Voluntary and involuntary orienting of attention elicit similar lateralized changes in alpha activity and slow potential shifts over visual cortex

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Abstract

There is a common distinction between endogenous attention, which refers to the volitional orienting of spatial attention according to current task goals, and exogenous attention, which is the involuntary orienting to salient events regardless of current goals. Both types of attention can facilitate the sensory processing of information at an attended location, however, *how* they influence visual processing and whether they affect visual-cortical processing in similar or different ways is unknown. In the present study, we sought to directly test this question by comparing event-related potentials (ERPs) and alpha activity (~10Hz oscillations) over visual cortex during the cue-target interval of a series of audiovisual attentional cueing tasks. Across two within-subject experiments including healthy male and female participants, we varied the two main dimensions over which voluntary and involuntary attention tasks typically differ: cue format (centrally vs. peripherally presented) and cue informativity (spatially predictive vs. non-predictive). Our data demonstrate that all of these cues elicit lateralized ERPs over parietal-occipital cortex and also trigger decreases in occipital alpha activity over contralateral sites with respect to the cued location. Critically, the magnitude and time courses of these neural effects differ considerably based upon cue format and informativity, mirroring the time courses of previously reported behavioral effects. While peripheral cues elicit rapid changes in visual cortex, these changes are sustained only when a cue is informative as to a future target's location. Broadly, these data suggest that voluntary and involuntary spatial attention are supported by the same changes in visual-cortical processing, shifted in time.

Significance Statement

The dichotomy between endogenous and exogenous attention is a pervasive concept in the attention literature, yet very few studies have directly compared whether and how they differ in terms of their neural effects on visual processing. Using a novel cross-modal cueing paradigm, we demonstrate that each of these types of attention elicits similar lateralized changes over visual cortex in response to the different attention cues, as evidenced in lateralized ERPs and oscillatory alpha (~10Hz) activity. Importantly, and consistent with previous behavioral results, the time course of these neural changes differs depending on cue format and cue informativity. Overall, this finding implicates changes in alpha activity and lateralized slow-waves of the ERP as universal indices of spatial attention.

Introduction

Selective spatial attention can be deployed endogenously (i.e., voluntarily), following the goals and intentions of an observer, or exogenously (i.e., involuntarily), through capture by a sudden event in the environment such as a bright flash or a salient sound (Reynolds & Chelazzi, 2004; Wright & Ward, 2008). Decades of research have shown that endogenous and exogenous attention result in behavioral benefits at the attended location, reflected in higher accuracy and faster response times in discrimination or detection tasks (Posner, 1980; Posner & Cohen, 1984; for a review, see Carrasco, 2011). However, these behavioral effects typically arise at different timescales, with endogenous attentional benefits emerging slowly and sustaining for an extended time and exogenous attention benefits emerging quickly but disappearing shortly after (with the possibility of behavioral costs thereafter, i.e., inhibition of return; Müller & Rabbit, 1989; Nakayama & Mackeben, 1989; Klein, 2000). Due to these differences in time course and origin (internal goals vs. external events), it is often assumed that these two modes of attention are fundamentally different, involving different neural substrates (Corbetta & Shulman, 2002) and having distinct effects on visual-cortical processing (Hopfinger & West, 2006). However, endogenous and exogenous attention must constantly work together, as we often orient our attention concurrently to physically salient and behaviorally relevant information in our environment. Accordingly, it would be beneficial for both types of attention to exert similar effects on visual-cortical processing.

Previous research has provided some evidence for how spatial attention affects sensory processing to support behavior. For example, several studies have shown that endogenously directing spatial attention enhances visual-cortical processing even prior to the appearance of a target stimulus. There are two particularly strong markers of these cue-triggered changes in

neural activity observed in the electroencephalogram (EEG). One is the occipital alpha rhythm, a 10 Hz oscillation that tends to decrease over occipital areas contralateral to an attended location while increasing at ipsilateral sites (Worden et al., 2000; Kelly et al., 2006; Thut et al., 2006; Green and McDonald, 2010). Another neural marker is a slow-wave in the event-related potential (ERP), termed the Late-Directing Attention Positivity (LDAP; Harter et al., 1989; Hopf & Mangun, 2000; Eimer, Van Velzen, & Driver, 2002; Green & McDonald, 2006). Both of these lateralized changes over occipital cortex emerge relatively late after the onset of an attention cue (typically ~ 500 to 700 ms later), presumably making them unique markers of endogenous attention. However, recent studies suggest that peripheral, non-predictive cues typically used to induce exogenous shifts of spatial attention can also induce changes in the occipital alpha rhythm (Störmer et al., 2016; Feng et al., 2017) and trigger slow positive deflections in the ERP (i.e., McDonald et al., 2013; Störmer, McDonald, & Hillyard, 2019; Feng et al., 2014), possibly resembling some EEG signatures of endogenous attention. Despite these similarities, it is currently unclear how these neural measures relate to each other and attentional orienting more broadly, as they have been studied separately across different participants and different tasks.

We here sought to directly test whether endogenous and exogenous attention elicit similar changes in visual-cortical processing prior to the onset of a target by comparing ERPs and alpha activity over visual cortex during the cue-target interval of an audiovisual attention task. We used auditory cues to orient spatial attention to avoid any confounds of differences in low-level visual processing triggered by different visual cues, allowing us to isolate neural activity related to the orienting of spatial attention. Across two experiments using a within-subject design, we varied the two main dimensions over which endogenous and exogenous attention tasks typically differ – cue format (centrally vs. peripherally presented) and cue informativity (spatially

predictive vs. non-predictive) – while holding all other parameters constant. Overall, our results point to similar influences on visual-cortical processing for both types of attention, in support of a highly cooperative attention system, although the time courses and magnitudes of these effects differ in important ways.

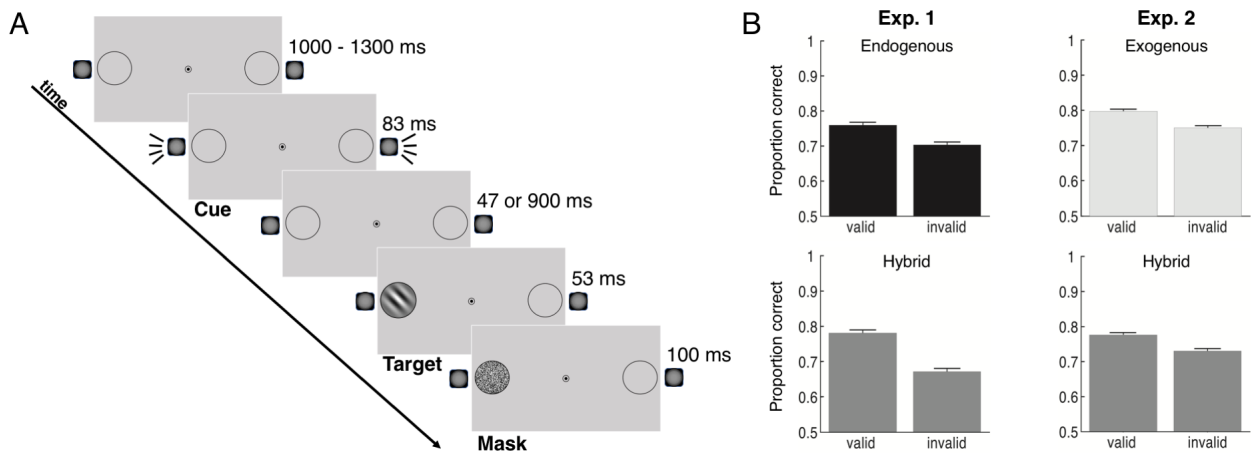

Figure 1. General task design and performance. (A) Participants discriminated the direction of rotation (clockwise or counterclockwise) of a masked Gabor patch target. Prior to the appearance of the target, participants were presented with an auditory cue that was either informative (80% valid) as to the future target's location following a ~1000 ms SOA (Endogenous and Hybrid tasks) or presented randomly just 130 ms prior to the target (50% valid; Exogenous task). This sound was an up-sweeping or down-sweeping tone in the endogenous attention task and a lateral pink noise burst in the hybrid and exogenous attention tasks. (B) Target discrimination accuracy, plotted as a function of cue validity for each of the tasks in Experiment 1 and Experiment 2, clearly reveals a benefit in accuracy at the cued vs. uncued location. Error bars represent ± 1 standard error of the mean.

Method

Participants

Sixteen participants were included in the final sample of Experiment 1 (12 female; mean age of 21.7 years) and another 16 participants were included in the final sample of Experiment 2 (11 female; mean age of 21.9 years). For Experiment 1, data from three participants were

excluded due to excessive artifacts in the EEG (affecting > 33% of trials). Data from an additional participant were excluded due to inability to perform the task (the participant reported seeing two targets of orthogonal orientation at the same location, leading them to report guessing the orientation of the target on every trial). For Experiment 2, data from three participants were excluded due to performance at or below chance level across all conditions (=/<~50% accuracy). An additional two participants did not complete the EEG task due to inability to suppress saccades to the cue and/or target in initial practice tasks.

All participants gave informed written consent as approved by the Human Research Protections Program of the University of California, San Diego and were paid for their time ($10/hour) or received course credit. All participants reported having normal or corrected-to-normal vision and normal hearing. Sample sizes were chosen a priori based upon a number of other studies utilizing similar cross-modal attentional cueing paradigms (McDonald, Teder-Salejarvi, & Hillyard, 2000; Green & McDonald, 2006; Störmer, McDonald, & Hillyard, 2009; McDonald et al., 2013; Feng et al., 2014).

Stimuli and Apparatus

Participants were seated approximately 45 cm in front of a 24” monitor in a sound-attenuated, electrically shielded booth. Stimuli were presented on the screen via the Psychophysics Toolbox in MATLAB (Brainard, 1997; Pelli, 1997). A small black fixation dot (0.5° x 0.5° of visual angle) was always present in the center of the screen, which was otherwise uniformly gray (RGB: 127, 127, 127). A black circle (0.1° x 0.1°) appeared around the fixation dot at the start of each trial to indicate to the participant that the trial had begun. We ran three different tasks across the two experiments that differed only in the type of cues that were

presented. In the hybrid (peripheral-informative cues; Experiments 1 and 2) and exogenous (peripheral-noninformative cues; Experiment 2) attention tasks, the cues were ~83 ms pink noise bursts (0.5–15 kHz, 78 dB SPL) played from external speakers mounted on either side of the computer monitor. The auditory stimuli were played in stereo and their amplitude was adjusted to give the impression that the sounds were emanating from the possible target locations on the screen. In the endogenous attention task (central-informative cues; Experiment 1), the attention cue was either an upward frequency sweep ranging from 750 Hz to 1,000 Hz or a downward frequency sweep from 1,250 Hz to 1,000 Hz, played from both speakers at the same time. The target was a Gabor patch with a spatial frequency of 1.3 cycles/degree, turned either -45° or 45° from vertical. The contrast of the Gabor patch was determined for each participant in a calibration task prior to the main experiment (see below). The target was presented in one of two peripheral locations indicated by a black circle with a diameter of 10° visual angle, centered 31° of visual angle to the left and right of fixation. Each target was followed by a visual noise mask of the same size.

Experiment 1 Procedures

All participants performed two cross-modal attention tasks, outlined in Figure 1A: an endogenous attention task and a hybrid attention task. In both of these tasks, participants were asked to keep their eyes on the central fixation dot throughout each experimental block. A black circle appeared around the central fixation dot at the beginning of each trial, indicating to the participants that the trial had begun. Following the onset of this circle at a variable stimulus onset asynchrony (SOA) of 1,000 – 1,300 ms, an 83-ms auditory attention cue was presented that indicated the location of a subsequent target with 80% validity (Posner, 1980). Participants were

informed about the relationship between cue and target location and were thus instructed to covertly shift their attention to the cued side in anticipation of the target. After a cue-target SOA of 983 ms, a Gabor patch target oriented 45° either clockwise or counterclockwise from vertical was presented at one of the two peripheral locations for 53 ms and was followed immediately by a visual noise mask for 100 ms. The noise mask always appeared at the location of the target to eliminate uncertainty about the location at which the target appeared. Following the noise mask at an ISI of 300 ms, the black circle surrounding the central fixation dot turned white, prompting a response from the participant as to which direction the target was oriented. Participants made this report using the "m" (clockwise) and "n" (counterclockwise) keys.

The hybrid and endogenous attention tasks differed only in the type of auditory cue presented. In the hybrid attention task, the cue was a pink noise burst presented at either the left or right speaker. The location of the cue indicated where the target was likely to appear. In the endogenous attention task, participants were presented with an up-sweeping or down-sweeping tone on each trial. The direction of the frequency sweep of that tone (up or down) indicated where the target was likely to appear on that trial (left or right; cf., Störmer, Green, McDonald, 2009). The sweep-direction-to-location mapping of this cue was counterbalanced across participants, such that the up-sweeping tone indicated that the target was likely to appear on the right side for half of the participants and the left side for the remaining half of participants. These different cue formats were chosen in order to dissociate the purported endogenous and exogenous components of attention; while the peripheral noise burst involved aspects of both exogenous and endogenous spatial attention tasks (i.e., peripherally presented and spatially predictive), the centrally presented sweeping tone involved aspects of only the traditional endogenous spatial attention tasks (i.eg., symbolic central cues that are spatially predictive). All

trial types were randomly intermixed, but the task performed (hybrid vs. endogenous) was blocked and the order counterbalanced between participants, such that half of the participants started with the endogenous attention task and the remaining half started with the hybrid attention task. Participants performed 7 consecutive blocks of 48 trials for each task (14 blocks overall), after completing 32 practice trials in each task. An additional short practice block (24 trials) was performed prior to the endogenous attention task in order to familiarize participants with the symbolic auditory cues. In this practice task, participants were presented the up-sweeping and down-sweeping tones and asked to report the side on which the cue indicated the target would be likely to appear, in the absence of any visual information on the screen.

Prior to the experimental tasks, task difficulty was adjusted for each participant using a thresholding procedure that varied the contrast of the Gabor patch target to achieve about 75% accuracy (i.e., QUEST; Watson & Pelli, 1983). In this thresholding task, participants discriminated the direction of the 45°-oriented Gabor patch in the absence of any sounds. Each participant performed 72 trials of the thresholding task and the individual contrast thresholds were used for the main experiment.

Experiment 2 Procedures

Participants performed both the hybrid and exogenous attention tasks in Experiment 2. The hybrid attention task was identical to the task described in Exp. 1 procedures. The exogenous attention task differed in three ways from the hybrid attention task. First, instead of being informative as to where a future target would appear, the cue of the exogenous attention task was presented randomly at the left or right side and did not carry any spatial information about the target. Consequently, participants were instructed to ignore the cue because it would

not be informative to the task. Second, the cue-target stimulus-onset asynchrony (SOA) in the exogenous task was much shorter than in the hybrid attention task (130 ms vs. ~1000 ms) in order to eliminate any effects of endogenous attention and maximize the effects of exogenous attention. Third, a target was only presented on a randomly selected 50% of trials in the exogenous attention task. This was done in order to separate the neural activity elicited by the uninformative peripheral cue and the target, which would otherwise overlap given the short SOA. This design allowed us to isolate neural activity elicited by the cue without the contamination of activity elicited by the visual target. Thus, the analysis of behavioral performance was performed only on trials in which a target appeared and the analysis of EEG activity was performed only on trials in which a target did not appear (i.e., cue-only trials). On the trials in which a target was not presented, participants were asked to keep their eyes on the central fixation dot and prepare for the next trial. All trial types were randomly intermixed within each experimental block. The hybrid attention task consisted of 7 consecutive blocks of 48 trials each, whereas the exogenous attention task consisted of 7 consecutive blocks of 96 trials each in order to collect a comparable number of ERP epochs and behavioral trials for the analysis across both tasks. Note that each experimental block took approximately the same amount of time since the trial time was much shorter in the exogenous attention task. Prior to performing either of the tasks, task difficulty was adjusted for each participant using the thresholding procedure described in Exp. 1. Following this thresholding procedure, participants performed the hybrid and exogenous attention tasks in an order counterbalanced across all participants. Participants performed 32 practice trials prior to each task.

EEG Recording and Analysis:

Electroencephalogram (EEG) was recorded continuously from 32 Ag/AgCl electrodes mounted in an elastic cap and amplified by an ActiCHamp amplifier (BrainProducts, GmbH). Electrodes were arranged according to the 10-20 system. The horizontal electrooculogram (HEOG) was recorded from two additional electrodes placed on the external ocular canthi which were grounded with an electrode placed on the neck of the participant. The vertical electrooculogram was measured at electrodes FP1 or FP2, located above the left and right eye, respectively. All scalp electrodes were referenced to the right mastoid online and were digitized at 500 Hz.

Continuous EEG data were filtered with a bandpass (butter filter) of 0.01-112.5Hz offline. Data were epoched from -1,000 ms to +2,000 ms with respect to the onset of the auditory cue. Trials contaminated with blinks, eye movements, or muscle movements were removed from the analysis. Artifacts were detected in the time window -800 to 1,100ms in two steps. First, we used automated procedures implemented in ERPLAB (Lopez-Calderon & Luck, 2014; peak-to-peak for blinks, and a step function to detect horizontal eye movements at the HEOG channel). Second, for each participant, each epoch was visually inspected to check the automated procedure and the trials chosen for rejection were updated (cf., Störmer, Alvarez, & Cavanagh, 2014). Artifact-free data was digitally re-referenced to the left mastoid. For the endogenous and hybrid attention tasks, all trials were included in the EEG analysis. For the exogenous attention task, only trials with no target stimuli were included to avoid overlap of the target-elicited neural activity with the cue-elicited neural activity.

ERPs elicited by the left and right noise bursts were averaged separately and were then collapsed across sound position (left, right) and hemisphere of recording (left, right) to obtain waveforms recorded ipsilaterally and contralaterally relative to the sound. The ERPs elicited by

the central cues (up- and down-sweeping tones) were averaged separately for attend-left and attend-right conditions and then also collapsed across hemisphere and hemifield. ERPs were low-pass filtered (half-amplitude cutoff at 25 Hz; slope of 12dB/octave) to remove high-frequency noise. Mean amplitudes for each participant and condition were measured with respect to a 200 ms prestimulus period (-200 to 0 ms from cue onset), and mean amplitudes were statistically compared using both repeated-measures Analyses of Variance (ANOVAs) and paired t-tests (contralateral vs. ipsilateral to attended location). Our analysis was focused on two ERP components that have previously been associated with exogenous and endogenous spatial attention. In particular, we examined the Auditory-Evoked Contralateral Occipital Positivity (ACOP) as an index of exogenous attention (McDonald et al., 2013), and the Late-Directing Attention Positivity (LDAP) as a signature of endogenous attention (Harter et al., 1989; Eimer et al., 2002; Green & McDonald, 2006). The exact time windows and electrode sites for each ERP analysis were chosen a priori based on previous research and matched across all analyses. Both ERP components were measured at the same four parietal-occipital electrode sites (PO7/PO8/P7/P8), but in different time windows. The ACOP was measured between 260-360 ms (McDonald et al., 2013), while the LDAP was measured between 500 - 800 ms (Green & McDonald, 2006). Additional pairwise comparisons (contralateral vs. ipsilateral) were performed on successive 50 ms sections of the ERP in order to better characterize the time course of these positive deflections in each task (cf. McDonald & Green, 2008; Störmer et al., 2009).

For the time frequency analysis, scalp channels were analyzed via complex Morlet wavelets before averaging, following the methods of Lakatos et al. (2004) and Torrence and Compo (1998). Spectral amplitudes were calculated via four-cycle wavelets at 60 different frequencies increasing linearly from 2 to 40 Hz separately for each electrode, time point (every 2

ms), attention condition (left, right), and participant. Spectral amplitudes were then averaged across trials separately for each condition and participant, and a mean baseline of −350 to –150 ms from cue onset was subtracted from each time point for each frequency separately (Pitts, Padwal, Fennelly, Martínez, & Hillyard, 2014; Störmer et al., 2016). Mean spectral amplitudes elicited by the left and right noise bursts (exogenous and hybrid attention tasks) and left-and right-directing central tones (endogenous attention task) were then collapsed across cued location (left, right) and lateral position of the electrode (left, right) to reveal attention-induced modulations ipsilateral and contralateral to the cued location. The statistical analysis was focused on alpha-band amplitude modulations over the range of 8 – 13 Hz at parietal-occipital electrode sites (PO7/PO8/P7/P8) and during the same time intervals as the ACOP (260 – 360 ms) and LDAP (500 – 800 ms) components. Replicating the ERP analysis, pairwise comparisons were performed on successive 50 ms sections of the average alpha-band amplitude values (i.e., average amplitude of oscillatory activity across 8-13 Hz) of the ipsilateral and contralateral hemispheres in each task. Data processing was carried out using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) toolboxes and custom-written scripts in MATLAB (The MathWorks, Natick, MA).

Topographical maps

To illustrate the scalp distribution of the different ERP and time-frequency measures, we created topographical maps using spline interpolation of the voltage differences between the contralateral and ipsilateral hemispheres for each of the time windows of interest. Specifically, the contralateral-minus-ipsilateral ERPs and alpha activity difference were calculated for homologous left and right electrode sites (e.g., PO7 and PO8), with the values at midline

electrode sites (e.g., POz) set to zero (Störmer et al., 2009). These difference voltage topographies were projected to the right side of the head.

Statistical Analyses

Behavior was analyzed by comparing accuracy (% correct) in the Gabor discrimination task separately for when the Gabor patch appeared at the cued location (valid trials) vs. at the uncued location (invalid trials). Behavioral and EEG data were statistically analyzed using paired t-tests and repeated-measures ANOVAs (alpha = 0.05) using MATLAB (The MathWorks, Natick, MA). In order to control for spurious results in the time window analyses of the EEG data, a statistical difference between the activity of each hemisphere in a time window was only considered reliable if it was significant and was a part of a cluster of four or more significant time windows (i.e., there were 4 or more consecutive time windows with $p < .05$; Luck, 2014).

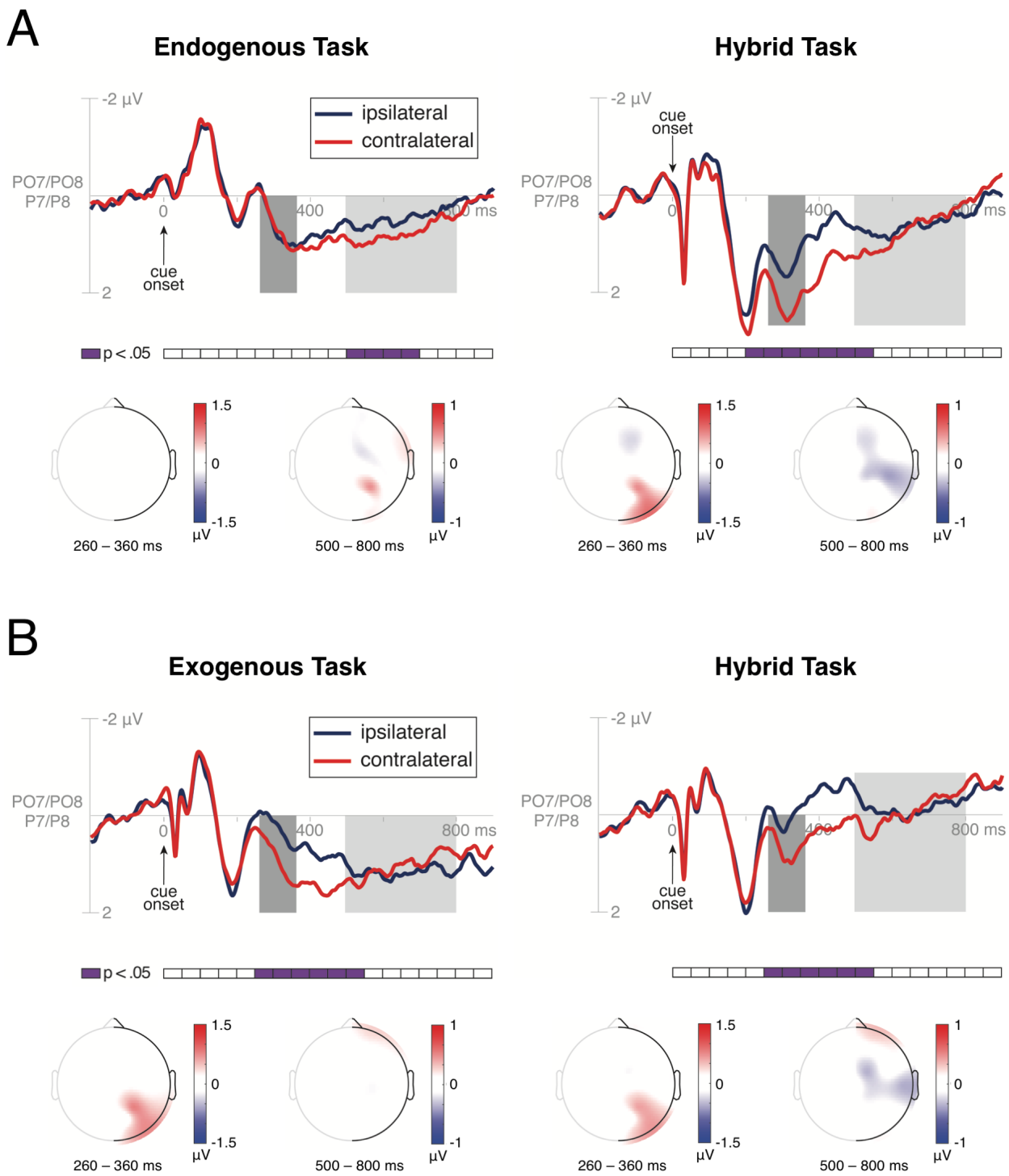

Figure 2. Grand-average ERP waveforms and topographies. ERPs at occipital scalp sites (PO7/PO8/P7/P8) were collapsed over left- and right-cue conditions and left and right hemispheres to obtain waveforms recorded ipsilaterally and contralaterally to the cued location. A priori defined ACOP and LDAP time windows are highlighted in dark gray and light gray,

respectively. Statistically significant ($p \leq 0.05$) differences between contralateral and ipsilateral waveforms are denoted in purple below the time axis. Topographical voltage maps show the contralateral-minus-ipsilateral ERP difference amplitudes, projected to the right side of the scalp during the ACOP and LDAP time windows. (A) A significant late positivity (i.e. LDAP) contralateral to the cued location was observed in response to the symbolic, central cues of the endogenous attention task of Experiment 1. An earlier contralateral positivity (i.e. ACOP) was observed in response to the informative, peripheral cues of the hybrid attention task. (B) A significant, early contralateral positivity (i.e. ACOP) was observed in response to the informative, peripheral cues of the hybrid attention task as well as the uninformative, peripheral cues of the exogenous attention task of Experiment 2. No LDAP was observed in the tasks containing peripheral sounds.

Results

Exp. 1 Behavior

As shown in Figure 1B, accuracy was higher following valid vs. invalid cues in both the endogenous and hybrid attention task of Experiment 1. In order to confirm the presence of this behavioral cueing benefit in each task, a two-way repeated-measures ANOVA with factors of cue validity (valid or invalid) and task (endogenous or hybrid) was performed. There was no significant main effect of task, $F(1, 15) = 0.15$, $p = 0.70$, $\eta^2 < 0.001$, but there was a significant main effect of cue validity, $F(1, 15) = 39.39$, $p < 0.001$, $\eta^2 = 0.28$, indicating that accuracy was significantly higher following valid relative to invalid cues. Interestingly, the magnitude of the observed behavioral benefits was greater in the hybrid attention task than in the endogenous attention task, as indicated by a significant interaction between cue validity and task, $F(1, 15) = 5.91$, $p = 0.03$, $\eta^2 = 0.03$. Follow-up t-tests confirmed that accuracy was higher following valid than invalid cues in both the endogenous task, $t(15) = 3.45$, $p = 0.004$, $d = 0.86$, and hybrid attention task, $t(15) = 6.12$, $p < 0.001$, $d = 1.53$.

Exp. 1 Cue-elicited ERPs

As shown in Figure 2A, the ERP waveform contralateral to the cued location was more positive than the waveform ipsilateral to the cued location during, and beyond, the ACOP time window (260 – 360 ms) in the hybrid attention task. Conversely, this early positivity was not present in the endogenous attention task. To provide statistical support for these observations, a two-way repeated-measures ANOVA with factors of hemisphere (ipsilateral vs. contralateral) and task (endogenous vs. hybrid) was performed on the ERP waveform during the ACOP time window. This analysis revealed a significant main effect of hemisphere, $F(1, 15) = 11.99$, $p = 0.004$, $\eta^2 = 0.02$, and task, $F(1, 15) = 26.78$, $p = < 0.001$, $\eta^2 = 0.14$, as well as a significant interaction between hemisphere and task, $F(1, 15) = 21.76$, $p < 0.001$, $\eta^2 = 0.02$, indicating that the main effects were driven by differences in the magnitude of the ACOP between tasks. Follow-up t-tests comparing the magnitude of the ipsilateral and contralateral ERP waveforms in each task revealed the presence of an ACOP in the hybrid attention task, $t(15) = 4.52$, $p < 0.001$, $d = 1.13$, but not the endogenous attention task, $t(15) = 0.08$, $p = 0.94$, $d = 0.02$.

Conversely, as can be seen in Figure 2a, a later contralateral vs. ipsilateral positivity (i.e., LDAP) was evident only in the ERP waveform of the endogenous attention task. In order to test for the presence of an LDAP in each task, a two-way repeated-measures ANOVA with factors of hemisphere (ipsilateral or contralateral) and task (endogenous or hybrid) was performed on the ERP waveform during the LDAP time window (500 – 800 ms). The analysis indicated that there was no significant main effect of task, $F(1, 15) = 0.16$, $p = 0.70$, $\eta^2 < 0.001$, nor an interaction between task and hemisphere, $F(1, 15) = 1.48$, $p = 0.24$, $\eta^2 = 0.002$. However, this analysis revealed a marginally non-significant main effect of hemisphere, $F(1, 15) = 3.82$, $p = 0.07$, $\eta^2 = 0.01$. In order to probe this marginal effect further, follow-up t-tests were performed comparing the ipsilateral and contralateral ERP waveforms during the LDAP time window for each task.

These comparisons indicated that there was no reliable LDAP in the hybrid attention task, $t(15) = 0.60$, $p = 0.56$, $d = 0.15$, but did indicate the presence of a significant LDAP in the goal-directed attention task, $t(15) = 2.54$, $p = 0.02$, $d = 0.64$. Altogether, these results indicate that a significant contralateral positivity emerged quickly following the informative, peripheral cue of the hybrid attention task (i.e., ACOP), and that an analogous – albeit smaller – contralateral positivity emerged on a later time frame (i.e., LDAP) following the informative, central cue of the endogenous attention task.

In order to examine the time course of each positivity in more detail, pairwise comparisons were performed on successive 50 ms sections of the ipsilateral and contralateral ERP waveforms of each task. These comparisons indicated the presence of a significant positivity from 200 – 550 ms in the hybrid attention task (i.e., ACOP; all ps < 0.02), and a significant positivity present from 500 – 700 ms (i.e., LDAP; all ps < 0.03) in the endogenous attention task.

Exp. 1 Cue-Elicited Alpha Oscillations

As demonstrated in the contralateral-minus-ipsilateral difference plots of Figure 3A, both the endogenous and hybrid attention tasks elicited lateralized changes in alpha frequency amplitude, such that there was a greater decrease in alpha amplitude over the hemisphere contralateral relative to ipsilateral with respect to the cued location. First, in order to probe the time course of this lateralized alpha oscillatory activity in each task, pairwise comparisons were performed on successive 50 ms sections of the average alpha-band amplitude values of the ipsilateral and contralateral hemispheres in each task. This analysis revealed significant differences in alpha activity between the two hemispheres in the endogenous attention task from

650 – 900 ms (all *p*s < 0.04), with marginally non-significant alpha activity stretching from 900 – 1000 ms (all *p*s < 0.09). In the hybrid attention task, however, significant lateralized alpha activity was present much earlier, lasting from 150 – 1000 ms (all *p*s < 0.04). Second, in order to compare the magnitude of this lateralized alpha activity across tasks, pairwise comparisons were performed on the alpha amplitude difference values (contralateral minus ipsilateral alpha amplitude) of each task in the a priori defined time windows of the ACOP (260 – 360 ms) and LDAP (500 – 800 ms). These comparisons revealed that the amplitude of lateralized alpha activity was higher in the hybrid than endogenous attention task at the early time window, $t(15) = 2.69$, $p = 0.02$, $d = 0.67$; this difference remained present numerically at the later time window (500-800 ms), but was marginally non-significant then, $t(15) = 1.92$, $p = 0.07$, $d = 0.48$. In sum, these results reveal the presence of lateralized alpha activity following informative cues, with this activity emerging more quickly and with greater magnitude following peripheral vs. central informative cues.

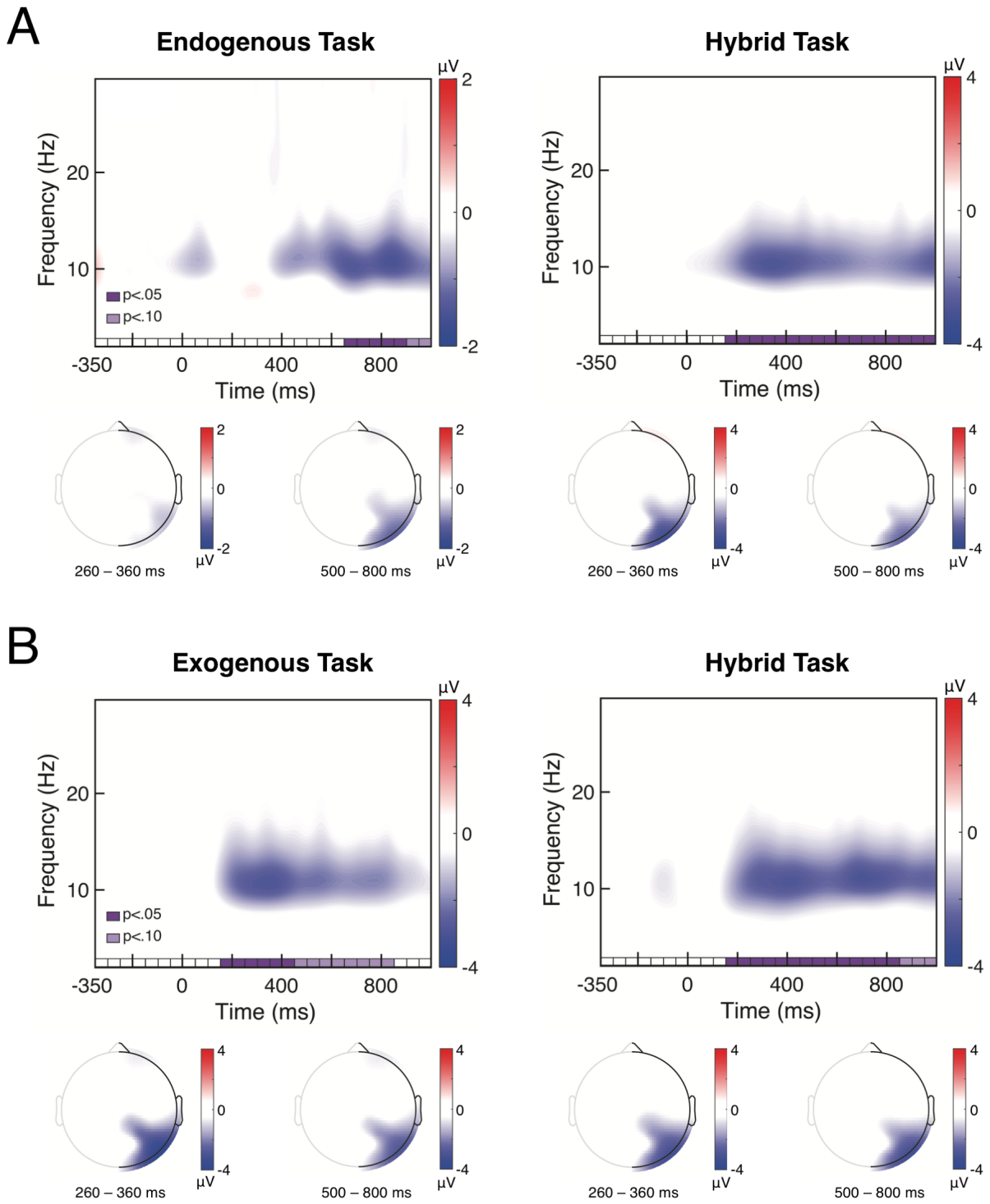

Figure 3. Grand-average time frequency plots of the contralateral-minus-ipsilateral activity over parietal-occipital scalp (PO7/PO8/P7/P8) shows clear lateralized alpha-band changes (8–13 Hz). Statistically significant ($p \leq 0.05$; dark purple boxes) and near-significant ($p \leq 0.10$; light purple boxes) differences between contralateral and ipsilateral alpha amplitude are denoted on the time

axis. Topographical voltage maps show the contralateral-minus-ipsilateral alpha-band difference amplitudes, projected to the right side of the scalp, during the pre-defined ACOP and LDAP time windows. (A) Lateralized and sustained decreases in contralateral (relative to ipsilateral) alpha-band amplitude emerged following both the symbolic, central cues of the endogenous attention task and the informative, peripheral cues of the hybrid attention task of Experiment 1. (B) Contralateral decreases in alpha-band amplitude emerged rapidly following both the informative, peripheral cues of the hybrid attention task and the uninformative peripheral cues of the exogenous attention task of Experiment 2. Topographical maps show a clear contralateral occipital focus of the alpha changes in all conditions.

Exp. 2 Behavior

As shown in Figure 1B, accuracy was higher following valid vs. invalid cues in both the exogenous and hybrid attention tasks of Experiment 2. Following the analysis strategy of Exp. 1, a two-way repeated-measures ANOVA with factors of cue validity (valid vs. invalid) and task (exogenous vs. hybrid) was performed. This analysis revealed a significant main effect of cue validity, $F(1, 15) = 33.42$, $p < 0.001$, $\eta^2 = 0.09$, confirming that the higher accuracy following valid than invalid cues was reliable. There was no main effect of task, $F(1, 15) = 1.38$, $p = 0.26$, $\eta^2 = 0.02$, nor an interaction between cue validity and task, $F(1, 15) = 0.00$, $p = 0.95$, $\eta^2 < 0.001$, indicating that neither overall task performance nor the magnitude of the observed behavioral cueing benefits differed between tasks. To align the analyses with Exp. 1, we also conducted follow-up paired t-tests which confirmed that accuracy was higher following valid than invalid cues in both the exogenous, $t(15) = 3.87$, $p = 0.002$, $d = 0.97$, and hybrid attention tasks, $t(15) = 3.24$, $p = 0.006$, $d = 0.81$.

Exp. 2 Cue-elicited ERPs

As shown in Figure 2B, the ERP waveforms were more positive over the hemisphere contralateral vs. ipsilateral with respect to the cued location during, and beyond, the ACOP time window (260 – 360 ms) of both the exogenous and hybrid attention tasks, similar to the hybrid

task in Experiment 1. A two-way repeated-measures ANOVA with factors of hemisphere (ipsilateral vs. contralateral) and task (exogenous vs. hybrid) was performed on the ERP waveforms during the ACOP time window. This analysis revealed a main effect of hemisphere, $F(1, 15) = 20.88$, $p < 0.001$, $\eta^2 = 0.07$, indicating a significant difference between the amplitude of the ipsilateral and contralateral waveforms (i.e., ACOP). The magnitude of the ACOP was comparable across both tasks, as there was no significant main effect of task, $F(1, 15) = 0.78$, $p = 0.39$, $\eta^2 = 0.01$, nor an interaction between hemisphere and task, $F(1, 15) = 0.02$, $p = 0.90$, $\eta^2 < 0.001$.

Conversely, as can be seen in Figure 2B, a later contralateral vs. ipsilateral positivity (i.e., LDAP) was not readily evident in the ERP waveforms of either task. In order to test this statistically, a two-way repeated-measures ANOVA with factors of hemisphere (ipsilateral vs. contralateral) and task (exogenous vs. hybrid) was performed on the ERP waveform during the LDAP time window (500 – 800 ms). This analysis confirmed that there was no effect of hemisphere, $F(1, 15) = 0.24$, $p = 0.63$, $\eta^2 < 0.001$, nor an interaction between hemisphere and task, $F(1, 15) = 1.63$, $p = 0.22$, $\eta^2 = 0.002$, indicating that there was no hint of an LDAP. However, there was a significant main effect of task, $F(1, 15) = 24.01$, $p < 0.001$, $\eta^2 = 0.29$, indicating a general difference in average ERP magnitude between the two tasks. Altogether, these results show that a reliable contralateral positivity of comparable magnitude emerged quickly after cue onset (i.e., ACOP), regardless of whether the cue was spatially informative (hybrid task) or uninformative (exogenous task).

To examine the time course of these positivities in more detail, pairwise comparisons were performed on successive 50 ms sections of the ipsilateral and contralateral ERP waveforms

of each task. These comparisons indicated that the ACOP stretched from 250 – 550 ms in both the exogenous attention task (all *p*s < 0.05) and the hybrid attention task (all *p*s < 0.04).

Exp. 2 Cue-Elicited Alpha Oscillations

As demonstrated in the contralateral-minus-ipsilateral difference plots of Figure 3B, cues in both the exogenous and hybrid attention tasks elicited lateralized changes in alpha frequency amplitude, such that there was a greater decrease in alpha amplitude contralateral relative to ipsilateral to the cued location. In order to probe the time course of this lateralized oscillatory alpha activity in each task, pairwise comparisons were performed on successive 50 ms sections of the average alpha-band amplitude values of the ipsilateral and contralateral hemispheres in each task. This analysis revealed significant lateralized alpha activity in the exogenous attention task from 150 – 450 ms (*p*s < 0.04), with marginally non-significant alpha activity stretching from 450 – 850 ms (*p*s < 0.10). In contrast, significant lateralized alpha activity was present in the hybrid attention task from 150 – 850 ms (*p*s < 0.05), with marginally non-significant alpha activity from 850 – 1000 ms (*p*s < 0.07). In order to compare the magnitude of this lateralized alpha activity across tasks, pairwise comparisons were performed on the alpha amplitude difference values (contralateral minus ipsilateral alpha amplitude) of each task in the a priori defined ACOP (260 – 360 ms) and LDAP (500 – 800 ms) time windows. These comparisons indicated that there was not a significant difference in the amplitude of lateralized alpha activity at the early time window, $t(15) = 0.01$, $p = 0.99$, $d = 0.003$, or at the late time window, $t(15) = 1.49$, $p = 0.16$, $d = 0.37$. In sum, these results show that lateralized alpha activity of similar magnitude emerges rapidly (~150ms post cue) following peripheral auditory cues, regardless of

their spatial informativity, but tends to decay earlier (~450ms) when the cue is not informative about the spatial location of a target relative to when it predicts the target location (~850ms).

Discussion

A classic distinction in the attention literature is that between endogenous, or voluntary attention, and exogenous, involuntary attention. The differentiation of these two types of attention is well-motivated, as they are each initiated by different events and have also been shown to differ in terms of their temporal dynamics (Kröse & Julesz, 1989; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989; Cheal & Lyon, 1991). However, despite their differences, it has also been shown that each results in similar behavioral effects – improving perception of stimuli appearing at the attended location relative to unattended locations (for a review, see Carrasco, 2011) – and that similar frontal-parietal brain networks can be engaged in both (Peelen, Heslenfeld, Theeuwes, 2004; but see also, Corbetta & Shulman 2002). Here, we show that both endogenous and exogenous attention exert similar influences on visual-cortical processing in response to a cue and prior to the onset of a target. In particular, we found two neural signatures associated with the orienting of attention initiated by different cue types. First, oscillatory alpha activity was decreased over occipital cortex contralateral to the attended side for both endogenous (voluntary) and exogenous (involuntary) attention, though these changes in lateralized alpha differed in their temporal profile. Secondly, we observed positive deflections over parietal-occipital cortex in the ERP waveforms. We found an early positivity over contralateral occipital cortex in response to salient peripheral cues regardless of their spatial predictability (the ACOP), and a later and relatively weaker positive deflection distributed over parietal cortex in response to central, spatially informative symbolic cues (the LDAP).

Several studies have shown that alpha activity decreases over contralateral occipital cortex with respect to a voluntarily attended location following an attention cue (Worden et al., 2000; Rihs, Michel, & Thut, 2007; Jensen & Mazaheri, 2010; Doesburg, Bedo, & Ward, 2016). These studies used spatial cueing paradigms where a centrally presented symbolic (visual) cue predicted the location of a subsequent visual target. The observed changes in alpha activity have been interpreted as reflecting anticipatory visual-spatial attention signals that prepare visual cortex to bias subsequent inputs in favor of the attended location – and have often been discussed as a hallmark of voluntary attention (Doesburg et al., 2016; Klimesch et al., 1998; Worden et al., 2000; Thut et al. 2006). These lateralized changes in alpha activity emerged on a relatively slow time scale in these studies, implying that spatially specific changes in alpha oscillations may be inherently sluggish and require time to evolve, thereby making them a unique marker of voluntary attention. However, recent evidence points to the possibility of a much more rapid onset of lateralized alpha activity. Using peripheral, salient sounds, it was shown that lateralized changes in alpha oscillations can be induced quickly and can be relatively short-lived (Störmer et al, 2016; Feng et al., 2017; see also, Bacigalupo, & Luck, 2019). Here, by systematically varying the presentation format of the cue and its spatial informativity in a within-subject design, we were able to directly compare changes in alpha activity across voluntary and involuntary attention tasks. The data revealed clear lateralized changes in occipital alpha activity across all tasks. These lateralized alpha changes showed a similar topographical distribution with a clear focus over contralateral occipital scalp sites, suggestive of a common neural source, but they differed in their temporal dynamics across tasks. While lateralized alpha activity emerged quickly following peripheral cues and was already present at about 150ms after the cue, this activity emerged later for symbolic cues (at about 650ms) and persisted throughout the entire

cue-target interval only when the cue was spatially informative. These data point to two important aspects of occipital alpha oscillations. First, alpha activity appears to track spatial attention regardless of how attention was initially allocated. Secondly, the time course of alpha activity is sensitive to both the cue format (peripheral or central) and the spatial informativity (spatially informative or random) of the cue. Overall this indicates that lateralized alpha activity reflects a common effect of spatial attention, regardless of cue type, and suggests that enhanced excitability of visual cortex activity prior to the onset of a target (i.e., a shift of baseline activity) represents a general mechanism of attention.

We also observed similarities in the ERP waveforms in response to the different cues. Peripheral cues elicited a relatively early and transient positive deflection over parietal-occipital cortex contralateral to the cue location that was independent of the cue's spatial informativity (i.e., ACOP), whereas a smaller and later lateralized parietal positivity was observed following the central symbolic cues (i.e., LDAP). These ERP components have been reported previously, and they have each been linked to processes of involuntary and voluntary attention respectively (McDonald et al., 2013; Van Velzen, Forster, & Eimer, 2002). Both of these ERP components appeared as lateralized positive deflections in the ERP waveform; however, they varied substantially in timing and magnitude as well as their topographical distributions. In our tasks, the ACOP was distributed across both parietal and occipital scalp sites, whereas the LDAP showed a clear parietal focus, with no activation over occipital sites (see topographical maps in Fig. 2). While it has previously been proposed that both of these components may reflect the same attentional process, simply shifted in time (Hillyard et al., 2016), the current data suggest that this is not necessarily the case. The parietal focus of the LDAP, together with the finding that it dissipates prior to the onset of the target, is consistent with an account of the LDAP as

indexing the orientation of attention to a symbolically cued location (Green & McDonald, 2006; Nobre, Sebestyen, & Miniussi, 2000; Van Velzen, et al., 2002), rather than accounts that have suggested the LDAP as reflecting the anticipatory biasing of visual processing (Hopf & Mangun, 2000; Kelly et al., 2010). The ACOP, on the other hand, shows activation over parietal and occipital scalp sites, possibly indicating that it reflects a combination of the orienting response and initial biasing in visual cortex (Feng et al., 2014; Hillyard et al., 2016; McDonald et al., 2013). Together, these data suggest that the two ERP components reflect a shared process of attention – the initial orienting response – but that the occipital activation present in the ACOP may also represent early and reflexive biasing of neural activity in visual cortex.

The most prominent and well-established difference between voluntary and involuntary attention is the difference in their timing in affecting behavior (Nakayama & Mackeben, 1989; Müller & Rabbit, 1989). The present results further support these differences and show that the neural effects parallel the time course of behavioral benefits. What then explains these differences in timing? One possibility is that the slower timing of voluntary attention is simply due to the additional processes involved in interpreting the symbolic cue, mapping it to the corresponding target location, and planning the shift of attention to the appropriate location (Hazlett & Woldorff, 2004). Furthermore, the exact timing of these interpretation-and-mapping processes likely varies across trials, and this temporal variability could underlie the differences in magnitude of the peripheral and symbolic cueing effects observed here. Presumably, no such temporal variation occurs during the involuntary orienting of attention – where no additional mapping or planning processes are required. Thus, at this point it is difficult to disambiguate whether the differences in magnitude of ACOP and LDAP and lateralized changes in alpha activity are due to actual differences in the size of the effects on visual-cortical processing, or

whether they are simply a result of larger trial-by-trial variability in attentional shift time for voluntary relative to involuntary attention.

One challenge in comparing the effects of voluntary and involuntary attention is that, by definition, each is triggered by different events (e.g., cue types). Here, to tease apart the effects of different types of attention, we systematically varied cue format (peripheral vs. central) and cue informativity (spatially predictive or not). This was made possible by the inclusion of a novel, hybrid attention task that utilized an informative, peripheral cue – combining properties of cues typically used in voluntary and involuntary attention tasks. This hybrid attention task not only allowed us to disentangle the influence of cue format and informativity, but also represents a more ecologically valid cueing paradigm. In everyday life, salient events are often predictive of objects that we want to pay attention to. As such, it seems particularly adaptive for involuntary spatial attention, which may initially be captured by a salient event, to exert the same influences on visual-cortical processing as later-arriving effects of voluntary attention in order to optimize stimulus selection.

Overall, our data demonstrate that the orienting of spatial attention triggers changes in occipital alpha activity and slow deflections in the ERP waveforms – regardless of cue type. While these cue-elicited effects significantly differ in their time courses, similar to the behavioral effects of voluntary and involuntary attention, they appear strikingly similar in terms of neural processing. This suggests that voluntary and involuntary attention are supported by the same visual cortical biasing mechanisms, and can thus effortlessly work together to promote most effective stimulus processing.

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