), $t(23) = 10.78$, $p < .001$ (**Figure 7B**). By contrast, when the cue was non-target matching, RTs were significantly slower when the cue and target were presented at the same location ($M = 581$ms, $SD = 52$ms) than when they were presented at different locations ($M = 564$ms, $SD = 45$ms), $t(23) = 4.95$, $p < .001$.

The error results were analyzed using within-participant ANOVA with cue color (target matching, non-target matching) and cue-target location (same, different) as factors. The main effect of cue color was not significant, $F(1,23) = 0.32$, $p = .577$, $\eta^2 = .01$. There was a significant main effect of cue-target location, $F(1,23) = 4.35$, $p = .048$, $\eta^2 = .16$, and a

significant cue color by cue-target location interaction, $F(1,23) = 12.74$, $p = .002$, $\eta^2 = .37$. Follow-up tests revealed that when the cue matched the target color, responses were more accurate when the cue and target were at the same location ($M = 2.19\%$, $SD = 3.39\%$) than when the cue and target locations differed ($M = 4.29\%$, $SD = 3.31\%$), $t(23) = 3.50$, $p = .002$. When the cue matched a non-target color there were no differences in accuracy for same cue-target locations ($M = 3.33\%$, $SD = 2.36\%$) and different cue-target locations ($M = 2.68\%$, $SD = 2.00\%$), $t(23) = 1.55$, $p = .135$. Thus, the error data are consistent with those of Experiment 1, and rule out any speed accuracy trade-off between conditions of interest.

ERP Analysis

Average EEG responses were broadly consistent with those of Experiment 1. Analyses revealed greater negativity contralateral to target matching cues around 160ms post cue onset, which was greatly reduced following non-target matching cues. This was confirmed by analyzing mean ERP amplitudes during the relevant N2pc time window (160–260ms), using within-participant ANOVA with cue color (target matching, non-target matching) and ROI (ipsilateral, contralateral) as factors. These revealed a significant cue color by ROI interaction, $F(1,23) = 25.79$, $p < .001$, $\eta^2 = .53$ (**Figure 8**). Follow-up paired-samples *t*-tests revealed that following target

matching cues, EEG responses were significantly more negative contralateral than ipsilateral to the cued location (M = -.68 μV), $t(23)$ = 5.35, p < .001 (**Figure 8C**, green line). Responses were also significantly more negative contralateral than ipsilateral to non-target matching cues (M = -.17 μV), $t(23)$ = 2.89, p = .008 (**Figure 8C**, blue line). N2pc magnitude, however, was significantly larger following target matching cues than following non-target matching cues, $t(23)$ = 5.08, p < .001.

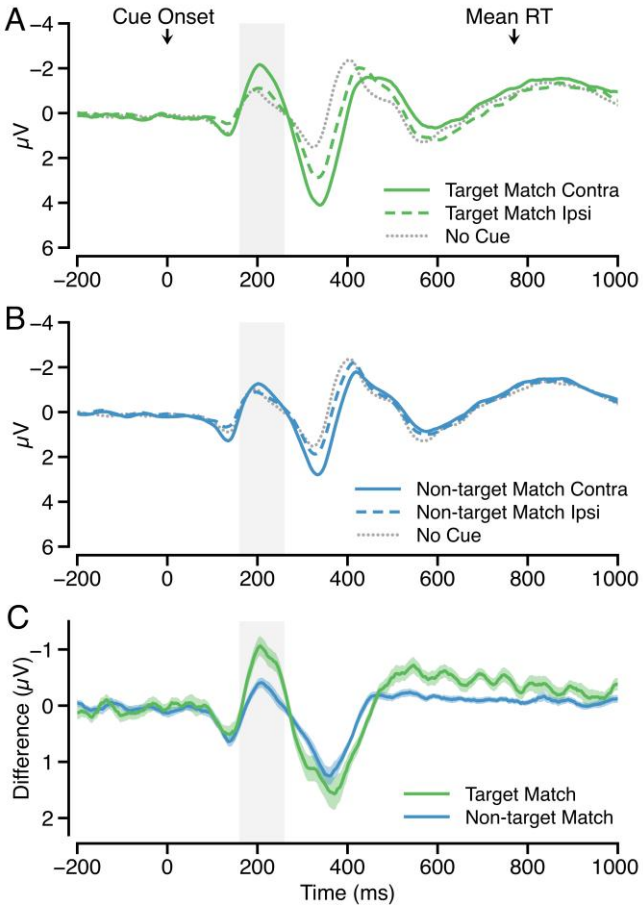

Figure 8. ERP results for Experiment 2. ***A***, Average ERP waveforms recorded at ROIs contralateral and ipsilateral to the target matching cues. The gray line shows

the ERP averaged across both left and right ROIs for the no-cue trials. The shaded region shows the period for analysis. ***B***, As above, but for non-target matching cues. ***C***, Waveforms showing the magnitude of the difference between contralateral and ipsilateral electrodes for each cue condition. Error shading reflects one within-participant SEM (Cousineau 2005; Morey 2008) of the difference between contralateral and ipsilateral responses.

Time-Frequency Analyses

Analysis of non-phase-locked spectral power change from baseline for frequencies from 2-80 Hz yielded results that closely mirrored those of Experiment 1. This revealed a significant power increase across the theta range (3-6.5 Hz) from 39ms post-cue onset in Experiment 2. The very early latency of this response is likely due to temporal smearing inherent to oscillatory analyses interacting with a stronger overall theta response in Experiment 2 versus Experiment 1. There were also significant power decreases in the alpha and beta bands across the 9-26 Hz range, from 109-648ms post cue onset, extending out to 757ms for the alpha frequencies around 10 Hz (**Figure 9**). Finally, there was a significant delta power increase from 2-4 Hz from 695ms until the end of the analysis window.

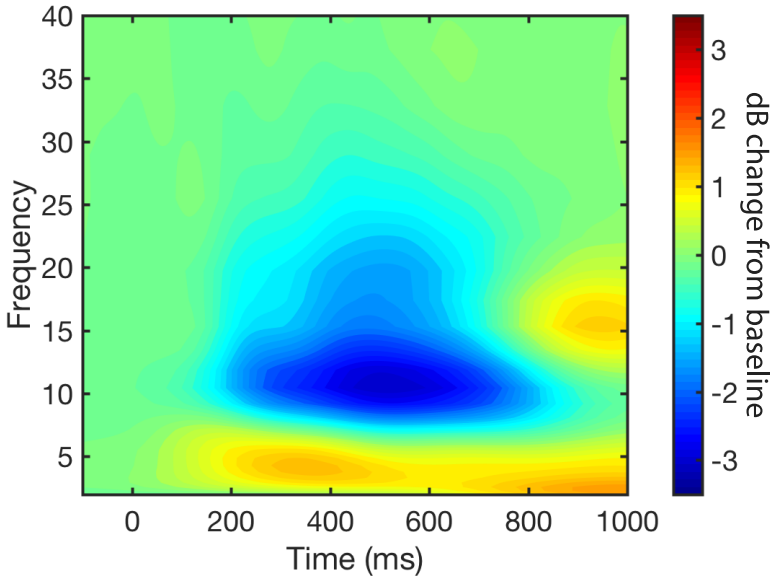

Figure 9. Change in non-phase-locked power relative to baseline (-500 to -200ms) for Experiment 2, averaged across left and right ROIs and averaged across all conditions. Frequency scale is limited to 40 Hz to show low frequency detail. There were no significant effects above 40 Hz.

Analysis of lateralization in the theta band revealed significant LI differences between trials in which the cue was on the target side and when it was opposite the target side, following both target matching and non-target matching cues (**Figure 10**). These differences lasted from 172-383ms after the onset of target matching cues (**Figure 10B**), and from 164-227ms after the onset of non-target matching cues (**Figure 10C**). For both of these cue types, LI values were negative when the cue and target appeared on the same side, indicating greater theta amplitude contralateral to the target side (i.e., contralateral to the cue). LI was

positive when the cue was presented opposite the subsequent target, indicating greater theta amplitude ipsilateral to the target side (contralateral to the cue). To compare the magnitude of theta lateralization for target matching versus non-target matching cues, we computed the average LI difference between same- and opposite-side cues during the period of overlap of their effects (172-227ms), and then compared these between target matching and non-target matching cues. These revealed that the magnitude of theta lateralization was significantly greater following target matching cues (M = 0.08, SD = 0.09) than following non-target matching cues (M = 0.04, SD = 0.05), $t(23) = 2.16$, $p = .042$.

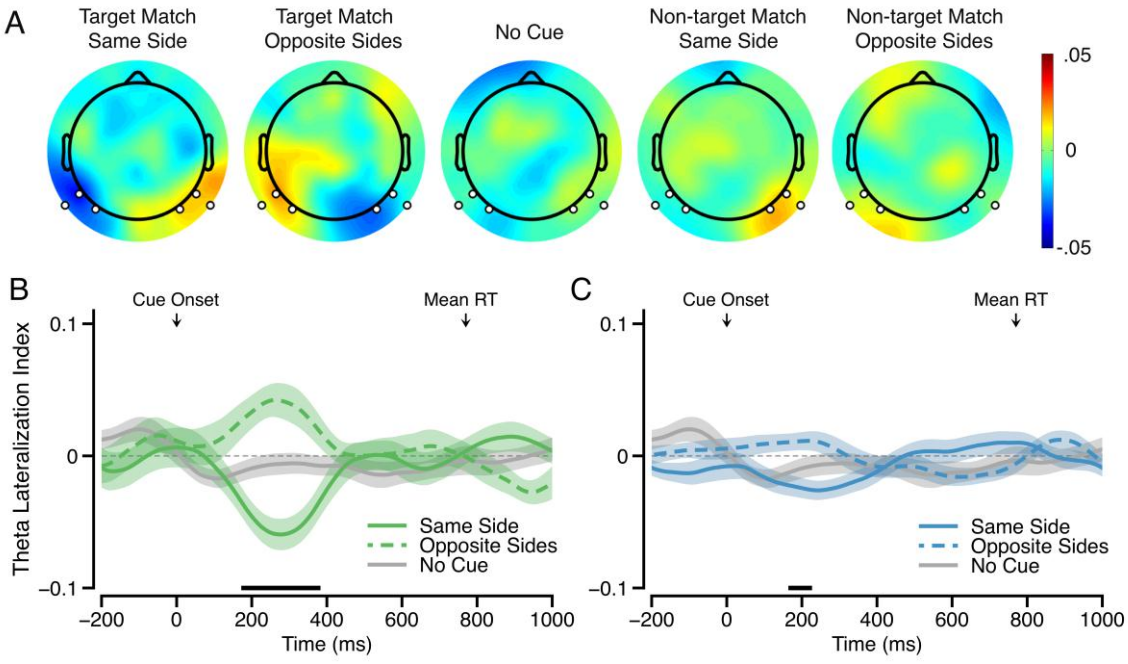

Figure 10. Lateralization of non-phase-locked theta amplitude for Experiment 2. ***A.*** Scalp topographies showing the distribution of non-phase-locked theta

amplitude averaged over the period from 172ms to 227ms post-cue onset. Topographies are presented relative to a target on the left (right-side target trials have had their topography flipped). Thus, in these topographies, 'same side' refers to a cue on the left, and 'opposite sides' refers to a cue on the right. White dots represent analyzed electrodes. ***B&C,*** Non-phase-locked theta lateralization index for trials in which the cue and target appeared in the same visual hemifield (solid colored lines) or in opposite hemifields (dashed colored lines), and for no-cue trials (solid gray lines). Positive numbers indicate greater theta amplitude ipsilateral to the target side. Negative values indicate greater theta amplitude contralateral to the target side. Solid black lines along the x-axis represent significant lateralization differences between Same Side and Opposite Side cue responses ($p < .05$), adjusted to control the false discovery rate (Benjamini & Hochberg 1995). Error shading represents one within-participant SEM (Cousineau 2005; Morey 2008).

Alpha lateralization analysis revealed significant LI differences between trials in which the cue was on the target side and trials in which it was opposite the target side, only following target matching cues (**Figure 11**). These differences lasted from 211-609ms after the onset of target matching cues, followed by a second period of difference from 758-906ms (**Figure 11B**). There were no significant lateralization differences in the alpha response to non-target matching cues (**Figure 11C**). Following target matching cues, alpha LI values were positive when the cue and target appeared on the same side, indicating decreased alpha amplitude contralateral to the target side (contralateral to the cue). LI was negative

when the cue was presented opposite to the subsequent target location, indicating decreased alpha amplitude ipsilateral to the target side (contralateral to the cue). Alpha lateralization averaged over the period of significant lateralization following target-matching cues (211-609ms) was significantly greater following target matching cues (M = -0.08, SD = 0.09) than following non-target matching cues (M = -0.02, SD = 0.05), $t(23)$ = 2.63, p = .015.

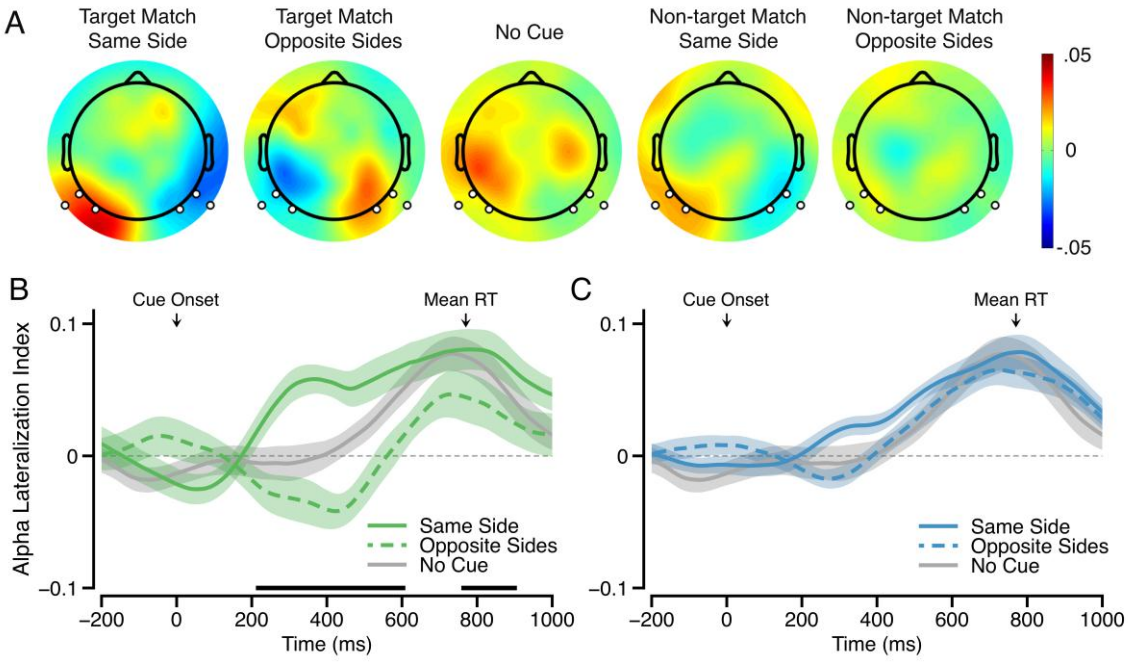

Figure 11. Lateralization of non-phase-locked alpha amplitude for Experiment 2. ***A.*** Scalp topographies showing the distribution of non-phase-locked alpha amplitude averaged over the period from 211ms to 609ms post-cue onset. Topographies are presented relative to a target on the left (right-side target trials have had their topography flipped). Thus, in these topographies, 'same side' refers to a cue on the left, and 'opposite sides' refers to a cue on the right.

White dots represent analyzed electrodes. ***B&C,*** Non-phase-locked alpha lateralization index data for trials in which the cue and target appeared in the same visual hemifield (solid colored lines) or in opposite hemifields (dashed colored lines), and for no-cue trials (solid gray lines). Green lines indicate target matching cue trials. Blue lines indicate non-target matching cue trials. No-cue responses are identical in both plots. Positive numbers indicate greater alpha amplitude ipsilateral the target side. Negative values indicate greater alpha amplitude contralateral the target side. Solid black lines along the x-axis represent significant lateralization differences between Same Side and Opposite Side cue responses ($p < .05$), adjusted to control the false discovery rate (Benjamini & Hochberg 1995). Error shading represents one within-participant SEM (Cousineau 2005; Morey 2008).

Once again, analysis of the beta band produced no significant differences in beta lateralization between cues appearing on the same side as the target compared with cues appearing on the opposite side to the target, for either target matching cues or non-target matching cues (**Figure 12**).

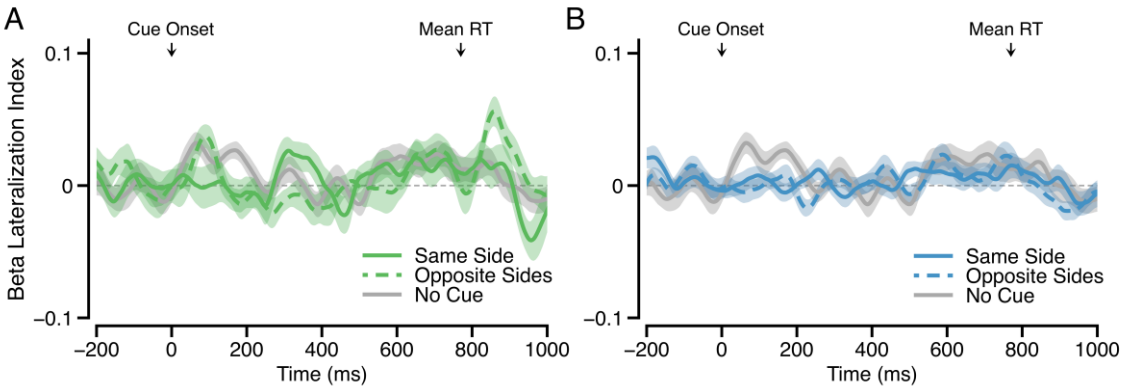

Figure 12. Lateralization of non-phase-locked beta amplitude for Experiment 2. ***A&B,*** Non-phase-locked beta lateralization index for trials in which the cue and target appeared in the same visual hemifield (solid colored lines) or in opposite hemifields (dashed colored lines), and for no-cue trials (solid gray lines). Green lines indicate target matching cue trials. Blue lines indicate non-target matching cue trials. No-cue responses are identical in both plots. Positive numbers indicate greater beta amplitude ipsilateral the target side. Negative values indicate greater beta amplitude contralateral the target side. Error shading represents one within-participant SEM (Cousineau 2005; Morey 2008). Same Side and Opposite Side cues did not produce significant differences in Beta lateralization in either condition.

Discussion

Here we investigated the roles of theta, alpha, and beta oscillations in goal-directed attentional capture. Participants performed a spatial cueing paradigm (Folk, Remington, & Johnston 1992) that allowed us to compare behavioral and neural responses between trials containing uninformative cues that possessed either a goal-relevant feature (the target color) or an irrelevant feature (a non-target color). Across two experiments, we observed the classic pattern of behavioral results (Folk & Remington 1998), showing strong modulation of response times by the location of task-irrelevant cues that matched the target color, and little or no modulation by non-target matching cues. ERPs also showed the typical pattern of

results, with an enhanced negativity contralateral to the location of target colored cues around 200ms post cue onset (the N2pc component; Lien et al. 2008; Luck & Hillyard 1994).

Our analyses of frequency-specific non-phase-locked neural oscillations showed that theta activity was lateralized following both target matching and non-target matching cues, but this lateralization was stronger following the target-matching cues. Alpha activity showed later lateralization, and only following target matching cues. These results suggest active and dissociable involvement of theta and alpha frequencies in goal-directed stimulus processing and attentional allocation. Beta oscillations showed a stimulus related amplitude reduction, but did not show lateralization following any cues, and thus may not be directly involved in the goal-directed allocation of spatial attention. We develop these conclusions in more detail below.

It is important to note that our lateralization results reflect *cue-related* activity specifically, because the analysis method we used normalizes out any temporal smearing from the target period. Temporal smearing is a problem inherent to oscillatory analyses, because it causes neural activity at a particular time-point to have its measured effect spread both

backwards and forwards in time from the time at which the activity occurs. This has the effect of blending oscillatory responses from events that occur close together in time, making them difficult to disambiguate. As noted earlier, however, this concern was avoided in the present study by analyzing lateralized responses produced by the cues, *relative to the normalized locations of the targets*. Thus, differences in cue-related lateralization between trials in which the cue was on the same side as the subsequent target, and trials in which the cue appeared opposite the subsequent target, are independent of any overlapping target-related activity.

Theta oscillations in this study lateralized in response to all color cues, but lateralization was strongest when those cues matched the target color. This is consistent with a role of theta oscillations in feature-based signal enhancement, and distinguishes this response from the well-studied medial-frontal conflict-related theta response, which is typically increased in the presence of *incongruent* stimuli (see Cavanagh & Frank, 2014, for review). The slow cycle of theta oscillations makes it unlikely that their amplitude is modulated rapidly enough to be the driving force behind feature-based response enhancements that occur in visual cortex at very early latencies (Bichot et al. 2005; Zhang & Luck, 2008). Rather, an

amplitude increase in the theta band produced by the presence of goal-relevant features may function to produce stronger temporal grouping of neural signals related to those features in downstream neural populations (Canolty et al. 2006; Liebe et al. 2012). This would effectively serve to strengthen the neural representation of goal-relevant features at downstream cortical areas, biasing competition for subsequent processing in favor of the goal-relevant stimulus (Desimone & Duncan, 1995). This hypothesized function of theta oscillations as carriers of goal-relevant information travelling up the visual hierarchy is consistent with recent work in nonhuman primates showing that theta oscillations are preferentially associated with feedforward signal transmission in the visual cortex (Bastos et al. 2015).

The lateralization of alpha oscillations in this study closely matched the behavioral results: alpha amplitude lateralized following target-matching cues, but showed no lateralization following non-target-matching cues. These results are consistent with the purported role of alpha oscillations in instantiating spatial attention (Capotosto et al. 2009; Händel et al., 2011; Jensen et al. 2012; Klimesch 2012). Furthermore, our results extend on past studies, which have linked alpha oscillations to the voluntary allocation of spatial attention. Here we show for the first time that alpha oscillations are

also involved in the *involuntary* capture of spatial attention by goal-relevant features. The involuntary nature of the attentional capture observed here is supported by several pieces of evidence. First, the cues were irrelevant to the task being performed, and were uncorrelated with the target location. Second, target matching cues were no more frequent than cues of any other color. Finally, both cues and targets were presented equally often at all locations. Thus, there was no incentive for participants to attend to the location of the target matching cues voluntarily, and there were no location biases that could provide an alternative explanation for our results. Furthermore, there is a large body of literature suggesting that under such conditions, target matching cues capture attention involuntarily (e.g., Eimer & Kiss, 2008; Folk et al. 1992, 2002; Zivony & Lamy, 2013), even when the cues occur outside of awareness (Ansorge et al., 2009; Lamy et al., 2014). Thus, the spatial modulation of alpha oscillations in our study, considered beside the evidence linking alpha oscillations to the voluntary allocation of spatial attention (e.g., Doesburg et al. 2016; Thut et al. 2006; Worden 2000), suggests that alpha oscillations may be linked to spatial attention in all its guises, not simply to voluntary attentional allocation.

Interestingly, while we observed a stimulus induced amplitude reduction in

the beta band, this response differed from the alpha response both in its timing and in that it did not lateralize in response to any of the cue conditions. Together these results suggest that alpha and beta oscillations are not simply arbitrary divisions between segments of the same underlying response (Michalareas et al. 2016), but instead are different signals with dissociable functions. Recent work has argued for a role of beta oscillations in the top-down transmission of identity predictions (Sedley et al. 2016), as compared with alpha' s role in spatial attention and prediction. The absence of a lateralized beta response in our experiments may thus reflect the fact that the cues possessed no relevant identity information, and target orientation was deliberately unpredictable from trial to trial.

Previous literature relating neural oscillations to involuntary attentional capture has focused on non-lateralized responses associated with bottom-up attentional capture by salient, goal-irrelevant stimuli (Landau et al. 2007; Mazaheri et al. 2011). One recent study relevant to the current work examined the interaction between spatial and feature-based attention in the lateralized responses of alpha oscillations (van Diepen et al. 2016). When a predictive target color in one visual hemifield was paired with a dissimilarly colored distractor in the opposite hemifield, alpha oscillations

subsequently lateralized such that they were decreased contralateral to the target location. By contrast, when the target-color was paired with a similarly colored distractor in the opposite hemifield, alpha oscillations did not lateralize to reflect the target location. These results suggest that spatial attention-related alpha oscillations lateralize to facilitate processing at locations signaled by the presence of a relevant feature, consistent with the present results. It is important to note, however, that in the van Diepen et al. (2016) study, the goal-relevant color was only ever present in the target display. As such, it is difficult to know whether their results reflect involuntary attentional capture, or the voluntary allocation of attention to locations that may contain a target.

The suggestion that alpha oscillations instantiate spatial attention assumes that alpha oscillations have a causal effect on stimulus processing, as would be required to bring about the behavioral effects commonly associated with spatial cueing manipulations. Several studies have demonstrated that this is in fact the case. For example, the phase of pre-stimulus alpha oscillations (VanRullen 2016) has been shown to influence saccade latency (Drewes & VanRullen 2011), perception of masked stimuli (Mathewson et al. 2009) and stimuli presented at detection threshold (Busch et al. 2009), as well as the probability that transcranial magnetic

stimulation (TMS) of occipital cortex will produce phosphenes (Dugue et al. 2011; Romei et al. 2012). Furthermore, inducing alpha oscillations, either with TMS (Romei et al. 2010), entrainment by flickering stimuli (de Graaf et al. 2013; Mathewson et al. 2010, 2012), or through real-time neurofeedback training (Okazaki et al. 2015), has been shown to modulate stimulus detection. This evidence suggests a causal role for alpha oscillations in perception and cognition.

Conclusions

Here we have shown that theta, alpha, and beta frequencies play dissociable roles in goal-directed visual attention. Across two independent experiments, theta oscillations lateralized to reflect the position of both goal-relevant and goal-irrelevant stimuli. Beta oscillations did not show location-specific responses to any stimuli, and alpha oscillations lateralized in a goal-directed manner. Furthermore, responses in the alpha band closely matched those observed in the behavioral results. These findings clearly demonstrate the involvement of alpha oscillations in involuntary goal-directed attentional capture (Folk et al. 1992; Yantis 1996), extending on previous studies that have been limited to examining the relationship between alpha oscillations and voluntary attentional allocation (Kelly et al. 2006; Thut et al. 2006; Worden et al. 2000).

Conflict of Interest:

The authors declare no competing financial interests

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