

UNIVERSITY OF CALIFORNIA SAN DIEGO

Evaluating Attention's Theoretical Dichotomy: A Comparison of Exogenous and Endogenous
Attention

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requirements for the degree Doctor of Philosophy

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Experimental Psychology

by

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University of California San Diego

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DEDICATION

To the family, friends, and mentors that made this dissertation possible.

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ABSTRACT OF THE DISSERTATION

Evaluating Attention's Theoretical Dichotomy: A Comparison of Exogenous and Endogenous Attention

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Selective attention is a critical cognitive capacity that enables us to navigate our information-dense world, allowing us to focus our limited processing resources on behaviorally relevant information while filtering the irrelevant. A large body of research demonstrates that selective spatial attention can be deployed both endogenously following the internal goals of an observer and exogenously in response to salient events in the environment. These findings have motivated the adoption of a dichotomy in attention between endogenous (i.e., voluntary) and

exogenous (i.e., involuntary) attentional orienting. The purpose of the present dissertation is to offer a critical evaluation of the dichotomy of attention by carefully characterizing and comparing the processes involved in exogenous and endogenous attention. Utilizing psychophysics, EEG, and both cross-modal as well as uni-modal cueing paradigms in which either auditory or visual cues preceded visual targets, I offer a novel approach to evaluate this dichotomy across 3 chapters. Chapter 1 examines whether exogenous attention elicits the same changes in neural activity as endogenous attention. Chapter 2 investigates whether exogenous attention facilitates and suppresses neural processing at cued and uncued locations, respectively, as previously demonstrated in studies of endogenous attention. Finally, Chapter 3 tests whether exogenous attention operates outside of an individual's control, as previously theorized, or whether it is possible to exercise control over this process as in endogenous attention. Altogether, the present dissertation demonstrates that there are striking similarities in the effects of exogenous and endogenous attention upon visual processing, but also important differences that distinguish each type of attention. I conclude with a brief exploration of whether this dichotomy is useful to progressing the study of attention.

GENERAL INTRODUCTION

While the human brain is capable of amazing computational feats, perhaps its most noted characteristic is its limitations. Much of the existing psychological literature is devoted to continuously rediscovering the ways in which human perception, memory, and decision-making are limited. However, in the face of a virtually unlimited amount of information, it is remarkable the extent to which humans effectively navigate their environment. Selective attention is a critical cognitive capacity that enables this ability, allowing us to focus our limited processing resources on behaviorally relevant information while filtering the irrelevant. Research has shown that selective attention can flexibly prioritize certain spatial locations, features, or even moments in time to optimize behavior.

The impact of attention upon our experiences is phenomenologically obvious in our everyday lives. For this reason, its effects were qualitatively described by philosophers and early psychologists well before a subfield of empirical research was devoted to the topic. Gottfried Wilhelm Leibniz, Wilhelm Wundt, and William James each picked out selective attention as a critical determinant of conscious perception; and Helmholtz described attention-mediated changes in his awareness of stimuli from experiments that he ran on himself. As the empirical study of the mind progressed over the next century, prominent models converged on the idea that attention indeed acts as a bottleneck between the sensation of a stimulus and one's response to (or awareness of) that stimulus by filtering irrelevant information while allowing one to focus on relevant information (Broadbent, 1958; Treisman, 1960; Deutsch & Deutsch, 1963).

These seminal studies laid the groundwork for the idea of attention as a mechanism for selecting and filtering information. One piece of evidence for attention as a selective process comes from the Posner cueing paradigm, named for the psychologist Michael I. Posner who

developed the task. In the Posner cueing paradigm, subjects are asked to monitor multiple peripheral locations for the appearance of a single target that must be reported later (Posner, 1980). Critically, prior to the appearance of the target, a cue appears that is meant to draw or direct spatial attention. This cue may be a sudden event at one of the target locations in the periphery (i.e., peripheral) or a central, symbolic stimulus (e.g., arrow) indicating one of the target locations (i.e., central). Regardless of whether these cues were central or peripheral, Posner and others found that targets were detected more quickly and discriminated more accurately when presented at a cued vs. uncued location in a cueing paradigm, indicating that the orienting of attention to a location selectively improves perception at that location (Eriksen & Rohrbaugh, 1970; Eriksen & Hoffman, 1972; Posner, Nissen, & Ogden, 1978; Shaw & Shaw, 1977; Bashinski & Bacharach, 1980; Jonides, 1980; Posner, Snyder, & Davidson, 1980; Downing, 1988). These studies and others revealed that this selective improvement in perception within the focus of attention can be complemented by worsened perception outside this focus, finding that targets presented at uncued locations are detected less quickly and discriminated less accurately than a neutral baseline (i.e., following a spatially non-selective cue; Posner & Snyder, 1975; Bashinski & Bacharach, 1980; Jonides, 1980; Posner et al., 1980; Downing, 1988). Altogether, these studies demonstrated that attention can selectively improve perception at a spatial location, which may result in attenuated perceptual processing at unattended locations.

However, previous research has found a critical distinction in the effects of attention following central and peripheral cues. Whereas peripheral cues direct attention quickly, transiently, and reflexively, central cues direct attention much slower and in a more sustained manner (Müller and Rabbit, 1989; Nakayama and Mackeben, 1989). These differences motivated the adoption of a dichotomy in attention between endogenous (i.e., voluntary) and exogenous

(i.e., involuntary) attentional orienting (Posner & Snyder, 1975; Jonides, 1981; Wright & Ward, 2008). This dichotomy extends beyond behavioral measures, as neuroscientific literature has found further evidence that these two types of attention are at least partially distinct.

Neuroimaging research suggests there are partially separable fronto-parietal networks (Corbetta and Shulman, 2002; Hahn, Ross, & Stein, 2006; Chica, Bartolomeo, & Lupiáñez, 2013) and unique changes in fronto-parietal connectivity (Bowling, Friston, & Hopfinger, 2020) responsible for the neural effects following endogenous and exogenous attentional orienting. Mirroring the differences in the time courses of behavioral changes, electroencephalography (EEG) studies show that exogenous attention seems to affect early visual processing of targets more strongly and endogenous attention tends to affect slightly later processing more strongly (Hopfinger & West, 2006; Busse, Katzner, & Treue, 2008). Altogether, these findings from behavioral and neuroimaging studies implicate a clear dichotomy in the orienting and effects of attention, such that exogenous and endogenous attentional orienting elicit different patterns of behavioral effects and involve dissociable brain areas.

The purpose of the present dissertation is to critically evaluate the dichotomy of attention by carefully characterizing the processes involved in exogenous attention and their relationship to those engaged in endogenous attention. Across 3 chapters, I examine whether exogenous attention elicits the same changes in neural activity as endogenous attention (Chapter 1), whether it facilitates or suppresses neural processing at cued and uncued locations (Chapter 2), and whether – and to what extent – it operates outside of an individual’s control (Chapter 3). By utilizing both EEG and cross-modal cueing paradigms, I offer a novel approach to addressing these unresolved questions. Altogether, the results suggest that, while there are several

similarities between each type of attention, there are indeed critical differences that distinguish exogenous attention from endogenous attention.

Chapter 1 investigates whether there is a strong dissociation between the changes in sensory neural processing elicited by exogenous and endogenous attentional orienting, as theorized by existing literature. To test whether similar neural changes emerge in each type of attention, we conducted two within-subject experiments varying the two main dimensions over which endogenous and exogenous attention tasks typically differ: cue informativity (spatially predictive vs. non-predictive) and cue format (centrally vs. peripherally presented). By employing a cross-modal cueing paradigm in which auditory cues preceded visual targets, we were able to directly measure attention-induced activity over visual cortex without interference by the sensory processing of the cue. Thanks to our novel factorial manipulation and this cross-modal paradigm, we demonstrate that both central and peripheral cues elicit lateralized event-related potentials (ERPs) and oscillatory activity over parietal-occipital cortex, despite demonstrating different time courses based upon the cue's format. Overall, these data indicate that exogenous and endogenous attention result in common neural effects over visual cortex. This suggests that the dissociation between the neural activity elicited in sensory cortex by each type of attention may not be as distinct as previously thought.

Chapter 2 offers a critical test of whether exogenous attention improves perception by enhancing neural activity at attended locations, suppressing neural activity at unattended locations, or a combination of the two. While previous literature suggests that both exogenous and endogenous attention result in facilitation and suppression, this evidence is entirely dependent upon behavioral measures in the exogenous attentional cueing paradigms. Therefore, we sought to investigate whether changes in cue-elicited neural activity mirror the pattern found

in previous behavioral measures. Accordingly, we measured both behavioral performance and cue-elicited neural changes in the electroencephalogram as participants performed a cross-modal cueing paradigm in which a spatially non-predictive auditory cue preceded a visual target, allowing us to clearly measure the effects of attention upon visual-cortical processing. By comparing behavior and neural activity at the cued and uncued locations to a neutral cue baseline (i.e., a cue presented centrally), we discovered that both behavior and attention-mediated changes in visual-cortical activity are enhanced at the location of a cue prior to the onset of a target. However, unlike endogenous attention, exogenous attention seems to neither decrease behavioral performance at the uncued location nor suppress neural activity at an unattended target location relative to the neutral baseline. These results demonstrate an unexpected divergence between exogenous and endogenous attention: whereas previous literature suggests that endogenous attention operates via both facilitation of attended information and suppression of unattended information, we show that exogenous attention operates solely via facilitation of information at an attended location.

Chapter 3 examines whether exogenous attention operates outside of an individual's control, as is assumed by the classic dichotomy of attention, or whether it is possible to exercise control over this process as in endogenous attention. The extent to which each type of attention is under volitional control is a critical factor to defining the dichotomy, therefore this chapter attempted to test the strength of this dissociation by testing whether exogenous attention can be modulated depending on task goals. To do this, we ran 3 online experiments utilizing two tasks: an exogenous cueing paradigm where a random visual cue briefly preceded a masked target and a nearly identical task in which the salient cue was now counter-predictive of where a target would appear. By making the cue counter-predictive of the target location, we hoped to test

whether subjects could quickly overcome or even re-map their reflexive response to the cue – as indexed by response time and perceptual sensitivity. We found that sensitivity (d') was higher at the location of the cue in both tasks, even when the target was very likely to appear on the opposite side of the display. Overall, these studies suggest that exogenous attention indeed operates reflexively and outside of individuals' control, supporting the distinctions drawn by the classic dichotomy.

Altogether, these three chapters demonstrate important similarities and distinctions between exogenous and endogenous attention. By considering exogenous attention and its relationship to endogenous attention, I demonstrate the strengths and weaknesses of the dichotomy of attention as it is typically characterized. Accordingly, the present dissertation highlights the importance of carefully characterizing and comparing the effects of each type of attention together to build a more comprehensive model of spatial attention.

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Chapter 1:

Lateralized alpha activity and slow potential shifts over visual cortex track the time course of both endogenous and exogenous orienting of attention

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Lateralized alpha activity and slow potential shifts over visual cortex track the time course of both endogenous and exogenous orienting of attention



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ABSTRACT

Spatial attention can be oriented endogenously, based on current task goals, or exogenously, triggered by salient events in the environment. Based upon literature demonstrating differences in the time course and neural substrates of each type of orienting, these two attention systems are often treated as fundamentally distinct. However, recent studies suggest that rhythmic neural activity in the alpha band (8–13 Hz) and slow waves in the event-related potential (ERP) may emerge over parietal-occipital cortex following both endogenous and exogenous attention cues. To assess whether these neural changes index common processes of spatial attention, we conducted two within-subject experiments varying the two main dimensions over which endogenous and exogenous attention tasks typically differ: cue informativity (spatially predictive vs. non-predictive) and cue format (centrally vs. peripherally presented). This task design allowed us to tease apart neural changes related to top-down goals and those driven by the reflexive orienting of spatial attention, and examine their interactions in a novel hybrid cross-modal attention task. Our data demonstrate that both central and peripheral cues elicit lateralized ERPs over parietal-occipital cortex, though at different points in time, consistent with these ERPs reflecting the orienting of spatial attention. Lateralized alpha activity was also present across all tasks, emerging rapidly for peripheral cues and sustaining longer for spatially informative cues. Overall, these data indicate that distinct slow-wave ERPs index the spatial orienting of endogenous and exogenous attention, while lateralized alpha activity represents a common signature of visual-cortical biasing in anticipation of potential targets across both types of attention.

1. 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 and Chelazzi, 2004; Wright and 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 and 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 attentional benefits emerging quickly but disappearing shortly after (with the possibility of behavioral costs thereafter, i.e., inhibition of return; Müller and Rabbit, 1989; Nakayama and 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.

This dissociation is supported by other evidence demonstrating that different neural substrates are involved in each type of attention, with partially separable fronto-parietal networks being responsible for the exogenous and endogenous orienting of attention (Corbetta and Shul-

man, 2002; Hahn et al., 2006; Chica et al., 2013) and unique changes in fronto-parietal connectivity emerging following each type of orienting (Bowling et al., 2020). There is also evidence that the changes in visual-cortical activity resulting from the orienting of attention differ between these two systems. For example, human electrophysiological studies suggest that early visual-cortical processing is affected differently depending upon how attention is deployed. Exogenous attention seems to affect early visual processing of targets more strongly, as indexed by changes in the P1 component of the visually-evoked potential that occurs in the first 100 ms following a target; and endogenous attention tends to affect later processing more strongly, as indexed by changes in the N1 and P3 components that consecutively follow the P1 over the next ~200 ms and beyond (Hopfinger and West, 2006). Separate work recording single-unit activity in the macaque middle temporal visual area (i.e., MT) demonstrates a similar pattern of earlier changes in firing rate following the onset of attention-grabbing (i.e. exogenous) cues and later changes following only cues that are relevant to the endogenous orienting of attention – further suggesting that separable mechanisms underlie each type of attention (Busse et al., 2008). These findings corroborate other research demonstrating that only informative cues elicit gamma-frequency EEG activity (Landau et al., 2007), which has been linked broadly to cognitive processes including attention (Tallon-Baudry, 2009). Altogether, findings like these have been

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taken as evidence that exogenous and endogenous attention represent two attention systems that affect sensory processing in different ways (for a review, see [Chica et al., 2013](#)).

However, other recent studies point to some commonalities in how the endogenous and exogenous orienting of attention affect neural processing in early sensory areas even prior to the onset of a target stimulus. Such early-arising similarities seem surprising given that both types of attention are initiated differently (salient bottom-up signals vs. endogenous top-down goals), and would imply that the behavioral benefits are supported by the same neural mechanisms. There are two particularly strong markers of these cue-triggered changes in neural activity observed in the electroencephalogram (EEG). During endogenous attention, the most commonly observed index is lateralized changes in the occipital alpha rhythm, an 8–13 Hz oscillation that tends to decrease over occipital areas contralateral to an attended location while increasing at ipsilateral sites in response to an attention cue. This lateralized decrease in alpha activity has been interpreted as representing the anticipatory biasing of visual-cortical activity in preparation of an impending target ([Worden et al., 2000](#); [Kelly et al., 2006](#); [Green and McDonald, 2010](#)). These changes in alpha activity have been shown to occur in endogenous cueing tasks around the same time as a slow-wave in the event-related potential (ERP), termed the Late-Directing Attention Positivity (LDAP), which has been interpreted as either reflecting anticipatory biasing of visual activity (similar to the alpha changes) or the shifting of spatial attention itself ([Harter et al., 1989](#); [Hopf and Mangun, 2000](#); [Eimer et al., 2002](#); [Green and McDonald, 2006](#); [Störmer et al., 2009b](#)). Both of these lateralized changes over occipital and parietal-occipital cortex typically emerge relatively late after the onset of an attention cue (~ 500 to 700 ms later), in line with the slow time course of endogenous attention. Consequently, changes in alpha activity and the slow potential shift over parietal-occipital areas have both been interpreted as unique signatures of the endogenous orienting of attention. However, a different set of studies provides initial evidence that this might not be the case. These studies show that peripheral, salient sounds sometimes used to induce exogenous shifts of spatial attention can modulate the occipital alpha rhythm ([Störmer et al., 2016](#); [Feng et al., 2017](#)) and trigger slow positive deflections in the ERP – in particular, the Auditory-Evoked Contralateral Positivity (ACOP; [McDonald et al., 2013](#); [Feng et al., 2014](#); [Störmer et al., 2019](#)).

However, to date it is unclear how these alpha changes and slow-wave ERPs found across different studies relate to each other, and whether they represent common mechanisms associated with both types of attention. Given that these neural effects have been studied in very different paradigms using diverse stimuli and separate participants, the inferences that can be made in this regard are limited. A direct comparison of how exogenous and endogenous attention influence neural processing prior to the onset of a target is therefore lacking. Furthermore, and of particular interest to the current study, it is unclear how these changes in neural processing triggered by different cue types interact when both modes of attention are engaged.

To fill this gap, we conducted two within-subject experiments and varied the two main dimensions over which endogenous and exogenous attention tasks typically differ – cue informativity (spatially predictive vs. non-predictive) and cue format (centrally vs. peripherally presented) – while holding all other parameters constant. Across all tasks, we used auditory cues to orient spatial attention to avoid any contamination of visually evoked responses elicited by a visual cue. This allowed us to isolate neural activity related to the effects of the spatial orienting of attention. Importantly, the design also included a hybrid attention task with peripheral cues that were spatially predictive, combining aspects of both exogenous and endogenous attention. Our analysis focused on the temporal dynamics of slow-wave ERPs and lateralized alpha to disentangle processes related to the shifting of spatial attention to a new location, and the resulting biasing of visual-cortical activity, triggered by salient bottom-up cues and top-down attentional goals.

With regards to the ERPs, we were particularly interested in whether the slow positive deflections elicited by endogenous cues (i.e., LDAP) and exogenous cues (i.e., ACOP) reflect shifts of spatial attention, the anticipatory biasing of activity in visual areas, or a combination of the two. Prior functional magnetic resonance imaging (fMRI) research demonstrates that shift-related and biasing-related signals follow distinct time courses and emerge in dissociable situations: shift-related activity emerges transiently and only when attention must be oriented, and biasing-related activity emerges in a sustained manner regardless of whether a shift of attention is prompted by a cue ([Yantis et al., 2002](#)). Consequently, if these ERPs reflect the shifting of spatial attention to a new location, we would expect them to occur transiently. It is also possible that this shift-related activity will emerge earlier for peripheral relative to central cues given the additional time needed for interpretation and mapping of shifts of attention following symbolic cues ([Hazlett and Woldorff, 2004](#)). Alternatively, if these slow positive deflections reflect pre-target biasing of visual-cortical activity or a combination of shifting and pre-target biasing, we would expect them to be present continuously throughout the cue-target interval in tasks where the cues contain reliable information about the location of a future target (endogenous and hybrid task).

With regards to alpha oscillations, we expected lateralized occipital alpha activity to emerge relatively early following exogenous cues and later following endogenous cues ([Feng et al., 2017](#); [Kelly et al., 2006](#)). The main question of interest was whether these alpha changes represent a common process of biasing visual-cortical activity across both types of attention. The hybrid attention task (peripheral, informative cues) allowed us to test this directly. Specifically, if alpha indexes a common biasing process, then we would expect parietal-occipital lateralized alpha activity to be continuously present through both early and late time windows. Alternatively, if there is a discontinuity in this alpha activity or a large change in topography across time (e.g., only occipital or only parietal), then this would suggest that alpha activity indexes separate biasing processes following each type of attentional orienting. In addition, comparing the magnitude and topography of lateralized alpha across exogenous and hybrid attention tasks allowed us to examine the sensitivity of early alpha changes to top-down task goals (i.e., spatial informativity of the cue).

To anticipate our results, we find that lateralized alpha represents a common index of visual-cortical biasing across both modes of attention, but that the slow-wave ERPs – ACOP and LDAP – represent partially differentiable attentional orienting processes.

2. Method

2.1. Participants

Sixteen participants were included in the final sample of Experiment 1 (11 female; mean age of 21.9 years) and another 16 participants were included in the final sample of Experiment 2 (12 female; mean age of 21.7 years). Each of the subjects participated in only one of the experiments. For Experiment 1, 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 an inability to suppress saccades to the cue and/or target in initial practice tasks. For Experiment 2, 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, as 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.

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

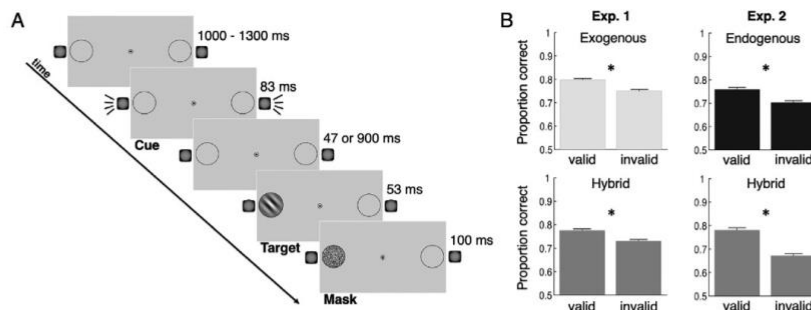


Fig. 1. General task design and performance. (A) Participants discriminated the direction of rotation (clockwise or counterclockwise) of a masked Gabor patch target. Prior to the appearance of the target, participants were presented with an auditory cue that was either presented randomly 130 ms prior to the target (50% valid; Exogenous task), or informative (80% valid) as to the future target's location following a \sim 1000 ms SOA (Endogenous and Hybrid tasks). This sound was a lateral pink noise burst in the hybrid and exogenous attention tasks, and a centrally presented up-sweeping or down-sweeping tone in the endogenous attention task. (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 across all tasks. Error bars represent ± 1 standard error of the mean. Asterisks indicate that there was a significant ($p < 0.05$) difference in accuracy following valid vs. invalid cues in the corresponding task.

vision and normal hearing. Sample sizes were chosen a priori based upon a number of other studies utilizing similar cross-modal attentional cueing paradigms, which reliably found the ACOP, the LDAP, cross-modal cueing effects, and/or lateralized alpha activity with 16 or fewer subjects (Hopf and Mangun, 2000; McDonald et al., 2000; Green and McDonald, 2006, 2008; Störmer et al., 2009a; Green and McDonald, 2010; McDonald et al., 2013; Feng et al., 2017).

2.2. Stimuli and apparatus

Participants were seated approximately 45 cm in front of a 27" 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 ($0.2^\circ \times 0.2^\circ$ of visual angle) was always present in the center of the screen, which was otherwise uniformly gray (RGB: 127, 127, 127). A black circle ($0.4^\circ \times 0.4^\circ$) 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 (informative peripheral cues; Experiments 1 and 2) and exogenous (uninformative peripheral cues; Experiment 1) attention tasks, the cues were \sim 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 (informative central cues; Experiment 2), the attention cue was either an upward frequency sweep ranging from 750 Hz to 1000 Hz or a downward frequency sweep from 1250 Hz to 1000 Hz, played from both speakers and perceived as emanating from the center/entirety of the screen. Across all tasks, 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 $\sim 9^\circ$ visual angle, centered $\sim 28^\circ$ of visual angle to the left and right of fixation. Each target was followed by a visual noise mask of the same size.

2.3. Experiment 1 procedures

In Experiment 1, we compared whether and how the changes in parietal-occipital activity elicited by a peripheral and spatially infor-

mative cue differ relative to a peripheral and spatially uninformative cue usually used in exogenous attention tasks. In other words, these cues were physically identical but differed as to whether they indicated where the target was likely to appear. This allowed us to isolate the rapid effects of exogenous attention upon visual-cortical processing, triggered by reflexive shifts of attention to salient and peripheral cues, from the later effects of endogenous attention, which are triggered only by cues that carry temporal/spatial information about a target. All participants performed two cross-modal attention tasks, outlined in Fig. 1A: the hybrid attention task and the exogenous attention task.

In the hybrid attention task, 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 1000 – 1300 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 \sim 980 ms, a Gabor patch target oriented 45° either clockwise or counterclockwise from vertical was presented at one of the two peripheral locations for \sim 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 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. \sim 980 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 oth-

erwise 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, but the task performed (exogenous vs. hybrid) was blocked and the order counterbalanced between participants, such that half of the participants started with the exogenous attention task and the remaining half started with the hybrid attention task. 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 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 and 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. Participants performed 32 practice trials prior to each task.

2.4. Experiment 2 procedures

In Experiment 2, we compared whether and how the changes in parietal-occipital activity elicited by a peripheral and spatially informative cue differ relative to a central and spatially informative cue usually used in endogenous attention tasks. In other words, these cues conveyed the same information regarding where the target was likely to appear but differed in their physical properties such that only one cue conveyed spatial information itself. This allowed us to isolate the effects of endogenous attention upon parietal-occipital processing, triggered by voluntary shifts of attention to cues that carry temporal/spatial information about a target, from the earlier effects of exogenous attention, which are triggered by salient and peripheral cues that capture attention. All participants performed both the endogenous attention task and the hybrid attention task.

The hybrid attention task was identical to the task described in Exp. 1 procedures. 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 and the location of the cue indicated where the target was likely to appear. In the endogenous attention task, participants were presented with a centrally presented 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 et al., 2009b). 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.e., 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. Prior to performing either of the tasks, task diffi-

culty was adjusted for each participant using the thresholding procedure described in Exp. 1. Participants performed 7 consecutive blocks of 48 trials for each task, 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.

2.5. EEG recording and analysis

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 (butterworth filter) of 0.01–112.5 Hz offline. Data were epoched from –1000 ms to +2000 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 1100 ms in two steps. First, we used automated procedures implemented in ERPLAB (Lopez-Calderon and 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 et al., 2014). To ensure that eye movements were fully removed using this artifact rejection method, we checked for any differences from zero in the HEOG channels separately for leftward and rightward cues. Specifically, we performed one-sample t-tests for the left and right HEOG at each time point (i.e., every 2 ms) in each task and corrected these t-tests for multiple comparisons using a false-discovery rate correction (Benjamini and Hochberg, 1995). We found no statistically significant drifts from baseline at any time points in any of the conditions (all p s > 0.15). Artifact-free data was digitally re-referenced to the average of the left and right mastoid off-line. 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 30 Hz; slope of 12 dB/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; Feng et al., 2014), and the Late-Directing Attention Positivity (LDAP) as a signature of endogenous attention (Harter et al., 1989; Eimer et al., 2002; Green and McDonald, 2006). The exact time win-

dows 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). These electrodes were chosen because they are typically used in ACOP paradigms (McDonald et al., 2013; Feng et al., 2017). Though prior LDAP studies have focused mainly on analyzing activity at PO7/8 (Green & McDonald, 2008; 2010), we included P7/8 to keep analyses consistent across the components. The ACOP was measured between 260 and 360 ms (McDonald et al., 2013), while the LDAP was measured between 500 – 800 ms (Green and McDonald, 2006).

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 et al., 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. Data processing was carried out using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon and Luck, 2014) toolboxes and custom-written scripts in MATLAB (The MathWorks, Natick, MA).

2.6. 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., 2009a). These difference voltage topographies were projected to the right side of the head.

2.7. Statistical analyses

Behavioral and EEG data were statistically analyzed using paired t-tests and repeated-measures ANOVAs ($\alpha = 0.05$) using MATLAB (The MathWorks, Natick, MA). 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). Though the behavioral measure of interest was accuracy, we also analyzed reaction time (i.e., RT) in order to rule out any speed-accuracy trade-offs. To compare accuracy and RT in each task following valid and invalid cues, we performed 2×2 repeated-measures ANOVAs with factors of cue validity (valid or invalid) and task (exogenous/endogenous or hybrid). To compare ERP and oscillatory activity in each hemisphere and task, we performed 2×2 repeated-measures ANOVAs with factors of hemisphere (contralateral or ipsilateral with respect to the cue) and task (exogenous/endogenous or hybrid) on the data separately for each of our time windows of interest (260 – 360 ms and 500 – 800 ms). All but two reported t-tests were planned a priori and were two-tailed and uncorrected and were led by a significant (or marginally non-significant) ANOVA effect or interaction.

The two post-hoc t-tests, performed in the analysis of the LDAP in Experiment 2, are noted as such and corrected for multiple comparisons using a Holm-Bonferroni correction (Holm, 1979).

To investigate the time course of the neural activity across the entire cue-target interval, we also performed a cluster-based permutation test (Maris & Oostenveld, 2007) on the cue-elicited ERP and alpha activity. This analysis allows for the identification of significant and sustained neural activity while controlling for the family-wise error rate. By accounting for the temporal dependence of EEG activity over time and using the data itself to build null distributions, cluster-based permutation tests maintain a great deal of statistical power and do not rely upon any of the assumptions of parametric statistics (see Chapter 13, Luck, 2014). Clusters of lateralized activity were identified by performing paired t-tests comparing the magnitude of neural activity in the hemisphere contralateral vs. ipsilateral to the cue at each time point (i.e. every 2 ms). For each cluster of significant values, which were defined by one or more significant ($p < 0.05$) t-tests of identical sign (e.g., all positive) surrounded by non-significant or opposite-sign tests, we calculated a cluster statistic that was defined as the sum of all t-values in that cluster. The significance of this cluster statistic was evaluated by comparing it to cluster statistic values from permuted data. In particular, we performed a whole-subject permutation test: a completely random subset of the subjects had the activity contralateral vs. ipsilateral to the cue location switched and we then found the cluster statistics for these randomly permuted data sets. We repeated this permutation protocol for 1000 iterations and found the largest cluster statistic in each iteration, whether positive or negative. Iterations yielding no significant clusters were assigned a value of 0. Finally, we found the 2.5th and 97.5th percentile values of these maximum cluster statistics and used these values as our critical cut-off for evaluating the significance of the clusters of neural activity (i.e., equivalent to a two-tailed t-test). If a cluster statistic in the data was more extreme than the 2.5th or 97.5th percentile values, we considered that cluster to be significant. P-values for these significant clusters were calculated by finding what percentage of the 1000 permuted cluster statistics were more extreme (i.e., either more positive or more negative) than the cluster statistic found in the non-permuted data. This was done separately for each task.

3. Results

3.1. Exp. 1 behavior

As shown in Fig. 1B, accuracy was higher following valid vs. invalid cues in both the exogenous and hybrid attention tasks 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. 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.

In order to confirm that these differences in accuracy were not the result of a speed-accuracy trade-off, we also analyzed reaction times (i.e. RTs) to the target. Numerically, we found that RT in the exogenous task was roughly equivalent following valid cues ($M = 1279$ ms, $sd = 997$ ms) and invalid cues ($M = 1291$ ms, $sd = 995$ ms); and RT in the hybrid task was faster following valid cues ($M = 920$ ms, $sd = 543$ ms) than invalid cues ($M = 1029$ ms, $sd = 549$ ms). In order to test whether this pattern held statistically, we performed a two-way repeated-measures ANOVA with factors of cue validity (valid or invalid) and task (endogenous or hybrid) on this RT data. This analysis revealed a significant main effect of cue validity, $F(1, 15) = 7.57, p = 0.01, \eta^2 = 0.001$, but there was no main effect of task, $F(1, 15) = 2.9, p = 0.11, \eta^2 = 0.04$, nor an interaction

between cue validity and task, $F(1, 15) = 1.35$, $p = 0.26$, $\eta^2 < 0.001$. Overall, these findings demonstrate that higher accuracy following the valid vs. invalid cues of each task in Experiment 1 cannot be explained by a trade-off between speed and accuracy, as responses were actually faster following validly cued targets.

3.2. Exp. 1 cue-elicited ERPs

Previous research has proposed that slow positive deflections in the ERP following informative central cues (the LDAP) and salient peripheral cues (the ACOP) may both represent either the orienting of spatial attention itself or the biasing of visual-cortical processing prior to the onset of a target (Hillyard et al., 2016). If these positive deflections do in fact index a common process, we expect to observe positivities of similar topography in both the exogenous and hybrid tasks. However, the expected time course of these ERPs would vary based upon whether the ERPs commonly index the shifting of attention or the biasing of visual cortex itself. Specifically, if these slow potentials reflect the shifting of attention to a spatial location, we would expect to see a positivity of similar time course in response to each of the cues – as attention should be exogenously shifted by the salient peripheral cues regardless of their informativity. Alternatively, if these positivities reflect the anticipatory biasing of visual-cortical activity, we would expect to observe only an early positivity in response to the uninformative cue of the exogenous task and both an early and late (or sustained) positivity in response to the informative cue of the hybrid attention task. Differences in spatial topography between these positivities or departures from the expected temporal patterns of these changes would argue against the interpretation of these positive ERPs as common indices of attentional shifts and/or visual-cortical biasing.

As shown in Fig. 2A, 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. 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, $F(1, 15) = 19.86$, $p < 0.001$, $\eta^2 = 0.01$, 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, $F(1, 15) = 0.99$, $p = 0.33$, $\eta^2 = 0.01$, nor an interaction between hemisphere and task, $F(1, 15) = 0.04$, $p = 0.84$, $\eta^2 < 0.001$.

Conversely, as can be seen in Fig. 2A, 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, $F(1, 15) = 1.07$, $p = 0.32$, $\eta^2 < 0.001$, nor an interaction between hemisphere and task, $F(1, 15) = 1.29$, $p = 0.27$, $\eta^2 < 0.001$, indicating that there was no hint of an LDAP. However, there was a significant main effect of task, $F(1, 15) = 22.61$, $p < 0.001$, $\eta^2 = 0.25$, 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 over occipital and parietal-occipital cortex (i.e., ACOP), regardless of whether the cue was spatially informative (hybrid task) or uninformative (exogenous task). Indeed, the additional cluster-based permutation test indicated that there was a significant difference between the neural activity contralateral and ipsilateral to the cue from 258 – 510 ms in the exogenous task and from 292 – 554 ms in the hybrid task ($ps < 0.001$).

These data argue against an interpretation of the early and late positivities previously observed in exogenous and endogenous attention tasks as common indices of visual-cortical biasing in anticipation of a

target, as there was no late or sustained response to the informative peripheral cues of the hybrid task. However, the emergence of an early positivity (i.e. ACOP) over occipital and parietal cortex in response to each of the peripheral cues suggests that the ACOP may represent a neural index of the shifting of attention and/or the initial and rapid biasing of visual-cortical processing. Notably, this shifting and/or biasing appears to occur regardless of the spatial informativity of the cue and is thus reflexive.

3.3. Exp. 1 cue-elicited alpha oscillations

If lateralized changes in alpha activity are an index of a common process of visual-cortical biasing across exogenous and endogenous attention, then we would expect to observe changes in alpha activity of similar topographies across each of the tasks of Experiment 1. Specifically, based upon prior literature, we might expect to observe a quick but relatively short-lived alpha change in response to the uninformative peripheral cues of the exogenous task and both an early and late (or sustained) alpha change in response to the informative peripheral cues of the hybrid task. Alternatively, if lateralized changes in alpha activity index processes unique to each type of attention, then we would expect to either not observe them in one of the tasks or find large differences in the topography of alpha modulations across tasks, which would suggest separate neural sources.

As demonstrated in the contralateral-minus-ipsilateral difference plots of Fig. 3A, cues in both the exogenous and hybrid attention tasks elicited lateralized changes in alpha frequency amplitude over parietal-occipital cortex, such that there was a greater decrease in alpha amplitude contralateral relative to ipsilateral to the cued location. In order to test whether this lateralized alpha activity was significant in each task, a two-way repeated-measures ANOVA with factors of hemisphere (ipsilateral or contralateral) and task (exogenous or hybrid) was performed on the alpha amplitude data during the ACOP time window (260 – 360 ms) and LDAP time window (500 – 800 ms). The analysis on the data during the ACOP time window indicated that there was a significant main effect of task, $F(1, 15) = 6.79$, $p = 0.02$, $\eta^2 = 0.08$, and a significant effect of hemisphere, $F(1, 15) = 9.18$, $p = 0.01$, $\eta^2 = 0.01$. However, there was not a significant interaction between task and hemisphere, $F(1, 15) = 0.00$, $p = 0.95$, $\eta^2 < 0.001$. The analysis on the data during the LDAP time window revealed a similar pattern. There was a significant main effect of task, $F(1, 15) = 5.62$, $p = 0.03$, $\eta^2 = 0.10$, and a significant main effect of hemisphere, $F(1, 15) = 5.65$, $p = 0.03$, $\eta^2 = 0.003$, but not a significant interaction between task and hemisphere, $F(1, 15) = 0.27$, $p = 0.61$, $\eta^2 < 0.001$. Altogether, these ANOVA results indicate that there was significant lateralized alpha activity of comparable magnitude present in both tasks during both the early and late time windows.

In order to more finely probe the time course of this lateralized oscillatory alpha activity in each task, we performed a cluster-based permutation test comparing alpha-band amplitude values of the ipsilateral and contralateral hemispheres separately in each task. Note that this analysis can provide us with a more detailed picture of the temporal pattern of alpha activity and effectively controls of multiple-comparisons, but may be less sensitive to smaller effects as a result of testing each time point on its own. This analysis revealed significant lateralized alpha activity in the exogenous attention task from 150 – 416 ms ($p = 0.03$); in contrast, significant lateralized alpha activity was present for a longer time period in the hybrid attention task, from 164 – 994 ms ($p = 0.002$). In sum, these results show that lateralized alpha activity of similar magnitude and topography emerges rapidly (~150 ms post cue) following peripheral auditory cues, regardless of their spatial informativity, but decays before the end of the cue-target interval only when the cue is not informative. When the cue predicts target location, however, this lateralized alpha activity sustains robustly for (nearly) the entire cue-target interval.

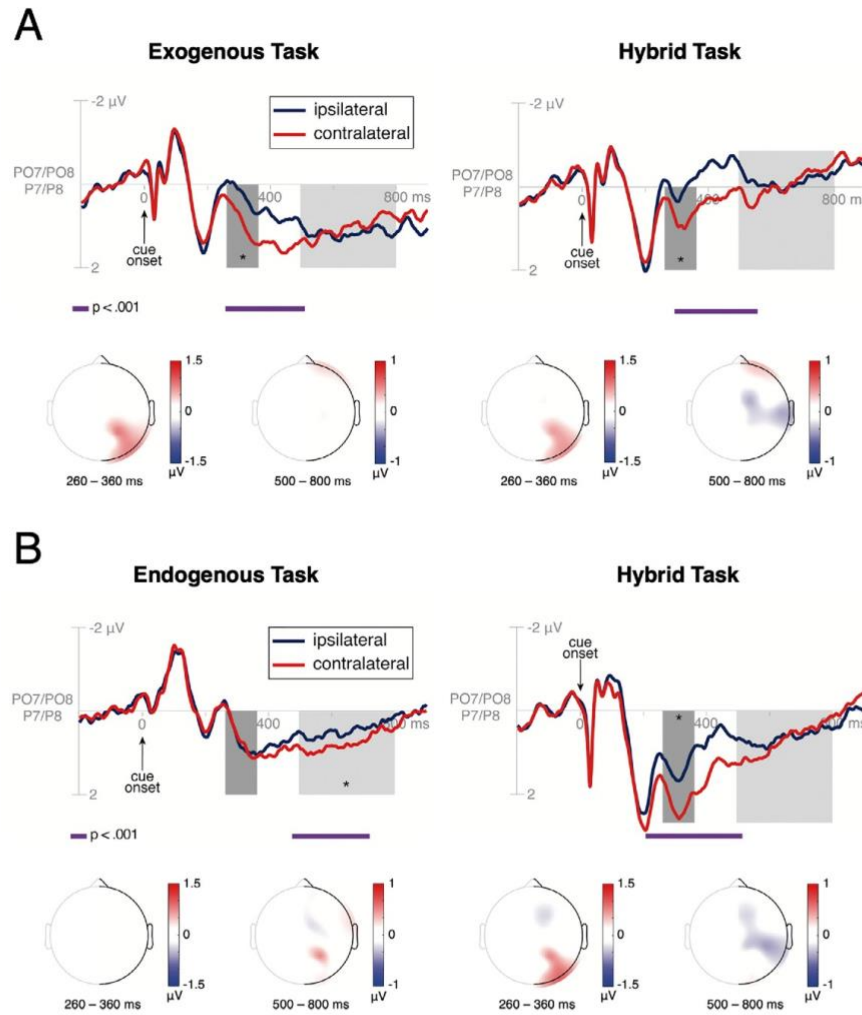


Fig. 2. Grand-average ERP waveforms and topographies. ERPs at parietal-occipital scalp sites (PO7/PO8/P7/P8) were collapsed over left- and right-cue conditions and left and right hemispheres to obtain waveforms recorded ipsilaterally and contralaterally to the cued location. A priori defined ACOP and LDAP time windows are highlighted in dark gray and light gray, respectively. Asterisks in these highlighted areas indicate that there was significant ($p < 0.05$) lateralized ERP activity in the task during that time window. Statistically significant ($p < 0.05$) clusters of lateralized ERP activity are indicated by the dark purple bar at the bottom of each plot. Though we used an alpha value of 0.05 to assess significance, all clusters in our analyses had p-values of less than 0.001 as indicated above. 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, early contralateral positivity (i.e. ACOP) was observed in response to the uninformative, peripheral cues of the exogenous attention task as well as the informative, peripheral cues of the hybrid attention task of Experiment 1. No LDAP was observed in the tasks containing peripheral sounds. (B) 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 2. An earlier contralateral positivity (i.e. ACOP) was observed in response to the informative, peripheral cues of the hybrid attention task.

3.4. Exp. 2 behavior

As shown in Fig. 1B, accuracy was higher following valid vs. invalid cues in both the endogenous and hybrid attention task 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 (endogenous vs. 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

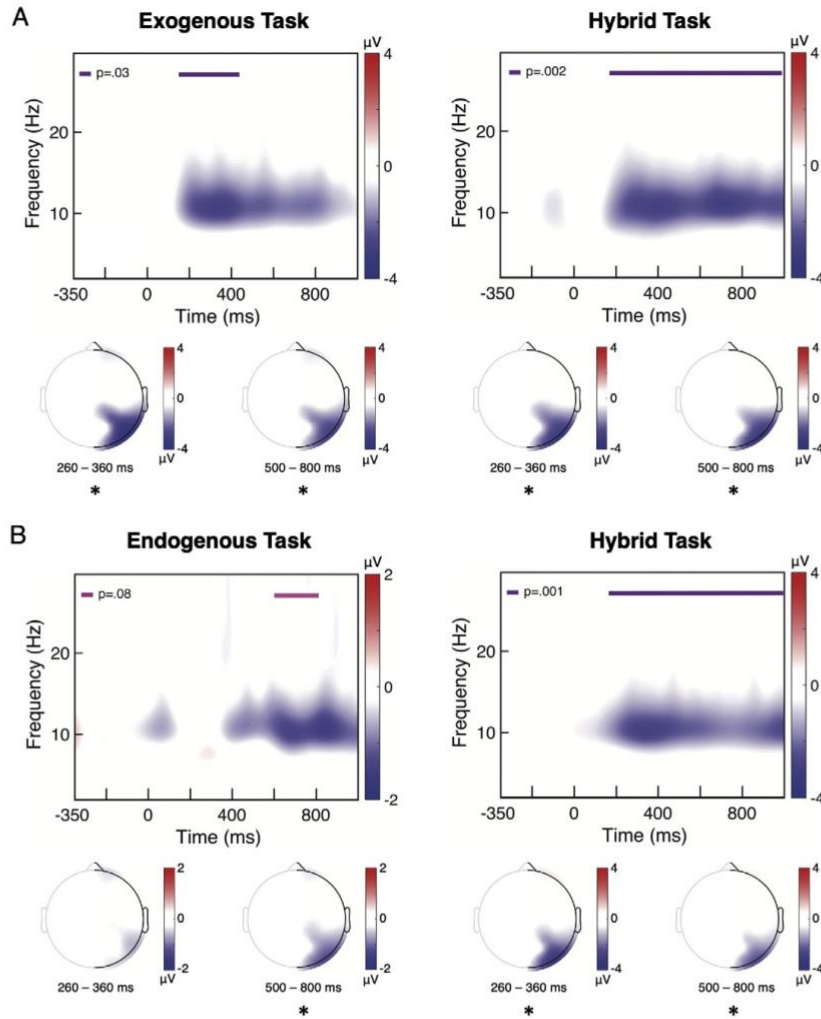


Fig. 3. Grand-average time frequency plots of the contralateral-minus-ipsilateral activity over parietal-occipital scalp (P07/P08/P7/P8) shows clear lateralized alpha-band changes (8–13 Hz). Statistically significant clusters of lateralized alpha activity are indicated by the dark purple bar at the top of each plot and the marginally non-significant alpha activity of the endogenous task is indicated in pink. Though we used an alpha value of 0.05 to assess significance, exact p-values from the cluster-based permutation test are indicated on each plot. 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. Asterisks below these topographies indicate that there was significant ($p < 0.05$) lateralized alpha activity in the corresponding task and time window. (A) Lateralized decreases in contralateral (relative to ipsilateral) alpha-band amplitude emerged rapidly following both the uninformative peripheral cues of the exogenous attention task and the informative, peripheral cues of the hybrid attention task of Experiment 1 but sustained longer during the hybrid attention. (B) Contralateral decreases in 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 2, though at difference time scales. Topographical maps show a clear contralateral occipital focus of the alpha changes in all conditions. Note the difference in the scale of the color bar in the endogenous task vs. other tasks.

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, $t(15) = 6.12, p < 0.001, d = 1.53$.

In order to confirm that these differences in accuracy were not the result of a speed-accuracy trade-off, we analyzed reaction times (i.e. RTs) to the target. Numerically, we found that RT in the endogenous task was faster following valid cues ($M = 923 \text{ ms}, sd = 737 \text{ ms}$) than

invalid cues ($M = 1089 \text{ ms}, sd = 797 \text{ ms}$); and that RT in the hybrid task was faster following valid cues ($M = 842 \text{ ms}, sd = 450 \text{ ms}$) than invalid cues ($M = 1022 \text{ ms}, sd = 564 \text{ ms}$). In order to test whether this pattern held statistically, we performed a two-way repeated-measures ANOVA with factors of cue validity (valid or invalid) and task (endogenous or hybrid) on this RT data. This analysis revealed a significant main effect of cue validity, $F(1, 15) = 10.07, p = 0.01, \eta^2 = 0.02$, but there was

no main effect of task, $F(1, 15) = 0.55$, $p = 0.47$, $\eta^2 = 0.003$, nor an interaction between cue validity and task, $F(1, 15) = 0.04$, $p = 0.85$, $\eta^2 < 0.001$. These findings demonstrate that subjects were generally faster to respond to validly vs. invalidly cued targets, indicating that the higher accuracy following the valid vs. invalid cues of each task in Experiment 2 cannot be explained by a trade-off between speed and accuracy.

3.5. Exp. 2 cue-elicited ERPs

Experiment 1 showed that the ACOP was elicited following peripheral informative and uninformative cues, indicating that the ACOP is robustly triggered by peripheral cues, regardless of their spatial predictability. However, it is unclear whether the ACOP and LDAP both index the shifting of spatial attention to a new location, especially given that the LDAP is usually observed in endogenous tasks using central cues. If this is the case, then we would expect to observe positivities of similar topography in the endogenous and hybrid tasks that differ only in their time course. Differences in spatial topography between these positivities or departures from the expected temporal patterns of these changes would argue against the interpretation of these positivities as common indices of attentional shifting.

As shown in Fig. 2B, 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, replicating Exp. 1. 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, $F(1, 15) = 10.91$, $p = 0.005$, $\eta^2 = 0.003$, and task, $F(1, 15) = 25.34$, $p < 0.001$, $\eta^2 = 0.13$, as well as a significant interaction between hemisphere and task, $F(1, 15) = 15.81$, $p = 0.001$, $\eta^2 = 0.002$, 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, $t(15) = 4.01$, $p = 0.001$, $d = 1.00$, but not the endogenous attention task, $t(15) = 0.70$, $p = 0.49$, $d = 0.18$.

Conversely, as can be seen in Fig. 2B, 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, $F(1, 15) = 0.72$, $p = 0.41$, $\eta^2 = 0.005$, nor an interaction between task and hemisphere, $F(1, 15) = 2.54$, $p = 0.13$, $\eta^2 < 0.001$. However, this analysis revealed a significant main effect of hemisphere, $F(1, 15) = 5.35$, $p = 0.04$, $\eta^2 = 0.002$. In order to probe this effect of hemisphere further, post-hoc t-tests were performed comparing the ipsilateral and contralateral ERP waveforms during the LDAP time window for each task. These comparisons, which were adjusted for multiple comparisons using the Holm-Bonferroni method (Holm, 1979), indicated that there was no reliable LDAP in the hybrid attention task, $t(15) = 0.56$, $p = 0.58$, $d = 0.14$, but did indicate the presence of a significant LDAP in the endogenous attention task, $t(15) = 3.35$, $p = 0.01$, $d = 0.84$.

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 probe the time course of these positivities in each task in more detail, we performed a cluster-based permutation test comparing ERP amplitude values of the ipsilateral and contralateral hemispheres

separately in each task. This analysis revealed significant clusters of lateralized ERP activity in the hybrid attention task from 208 – 514 ms and significant lateralized ERP activity in the endogenous attention task from 474 – 720 ms ($ps < 0.001$).

Together, these data indicate that shifting attention following both peripheral and central informative cues results in a positivity in the cue-locked ERP. However, the time course of this positivity differs based upon the format of the cue – with a much earlier positive deflection emerging following peripheral cues and a relatively late positivity following central cues. Neither of these positivities sustained over the entire cue-target interval, further arguing against an account of the ACOP and LDAP as indices of the sustained biasing of visual-cortical processing. Additionally, these components appear to differ in their spatial topography, with the ACOP showing both occipital and parietal-occipital foci and the LDAP showing only a parietal focus. This difference in topography may imply that each positivity indexes partially differentiable underlying processes, though such qualitative evaluation of topography is limited (see Discussion).

3.6. Exp. 2 cue-elicited alpha oscillations

In Experiment 1 we found that peripheral cues – regardless of their spatial informativity – elicited rapid changes in occipital alpha that sustained contiguously when the cue carried spatial information about the subsequent target, suggesting that lateralized alpha represents a common process underlying exogenous and endogenous attention. However, it is unclear from Experiment 1 whether the later changes in alpha activity observed in the hybrid task are similar to alpha changes elicited by central, symbolic cues typically used in endogenous cueing paradigms. If this is the case, then we would expect to observe late lateralized alpha activity of similar topography in response to informative peripheral and central symbolic cues of the hybrid and endogenous tasks, respectively.

As demonstrated in the contralateral-minus-ipsilateral difference plots of Fig. 3B, 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. In order to test whether this lateralized alpha activity was significant 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 ACOP time window (260 – 360 ms) and LDAP time window (500 – 800 ms). The analysis on the data during the ACOP time window indicated that there was a marginally non-significant main effect of task, $F(1, 15) = 3.58$, $p = 0.08$, $\eta^2 = 0.04$, a significant effect of hemisphere, $F(1, 15) = 8.11$, $p = 0.01$, $\eta^2 = 0.002$, and a significant interaction between task and hemisphere, $F(1, 15) = 9.00$, $p = 0.01$, $\eta^2 = 0.002$. Pairwise t-tests performed to probe this interaction revealed that there was significant lateralized alpha activity following cues in the hybrid attention task, $t(15) = 3.18$, $p = 0.01$, $d = 0.80$, but no significant alpha activity in the endogenous attention task, $t(15) = 0.19$, $p = 0.85$, $d = 0.05$, during the ACOP time window. The analysis on the data during the LDAP time window indicated that there was not a main effect of task, $F(1, 15) = 0.89$, $p = 0.36$, $\eta^2 = 0.008$, but that there was a significant effect of hemisphere, $F(1, 15) = 12.65$, $p = 0.003$, $\eta^2 = 0.001$, and a marginally non-significant interaction between task and hemisphere, $F(1, 15) = 4.21$, $p = 0.06$, $\eta^2 < 0.001$. Pairwise t-tests performed to further probe this marginal interaction revealed that there was significant lateralized alpha activity following cues in the hybrid attention task, $t(15) = 4.05$, $p = 0.001$, $d = 1.01$, and marginally non-significant alpha activity in the endogenous attention task, $t(15) = 2.00$, $p = 0.06$, $d = 0.50$, during the LDAP time window.

Following our previous analysis strategy, we also performed a cluster-based permutation test comparing alpha-band amplitude values of the ipsilateral and contralateral hemispheres separately in each task across time. This analysis revealed significant differences in alpha activity between the two hemispheres in the hybrid attention task lasting

from 154 – 1000 ms ($p = 0.001$), replicating the rapidly emerging and extended alpha activity following the hybrid cues in Exp. 1. The same analysis in the endogenous attention task revealed a marginally non-significant ($p = 0.08$) cluster of lateralized alpha activity that started much later, stretching from 644 – 808 ms. Experiment 2 demonstrates that lateralized alpha activity emerges following informative cues regardless of cue format, but that this activity emerges more quickly and with greater magnitude following peripheral vs. central informative cues. Overall, these data are consistent with the hypothesis that lateralized changes in alpha activity are a general neural marker of visual-cortical biasing following a cue, regardless of cue format or informativity, and are sensitive to both the time course of attentional deployment following a cue and the spatial information carried by that cue.

4. Discussion

A classic distinction in the attention literature is that between endogenous (i.e., voluntary) attention and exogenous (i.e., involuntary) attention. The differentiation of these two attention systems is well-motivated, as they are each initiated by different events, differ in terms of their temporal dynamics, and are implemented in separate (though partially overlapping) brain networks (Kröse and Julesz, 1989; Müller and Rabbitt, 1989; Nakayama and Mackeben, 1989; Cheal and Lyon, 1991; Corbetta and Shulman, 2002; Peelen et al., 2004; Chica et al., 2013). However, despite their differences, they each result in similar behavioral effects: improved perception of stimuli appearing at the attended location relative to unattended locations (for a review, see Carrasco, 2011). Here, we investigated the neural processes underlying each type of attention and asked how they interact to jointly influence behavior. We ran two within-subject experiments that systematically controlled for differences in task design between endogenous and exogenous attentional cueing paradigms by varying only the two main dimensions over which endogenous and exogenous attention tasks typically differ: cue informativity and cue format. By introducing a novel hybrid attentional cue (peripheral, informative cues), we were able to tease apart neural activity related to the shifting of spatial attention and the anticipatory biasing of visual-cortical activity for each type of attention, and also assess their interaction.

Our data reveal that endogenous and exogenous attention exert similar influences over parietal and occipital cortices in response to a cue and prior to the onset of a target. First, oscillatory alpha activity was decreased over occipital cortex contralateral vs. ipsilateral to the attended side following all of the cues. These changes showed a similar contralateral, parietal-occipital focus across the tasks, consistent with the hypothesis that they represent the same visual-cortical biasing in preparation for a potential target (i.e., a baseline shift in cortical excitability). Secondly, we observed positive deflections over parietal-occipital cortex in the ERP waveforms following informative and uninformative peripheral cues (the ACOP) and informative central cues (the LDAP). These slow-wave ERPs differed in terms of spatial topography and magnitude, suggesting that they represent partially distinct processes. Both lateralized alpha and slow-wave ERPs showed different temporal dynamics following each cue type, providing important insights into their functional roles during the deployment of spatial attention. Broadly, our data are consistent with the slow-wave ERPs reflecting the shifting of spatial attention and lateralized alpha activity representing the spatially selective biasing of visual cortical activity that is sensitive to, but does not depend on, endogenous top-down signals.

Several studies have shown that alpha activity decreases over contralateral occipital cortex with respect to a voluntarily attended location following a central attention cue (Worden et al., 2000; Rihls et al., 2007; Jensen and Mazaheri, 2010; Doesburg et al., 2016). The observed changes in alpha activity have been interpreted as reflecting top-down anticipatory visual-spatial attention signals that prepare visual cortex to bias subsequent inputs in favor of the attended location – and have often been interpreted as an important index of endogenous attention in

particular (Klimesch et al., 1998; Worden et al., 2000; Thut et al., 2006; Doesburg et al., 2016). However, recent studies have demonstrated that peripheral, salient sounds can elicit quick but relatively transient lateralized changes in alpha frequency activity, from ~200 to 400 ms after a cue in the absence of any visual information (Störmer et al., 2016; Feng et al., 2017; see also, Bacigalupo, and Luck, 2019). Still, to this point it has been unclear how lateralized alpha observed during endogenous spatial attention tasks relates to the alpha changes triggered by salient peripheral cues. The present results indicate that lateralized alpha can be triggered rapidly by peripheral cues, regardless of their informativity, but sustains throughout the cue-target interval only when a cue carries spatial information about the target. In particular, we found that lateralized alpha activity was already present at about 150 ms after the peripheral cues, but that it emerged later for symbolic cues (at about 475 ms) and persisted reliably throughout the entire cue-target interval only when the cue was predictive of the subsequent target location. Importantly, both early and late lateralized alpha changes were focused over parietal-occipital areas. Though this topographical similarity is only qualitatively assessed in the present study, it may be quantitatively tested in future studies using high-density EEG recording and source localization methods. It is indeed important to note that topographical maps of EEG activity cannot be directly linked to specific neural sources without more intensive source-modeling methods. Regardless, the finding of parieto-occipitally focused EEG activity in all tasks and in both early and late time windows is generally consistent with the hypothesis that lateralized alpha activity indexes a common process of biasing activity in visual cortex even when triggered by distinct cues (Frey, Ruhnau, & Weisz, 2015). This spatially selective pre-activation of visual cortex in anticipation of an impending target stimulus is one of the main principles of the biased-competition model of attention (Desimone and Duncan, 1995), effectively facilitating processing of attended items by biasing neural processing even before any stimulus is presented (Kastner et al., 1999). The present data show that such anticipatory biasing occurs across exogenous and endogenous attention tasks and is possibly implemented by the same mechanism indexed by the occipital alpha rhythm, consistent with other research suggesting that pre-stimulus alpha power modulations may be associated with both exogenous and endogenous spatial attention (Zazio et al., 2020). Thus, these data significantly add to our understanding of occipital alpha oscillations more broadly. First, lateralized alpha over parietal-occipital cortex appears to track the location and time course of both endogenous and exogenous spatial attention. Second, the rapidly emerging portion of alpha – triggered by peripheral cues – is independent of top-down goals, while the later sustained portion is modulated by current task goals.

It is worth noting that lateralized alpha activity following the peripheral, salient cues of the exogenous task appeared to sustain much longer relative to what is expected from the typical time course of exogenous attention. While other studies often found lateralized alpha activity only between ~200–500 ms following peripheral non-predictive sounds (Störmer et al., 2016; Feng et al., 2017), we here found reliable lateralized alpha activity during early (260–360 ms) and late (500–800 ms) time windows. The cluster-based analysis homing in on the exact time course revealed that the later portion of lateralized alpha was less robust than the earlier portion. This may indicate that lateralized alpha activity became weaker in the later time windows, but it could also be the result of a loss of power at later time periods because of increasing noise in the EEG signal over time – though this seems unlikely given the reliable long-lasting effects in the hybrid attention task. In either case, why would lateralized alpha tend to last longer in our current experiment and go beyond the typically observed transient time course of exogenous attention? It may well be the case that this sustained activity is the result of the present task design, in which there was little incentive for subjects to quickly re-orient their attention to the center of the screen in anticipation of the next trial. Thus, it is likely that for some participants – or on some proportion of trials – attention was not

rapidly disengaged from the location of the salient, uninformative cue, but instead lingered at the cued location until the end of the trial. Future studies could address this by designing tasks that require participants to quickly disengage from the cued location to detect or discriminate a target elsewhere in the visual field.

Of particular interest was how these changes in alpha activity interact with each other when both exogenous and endogenous attention are engaged. Our novel hybrid attention task shows that the biasing activity indexed by alpha oscillations can be effectively “handed off” from exogenous to endogenous attention when an attention-grabbing cue also contains task-relevant information. As can be seen in the hybrid task plots of Fig. 3, there is no evidence of a discontinuity in alpha activity following the informative, peripheral cues. Additionally, the topography of this alpha activity remains constant. In other words, it appears that the biasing activity engaged by each system can be effortlessly coordinated when both types of attention are engaged by a novel cue that combines aspects of exogenous and endogenous cueing paradigms.

Indeed, this hybrid attention task not only allowed us to disentangle the influence of cue format and informativity on lateralized alpha activity, 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 exogenous 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 endogenous attention in order to optimize stimulus selection. The cue-elicited alpha activity of the hybrid attention task indicates that endogenous and exogenous attention do indeed work together to orient and sustain attentional biasing at a location. This argues strongly against fully segregated systems underlying each type of attention and demonstrates a novel example of how these two systems may coordinate in the real world.

The present results also illuminate the functional significance of the positive slow-wave ERPs typically observed in response to attentional cues, plotted in Fig. 2. Peripheral cues elicited an early positive deflection from ~200 – 500 ms over parietal-occipital cortex. This deflection was focused contralateral to the cue location and was independent of the cue’s spatial informativity (i.e., ACOP). Analogously, a smaller and later lateralized parietal positivity was observed from ~500 – 700 ms following the central symbolic cues (i.e., LDAP). These ERP components have been reported previously, and they have each been linked to processes of exogenous and endogenous attention respectively (McDonald et al., 2013; Van Velzen et al., 2002). Though both of the ERP components appeared as lateralized positive deflections in the ERP waveform, they varied substantially in timing and magnitude as well as their topographical distributions. Therefore, 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.

In the present study, we found the ACOP to be transient and distributed over both parietal and occipital scalp sites, consistent with attentional shift-related activity (Posner et al., 1984; Yantis et al., 2002); however, the extensive spread of this activity over visual cortex is also consistent with the biasing of visual activity (Yantis et al., 2002). This activation over visual cortex is not present during the LDAP and is not clearly predicted by an account of the ACOP as reflecting the shifting of attention alone. Therefore, this finding suggests that the ACOP uniquely reflects a combination of the shifting of attention and initial biasing in visual cortex (McDonald et al., 2013; Feng et al., 2014; Hillyard et al., 2016). It should be noted that this conclusion is somewhat speculative given the limitations of inference based upon visual inspection of EEG topographies alone, but future studies may seek to critically test this hypothesis by attempting to dissociate these shifting and biasing components of the ACOP with higher density EEG recording and source localization methods. Our results also demonstrate that the ACOP occurs regardless of the top-down significance of a cue. Specifically, in the hybrid attention task, where the peripheral cues were both salient and

informative, the ACOP did not differ in magnitude or time course from the positivity elicited by the uninformative peripheral cues of the exogenous task. The similarity of the ACOP following both informative and uninformative peripheral cues indicates that the ACOP is robust to changes in endogenous attention, offering a novel example of the reflexive nature of exogenous attention.

While the ACOP was distributed across both parietal and occipital areas, the LDAP was evident only over parietal areas and was absent when attention was shifted more quickly by the peripheral and spatially informative cues of the hybrid tasks in Experiment 1 and 2. In sum, we find that the LDAP is transient, does not occur when attention is already shifted, and is focused only over the parietal scalp. These findings are consistent with an account of the LDAP as indexing the shifting of attention to a symbolically cued location (Nobre et al., 2000; Van Velzen, et al., 2002; Green and McDonald, 2006) rather than reflecting the anticipatory biasing of visual processing (Hopf and Mangun, 2000; Kelly et al., 2010). Critically, the sensitivity of the LDAP to whether attention was already deployed exogenously to a location is a further demonstration of how endogenous and exogenous attention cooperate (and sometimes compete) to determine where attention is focused following a cue. Therefore, these findings demonstrate that the ACOP and LDAP likely reflect a shared process of attention – the shifting response to a new location – but that the occipital activation observed in the ACOP may additionally represent early and reflexive biasing of neural activity in visual cortex by exogenous attention.

Across our experiments, both lateralized ERPs and lateralized alpha closely followed the purported time courses of each type of attention. There was a rapid shifting response and transient visual-cortical enhancement (i.e., biasing) following exogenous attentional cues; and there was a relatively later shifting response and later but longer-lasting visual-cortical biasing following endogenous attentional cues. This nicely demonstrates the temporal sensitivities of these neural markers across different spatial attention tasks. However, both the ERPs and later alpha activity also differed significantly in amplitude in each of our tasks. While it is possible that these amplitude differences represent a true divergence between the magnitude of neural activity elicited by endogenous and exogenous attentional cues, it also may be the case that differences in the trial-by-trial temporal dynamics of endogenous vs. exogenous attention explain these differences. Specifically, previous research suggests that the endogenous orienting of attention consists of several additional processes relative to the exogenous orienting of attention: such as interpreting the symbolic cue, mapping it to the corresponding target location, and planning the shift of attention to the appropriate location (Hazlett and Woldorff, 2004). 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, there is much less temporal variation accompanying the exogenous 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, or whether they are simply a result of larger trial-by-trial variability in attentional shift time for endogenous relative to exogenous attention. However, future work manipulating the interpretability of a cue as well as the difficulty of the cue-location mapping process may help to distinguish between these accounts.

Overall, our data demonstrate that the orienting of spatial attention triggers lateralized changes in occipital alpha activity and slow deflections in the ERP waveforms – regardless of whether attention is shifted endogenously or exogenously. By directly comparing exogenous and endogenous attention separately and jointly (using a hybrid task), we were able to show distinct functional roles of the lateralized ERPs, which appear to primarily represent the initial spatial orienting of attention, and lateralized alpha, which reflects the sustained biasing of visual-cortical activity in preparation of an impending target. The finding that lateral-

ized alpha activity emerges following different cue types, albeit at different time scales, suggests that endogenous and exogenous attention are – at least in part – supported by the same anticipatory visual-cortical biasing mechanisms, enabling them to effortlessly work together to promote most effective stimulus processing.

Data availability statement

Preprocessed data and MATLAB scripts re-creating the analyses of main effects in the data are available at <https://osf.io/3gjfik>. Raw data will be available upon reasonable request, made via email to the corresponding author (jmkeefe@ucsd.edu).

Credit authorship contribution statement

Jonathan M. Keefe: Conceptualization, Methodology, Software, Formal analysis, Validation, Investigation, Visualization, Writing - original draft, Writing - review & editing. **Viola S. Störmer:** Conceptualization, Methodology, Software, Formal analysis, Validation, Resources, Visualization, Writing - review & editing.

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Chapter 2:

Cross-modal orienting of exogenous attention results in visual-cortical facilitation, not suppression

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**OPEN** **Cross-modal orienting of exogenous attention results in visual-cortical facilitation, not suppression**Jonathan M. Keefe^{1✉}, Emilia Pokta¹ & Viola S. Störmer^{1,2}

Attention may be oriented exogenously (i.e., involuntarily) to the location of salient stimuli, resulting in improved perception. However, it is unknown whether exogenous attention improves perception by facilitating processing of attended information, suppressing processing of unattended information, or both. To test this question, we measured behavioral performance and cue-elicited neural changes in the electroencephalogram as participants (N = 19) performed a task in which a spatially non-predictive auditory cue preceded a visual target. Critically, this cue was either presented at a peripheral target location or from the center of the screen, allowing us to isolate spatially specific attentional activity. We find that both behavior and attention-mediated changes in visual-cortical activity are enhanced at the location of a cue prior to the onset of a target, but that behavior and neural activity at an unattended target location is equivalent to that following a central cue that does not direct attention (i.e., baseline). These results suggest that exogenous attention operates via facilitation of information at an attended location.

In order to deal with the surfeit of information entering our senses, we can engage spatial selective attention voluntarily based on current goals or orient attention reflexively to a salient event in the environment, which both result in improved perception at the attended location¹. Foundational theories of attention propose that two mechanisms are involved during spatial selection: enhancement of sensory processing at the attended location and suppression of sensory processing at unattended locations^{2,3}. This is based on the idea that visual processing is a strictly limited resource, and that if visual processing is increased at one location then it should be paralleled by a decrease in visual processing elsewhere. Studies of endogenous (i.e., voluntary) spatial attention have used electroencephalography (EEG) to examine neural activity following spatial attention cues, and found that when a location is attended, neural activity in parts of the visual cortex that represent that location is increased relative to other unattended locations even before a target stimulus is presented (e.g.,⁴). Several studies have argued that these preparatory biasing signals not only reflect neural enhancement of attended regions, but also suppression of unattended areas prior to target presentation^{5–9}. More recently, a similar effect on visual-cortical processing was observed during the exogenous orienting of attention. Following peripheral salient sounds that reflexively oriented attention to the left or right side of space, neural activity was increased over the occipital cortex contralateral to the sound's location relative to ipsilateral, even prior to or in absence of visual targets¹⁰. Given that these peripheral sounds were completely random—predicting neither the occurrence, timing, nor location of a target¹⁰—this lateralized neural activity has been interpreted as representing the reflexive enhancement of visual processing following the exogenous orienting of attention at the location of the cue¹¹. However, based on this relative difference in neural activity between the hemispheres, it cannot be distinguished whether this modulation reflects signal enhancement at the attended location, suppression of the unattended location, or a combination of the two. Thus, while many studies have attempted to tease apart mechanisms of enhancement and suppression during endogenous attentional orienting, research on how exogenous attention modulates neural activity following a salient cue is lacking.

We addressed this issue by adapting a cross-modal cueing paradigm to include a baseline ‘no-shift’ cue that allowed us to isolate neural activity related to the attended and unattended locations. Prior behavioral studies have used such baseline cues to separate behavioral benefits and costs of target processing, finding evidence for both attentional benefits (i.e., increases in performance for the cued location relative to baseline; e.g.,^{12,13}) as well

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as attentional costs (i.e., decreases in performance at the uncued location relative to baseline;^{14–16}). However, based on behavioral responses alone it is difficult to infer how orienting spatial attention is implemented in sensory cortex, given that responses are the result of multiple processing stages including changes in sensory activity prior to the onset of a target, perceptual processing of the target itself, and subsequent cognitive stages that involve decision-making, response preparation and response execution. Thus, in addition to behavior, we here directly assessed visual-cortical processing elicited by an auditory cue during exogenous attentional orienting using EEG.

Participants performed a visual discrimination task, and shortly before a visual target appeared, an auditory cue was presented either at the left or right target location to orient spatial attention, or at a central location—in this case acting as an alerting signal without eliciting lateralized shifts of attention (no-shift cue). Note that we used sounds as attention cues to eliminate any early visual responses elicited by the cues themselves. Our EEG analysis focused on two event-related potentials (ERPs). First, we examined the Shift-Related Positivity (SRP) over frontal electrode sites to confirm that our no-shift cue differed from the shift-cues in terms of engaging attentional control areas¹⁷, second, we examined the Auditory-Evoked Contralateral Occipital Positivity (ACOP), a positive deflection over contralateral relative to ipsilateral occipital cortex with respect to the cue location^{10,18}. The main question was how these lateralized changes over occipital cortex would compare to activity elicited by the no-shift baseline cues. Specifically, if exogenous attention is primarily supported by neural enhancement, we would expect increased neural activity over contralateral cortex relative to the no-shift cue; alternatively, if exogenous attention is primarily supported by neural suppression, we would expect decreased activity over ipsilateral cortex relative to the central no-shift cue; finally, an intermediate level of activity elicited by the no-shift cue would suggest the involvement of both enhancement and suppression. In addition to these neural measures, we also analyzed behavioral performance examining costs and benefits at the cued and uncued location relative to the central cue. Together, these measures would provide converging evidence of how spatial exogenous attention improves perceptual processing of a target at attended relative to unattended locations.

Method

Participants. Nineteen participants were included in the final sample of the experiment (14 female; mean age of 19.9 years). Data from five participants were excluded due to excessive artifacts in the EEG (affecting >30% of trials). Data from two additional participants were excluded due to issues with the EEG system that resulted in significant lost data: an HEOG electrode came loose for one subject and a battery died for the other. Two subjects lost a small number of trials (11 and 14 trials) due to sampling errors of the EEG system but are included here, as each subject had greater than 70% of the full sample trial number remaining following artifact rejection.

All participants gave informed written consent in accordance with the IRB guidelines of 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. The sample size was chosen a priori based upon a number of other studies utilizing similar cross-modal attentional cueing paradigms that effectively measured the ACOP and/or related behavioral effects^{10,17–21}. We preregistered our predictions and analysis on AsPredicted (<https://aspredicted.org/rw2it.pdf>) and planned to collect data from 20 participants after exclusion. Our sample has one fewer subject than planned due to data collection being disrupted by COVID-19.

Stimuli and Apparatus. Participants were seated approximately 45 cm in front of a 27" monitor in a sound-attenuated, electrically shielded booth. Stimuli were presented on the screen via the Psychophysics Toolbox in MATLAB^{22,23}. A small black fixation dot (0.2° × 0.2° of visual angle) was always present in the center of the screen, which was otherwise uniformly gray (RGB: 127, 127, 127). A black circle (0.4° × 0.4°) appeared around the fixation dot at the start of each trial to indicate to the participant that the trial had begun. Peripheral auditory 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. Consistent with previous cross-modal cueing work from our lab and others^{10,17–20,24}, these cues 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. For example, for a left cue, the amplitude of the sound coming from the left speaker was adjusted to be louder than the amplitude of the sound coming from the right speaker, so that the sound appeared to come from the visual target location. The central auditory cue was the same pink noise burst played from a speaker mounted on the top of the monitor that was slightly tilted downwards (hereafter referred to as *central cue*) and adjusted to be equal in intensity to the peripheral stimuli. This central cue appeared to emanate from the center of the screen, and thus would not elicit any lateralized shifts of spatial attention. Indeed, as the main goal of this cue was to not elicit any spatial attention shifts but maintain attention focused in the central area of the screen, we opted to present a sound from a speaker located centrally as well. We believe this central sound—rather than, for example, bilateral sounds from both peripheral speakers simultaneously—eliminated any possibility of this sound directing attention to each of the possible target locations simultaneously²⁵. Additionally, because all cue conditions should be intermixed throughout the entirety of the study²⁶, and shift cues were themselves already played in stereo from both speakers, we opted for a no-shift cue played from a separate speaker in order to eliminate the possibility of an interaction between the shift and no-shift cues that may have influenced the perception of each. 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 ~9° visual angle, centered ~28° of visual angle to the left and right of fixation. Each target was immediately followed by a visual noise mask of the same size.

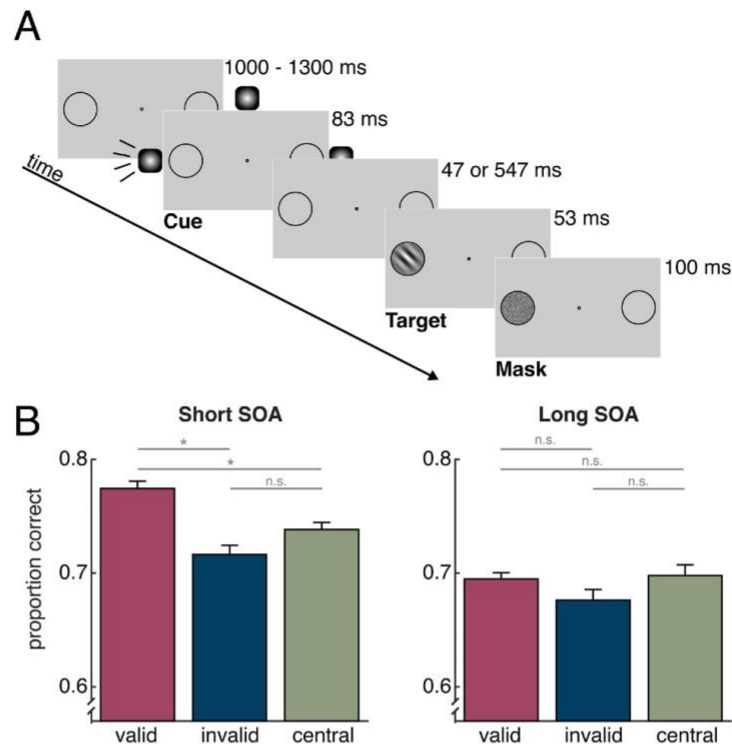


Figure 1. Example trial and performance. (A) Participants discriminated the direction of rotation (clockwise or counterclockwise) of a masked Gabor patch target. Prior to the appearance of the target, participants were presented with an auditory cue that was played randomly either 130 ms or 630 ms prior to the target. This sound was a pink noise burst played either in stereo from peripheral speakers such that it appeared to emanate from either the left or right of the screen, or from a speaker at the top center of the screen such that it appeared to emanate from the center of the screen. On one third of the trials, no visual target was presented. (B) Target discrimination accuracy, plotted as a function of cue condition for each of the cue-target SOAs. Error bars represent ± 1 standard error of the mean. Asterisks indicate a significant ($p < .05$) difference between conditions.

Procedures. All experimental procedures were approved by and conducted in accordance with the guidelines and regulations of the University of California, San Diego Institutional Review Board. An example of a full trial presentation is outlined in Fig. 1A. Participants were asked to keep their eyes on the central fixation dot throughout each experimental block. Each trial began with the presentation of a black circle that appeared around the central fixation dot, indicating to the participants that the trial had started. Following the onset of this circle at a variable stimulus onset asynchrony (SOA) of 1000–1300 ms, an 83-ms auditory attention cue was presented randomly at either the left, right, or center and was not predictive of the spatial location of the visual target. Consequently, participants were instructed to ignore the sounds because they would not be informative to the task. On 1/3 of trials, a target was presented following the cue at an SOA of 130 ms, and on another 1/3 of trials the target was presented following the cue after 630 ms. The target Gabor patch 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 offset of the noise mask at an interstimulus interval (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. On the remaining 1/3 of trials, neither a target nor a mask appeared following the cue. These trials ended 900 ms after cue onset, and participants pressed the spacebar to continue to the next trial. The target display was omitted or presented after a longer cue-target SOA (630 ms) to allow recording of the event-related potential (ERP) to the cue separately from the otherwise overlapping ERP to the visual target.

We included the 1/3 of trials in which the target appeared at a short SOA from the cue in order to investigate whether the salient auditory cue influenced behavior, as exogenous attentional benefits in perception typically last only a few hundred milliseconds^{27,28}. We included the 1/3 of trials in which the target appeared at a long

SOA from the cue in order to eliminate any clear temporal relationship between the cue and the target, and we included the 1/3 of trials in which no visual information was presented in order to make the cue nonpredictive of whether a target would appear at all. This ensured that neural responses to the cue were representative of purely exogenous activity and not any expectations related to the appearance of the target, as the cue was not predictive of where, when, or even if a target would appear. Additionally, because neither the long SOA nor the no-target trials presented any visual information during and beyond our a priori time window of interest, we were able to include each of these trial types (2/3 of all trials) in the EEG analysis. All trial types were randomly intermixed within a block. Subjects performed 12 blocks of 72 trials each. 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;²⁹). 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. Prior to performing the thresholding task, participants performed 36 practice trials without a cue.

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.

Data processing was carried out using EEGLAB³⁰ and ERPLAB³¹ toolboxes and custom-written scripts in MATLAB (The MathWorks, Natick, MA). Continuous EEG data were filtered with a bandpass (butterworth filter) of 0.01–112.5 Hz offline. Data were epoched from -1000 ms to +1200 ms with respect to the onset of the auditory cue. Artifacts were detected in the time window -800 to 800 ms, and trials contaminated with blinks, eye movements, or muscle movements were removed from the analysis. First, we used automated procedures implemented in ERPLAB³¹, 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.³²). Artifact-free data was digitally re-referenced to the average of the left and right mastoids. In order to avoid overlap of the target-elicited neural activity with the cue-elicited neural activity, only trials without a target and trials with a 630 ms cue-target SOA were included in the cue-elicited ERP analysis.

ERPs elicited by the left and right noise bursts were averaged separately and were then collapsed across cue 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 were obtained by averaging across the same lateral electrode positions across both hemispheres (bilateral) that were included in the peripheral cue analysis. ERPs were low-pass filtered (half-amplitude cutoff at 25 Hz; slope of 12 dB/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 planned follow-up paired t-tests. Our main analysis was focused on the ERP activity during the Auditory-Evoked Contralateral Occipital Positivity (ACOP) time window. The ACOP—usually measured as a contralateral-vs.-ipsilateral ERP component—has been proposed as an index of exogenous attention¹⁰. Thus, based on previous studies on the ACOP^{10,18}, the ERP amplitude was measured between 260 and 360 ms at four parietal-occipital electrode sites (PO7/PO8/P7/P8) separately for the hemisphere contralateral to the cued location, ipsilateral to the cued location, and over bilateral electrode sites following the central cue. A separate and more exploratory (though preregistered) analysis focused on frontal activity related to shifting vs. not shifting attention to peripheral and central cues respectively. Based upon prior research demonstrating shift-related activity at frontal sites in endogenous attentional cueing paradigms¹⁷, activity was measured between 300–500 ms at four frontal electrode sites (F3/F4/FC1/FC2).

Topographical maps. To illustrate the scalp distribution of the different ERP measures, we created topographical maps using spline interpolation of the voltage differences between the cue conditions. To isolate the activity related to the three different cues, we created maps for the contralateral-minus-ipsilateral activity (the ACOP), as well as for the voltage differences between each lateralized activity and the non-lateralized activity elicited by the central cue (i.e., contralateral-minus-central; ipsilateral-minus-central). For contralateral-minus-ipsilateral topographies, values at midline electrode sites (e.g., POz) were set to zero^{17,19}, and these difference voltage topographies were projected to the right side of the head. The contralateral/ipsilateral-minus-central topographies were plotted together, with differences in the ipsilateral hemisphere projected to the left side of head and differences in the contralateral hemisphere projected to the right side.

Statistical analyses. Behavior was analyzed by comparing accuracy (% correct) in the Gabor discrimination task separately for when a cue was presented at the same location as the visual target (valid trials) vs. at the opposite location (invalid trials) vs. at the center (central trials). Though the behavioral measure of interest was accuracy, we also analyzed reaction time (i.e., RT) in order to rule out any speed-accuracy trade-offs. Behavioral and EEG data were statistically analyzed using repeated-measures ANOVAs and paired t-tests (alpha = 0.05) using MATLAB (The MathWorks, Natick, MA). To compare accuracy and RT in each task following the different cue conditions, we performed 3 × 2 repeated-measures ANOVAs with factors of cue type (valid, invalid, or central) and cue-target SOA (130 ms or 630 ms). Note that the inclusion of the cue-target SOA factor is a departure

from our pre-registered analysis but was necessary in order to compare the strength of the alerting response elicited by each cue. To compare ERP activity following each cue, we performed repeated-measures ANOVAs with a factor of hemisphere relative to cue type (contralateral to peripheral cue, ipsilateral to peripheral cue, bilateral for central cue) on the data separately for each of our a priori chosen electrode clusters and time window pairs. Both pre-registered and post-hoc t-tests were performed on the data and are appropriately noted in the Results section. Post-hoc t-tests were corrected for multiple comparisons using a Holm-Bonferroni correction³³ and reported in corrected form.

An additional time–frequency analysis of lateralized and nonlateralized oscillatory activity in the alpha-band (8–13 Hz) was pre-registered. These data are not reported here due to the critical a priori ANOVA comparing alpha-frequency activity across the three cue conditions (contralateral vs. ipsilateral vs. central) failing to reach statistical significance. However, the method and results of this analysis are outlined in the Supplementary Alpha Analysis Method and Supplementary Alpha Analysis Results.

Results

Behavior. Accuracy following each cue and cue-target SOA in the target discrimination task is plotted in Fig. 1B. In order to test for the presence of a behavioral cueing benefit at each SOA, a two-way repeated-measures ANOVA with factors of cue condition (valid, invalid, central) and SOA (short, long) was performed. This analysis revealed a significant main effect of SOA, $F(1, 18) = 36.00, p < 0.001, \eta_p^2 = 0.59$, indicating that overall accuracy was higher in short SOA trials than long SOA trials. Additionally, there was a main effect of cue condition, $F(2, 36) = 7.79, p = 0.002, \eta_p^2 = 0.33$, indicating that accuracy varied by cue condition. Finally, there was trend towards a significant interaction between cue condition and SOA, $F(2, 36) = 3.08, p = 0.06, \eta_p^2 = 0.15$. Preregistered follow-up t-tests were performed for the short SOA condition, revealing that accuracy was significantly higher following valid cues compared to invalid cues, $t(18) = 4.39, p < 0.001, d = 1.01$, and central cues, $t(18) = 3.67, p = 0.002, d = 0.84$. Critically, there was no significant difference between performance following invalid and central cues, $t(18) = 1.69, p = 0.11, d = 0.39$. This pattern of findings is generally in line with the predictions of a facilitation-only account of exogenous attention: there were behavioral benefits at the cued location relative to baseline, but no costs for the uncued location relative to baseline. Post-hoc t-tests were also performed on the long SOA data in order to test for the presence of cueing effects, which were not predicted given that exogenous attention effects are typically largest at short SOAs²⁸. These t-tests, which were corrected for multiple comparisons because we did not pre-register them, demonstrated that accuracy was comparable across all cue conditions. Accuracy was not significantly different following valid and invalid cues, $t(18) = 1.53, p = 0.52, d = 0.35$, or central cues, $t(18) = 0.25, p = 0.81, d = 0.06$. Additionally, performance did not significantly differ following central and invalid cues, $t(18) = 1.20, p = 0.50, d = 0.28$.

In order to confirm that any differences in accuracy were not the result of a speed-accuracy trade-off, we analyzed reaction times (i.e. RTs) to the target, plotted in Supplementary Fig. 1. We tested whether there were any differences in RT between our conditions of interest by performing a two-way repeated-measures ANOVA with factors of cue validity (valid, invalid, central cue) and SOA (short vs. long) on the RT data. Neither the main effect of SOA, $F(1, 18) = 3.20, p = 0.09, \eta_p^2 = 0.08$, nor the main effect of cue condition, $F(2, 36) = 1.23, p = 0.30, \eta_p^2 = 0.08$, reached significance. Additionally, there was no significant interaction between cue condition and SOA, $F(2, 36) = 1.40, p = 0.26, \eta_p^2 = 0.07$. These findings demonstrate that higher accuracy following the valid vs. invalid and central cues at the short SOA cannot be explained by a trade-off between speed and accuracy.

Frontal ERPs. Previous research has demonstrated that slow positive deflections in the ERP emerge bilaterally over frontal areas following endogenous symbolic cues that prompt a shift of attention to peripheral locations vs. symbolic cues that do not prompt a shift of attention, termed the Shift-Related Positivity (SRP;^{17,19}). Based upon this finding, we investigated whether a similar ERP signature associated with the spatial shifting of attention emerged following the random peripheral (shift) vs. central (no-shift) cues over the same time interval in the present study. This would provide support for the idea that our central and peripheral cues oriented attention differently and would also demonstrate the presence of a novel frontal ERP signature of exogenous attentional deployment to uninformative, peripheral auditory cues.

As can be seen in Fig. 2, we found a sustained bilateral positivity at frontal sites following the shift vs. no-shift cues. A one-way repeated-measures ANOVA with a factor of cue condition (contralateral to cued location, ipsilateral to cued location, bilateral for central cue) was performed on the ERP waveforms during the predefined SRP time window (300–500 ms post-cue). This analysis revealed a main effect of cue condition, $F(2, 36) = 14.67, p < 0.001, \eta_p^2 = 0.45$, indicating a significant difference between the amplitudes of the waveforms. Planned follow-up t-tests indicated that both the ipsilateral waveform, $t(18) = 4.03, p < 0.001, d = 0.93$, and contralateral waveform, $t(18) = 3.95, p < 0.001, d = 0.91$, were significantly more positive than the waveform elicited by the central cue. Critically, there was no significant difference between the amplitude of the ipsilateral and contralateral waveforms, $t(18) = 0.90, p = 0.38, d = 0.21$, indicating that this bilateral frontal component was not sensitive to the specific peripheral location attention was shifted to, but instead indexes control processes related to the spatial orienting response more generally.

Occipital ERPs. In order to investigate whether cross-modal exogenous attention improved performance on the visual task by facilitating visual-cortical processing at the cued location, suppressing visual-cortical processing at the uncued location, or both, we examined the ERPs elicited by the peripheral cues relative to the central cues at parietal-occipital electrode sites. In particular, we focused on the time window of the ACOP—an ERP component that has previously been associated with the exogenous orienting of attention^{10,18}. The ACOP is based on a relative difference between neural activity across the hemispheres, so it is unclear whether it reflects

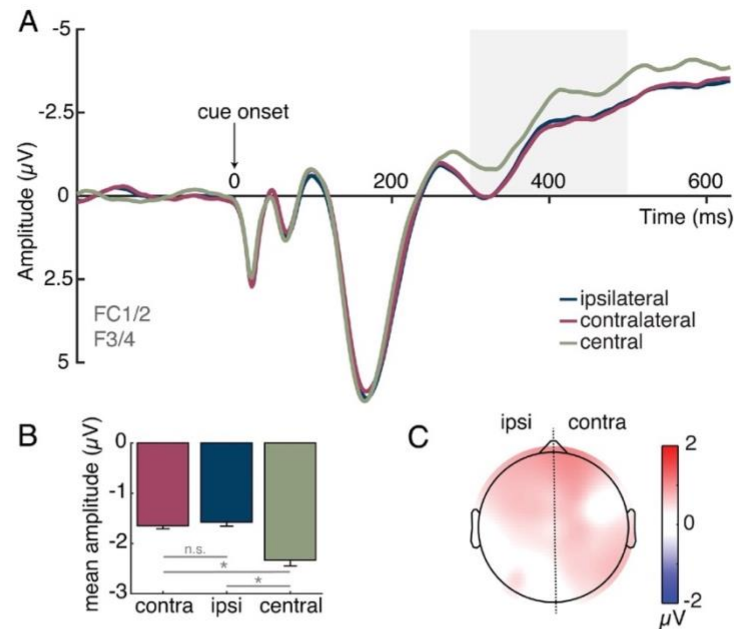


Figure 2. Grand-average ERP waveforms, mean amplitudes, and ERP topography during the shift-related potential (SRP) time window (300–500 ms). ERPs at frontal scalp sites (F3/F4/FC1/FC2) were collapsed over left- and right-cue conditions and left and right hemispheres to obtain waveforms recorded ipsilaterally and contralaterally to the cued location. For the central-cue condition, ERPs were computed by averaging bilaterally across the same set of electrodes. (A) Plot of cue-elicited ERP. There was a significant positivity in ipsilateral and contralateral hemispheres in comparison to the no-shift cue (central) during the a priori defined SRP time window (highlighted in gray). (B) Plot of average ERP magnitude during the a priori SRP time window (300–500 ms). There was a positivity in ipsilateral (ipsi) and contralateral (contra) cortex relative to the central cue. Error bars represent ± 1 standard error of the mean. Asterisks indicate a significant ($p < .05$) difference between conditions. (C) Topographical voltage map of the contralateral-central and ipsilateral-central ERP difference amplitudes during the SRP time window, with contralateral and ipsilateral differences projected to the right and left sides, respectively. The map demonstrates that the SRP was broadly distributed over bilateral frontal areas, concurrent with the posterior lateralized positivity.

a contralateral positivity, which would be consistent with visual-cortical enhancement of the attended location; or an ipsilateral negativity, which would be consistent with visual-cortical suppression of the unattended location; or both. If the ACOP reflects facilitation of information at the cued location, then we would expect the contralateral waveform (which reflects activity at the cued location) to be significantly greater in amplitude than the central-cue waveform. In this case, activity ipsilateral to the cue (which reflects activity at the uncued location) should be roughly equivalent to the central-cue baseline. Conversely, if the ACOP reflects suppression of unattended information, then we would expect the ipsilateral waveform to be significantly lower in amplitude than the central-cue waveform. In this case, the contralateral waveform should be comparable to the central-cue baseline. Finally, if the ACOP reflects both facilitation and suppression, then we would expect to observe both a contralateral increase and ipsilateral decrease relative to the central-cue baseline.

As shown in Fig. 3, the contralateral ERP waveform was more positive than both the waveform elicited over the ipsilateral hemisphere in response to the peripheral cue as well as the waveform elicited by the central cue over bilateral sites. Critically, there was no difference between the ipsilateral and central-cue waveforms. A one-way repeated-measures ANOVA with a factor of cue condition (contralateral to cued location, ipsilateral to cued location, bilateral for central cue) was performed on the ERP waveforms during the ACOP time window (260–360 ms post-cue). This analysis revealed a main effect of cue condition, $F(2, 36) = 11.91, p < 0.001, \eta_p^2 = 0.40$, indicating a significant difference between the amplitudes of the waveforms. Planned follow-up t-tests indicated that the contralateral waveform was significantly more positive than both the ipsilateral, $t(18) = 4.39, p < 0.001, d = 1.01$, and central-cue waveform, $t(18) = 4.57, p < 0.001, d = 1.05$. There was no significant difference between the amplitude of the ipsilateral and central-cue waveforms, $t(18) = 0.76, p = 0.46, d = 0.18$.

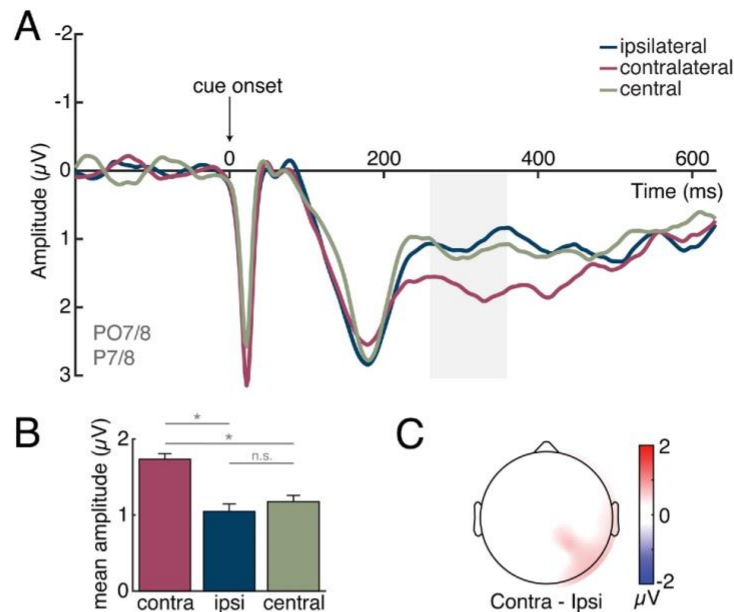


Figure 3. Grand-average ERP waveforms, mean amplitudes, and ERP topography during the ACOP time window. For peripheral cues, ERPs were collapsed over left- and right-cue conditions and left and right hemispheres to obtain waveforms recorded ipsilaterally and contralaterally to the cued location. For the central-cue condition, ERPs were computed by averaging bilaterally across the same set of electrodes. (A) Plot of cue-elicited ERP. There was a significant positivity over the contralateral hemisphere in comparison to the no-shift cue baseline during the a priori defined ACOP time window (highlighted in gray), whereas the ipsilateral waveform was roughly equivalent to the baseline. (B) Plot of average waveform magnitude during the a priori ACOP time window (260–360 ms). There was a positivity over contralateral (contra) cortex relative to ipsilateral (ipsi) cortex and relative to the central cue. Error bars represent ± 1 standard error of the mean. Asterisks indicate a significant ($p < .05$) difference between conditions. (C) Topographical voltage map of the contralateral-minus-ipsilateral ERP difference amplitudes, projected to the right side of the scalp during the ACOP time window. This map demonstrates that the topography of the ACOP was distributed over parietal and occipital areas, with no evidence of lateralized frontal activity.

Discussion

How does exogenous attention improve visual perception? While several studies have looked at how endogenous attentional orienting affects visual-cortical processing prior to the onset of a target, it is largely unknown how an exogenous attention cue modulates visual-cortical responses. To fill this gap, we had subjects perform a cross-modal, exogenous cueing task in which either peripheral left and right sounds or a central, no-shift sound preceded a masked visual target while we recorded EEG. This central cue did not evoke lateral shifts of attention, which allowed us to use this condition as a baseline to differentiate between spatially specific increases and decreases in neural activity and behavioral performance triggered by the peripheral cues. In accordance with a classic cost–benefit analysis, any increases above this baseline performance or neural activity were interpreted as evidence of facilitation whereas any decreases below this baseline were interpreted as evidence of suppression. Therefore, if exogenous attention improves perception by facilitating visual processing at attended locations, we expected to see an increase in activity at the cued location; and, conversely, if exogenous attention improves perception by suppressing visual processing at unattended locations, we expected to see a decrease in activity at the uncued location. We found that accuracy on the target discrimination task was higher following valid vs. no-shift and invalid cues. Critically, this effect of cue validity was accompanied by an increase in neural activity over parieto-occipital cortex in the hemisphere contralateral to the cue location, responsible for processing the cued location, relative to the ipsilateral hemisphere as well as the no-shift cue condition baseline. These results indicate that exogenous orienting of spatial attention results in visual-cortical facilitation in the hemisphere contralateral to the attended location, with no signs of suppression in the opposite hemisphere.

Several previous studies have used no-shift cues in behavioral paradigms with the goal of isolating costs and benefits during attentional orienting, with some studies finding costs, others benefits, and some both (e.g.,^{13,14}). We believe that the discrepancies between studies are likely due to differences in the exact stimuli and response measures used. For example, other studies have used dependent measures such as RT¹⁶, gap size threshold in a

Landolt square spatial acuity task¹⁴, and d^{34} or contrast threshold¹⁵ in a variable-contrast orientation discrimination task. As behavioral responses are the accumulation of multiple sensory and cognitive processing steps, and different measures may vary in their sensitivity to these processes, it is difficult to pinpoint at what stage costs and benefits arise in these behavioral studies. Using neural measures, as done here, allows for direct assessment of costs and benefits prior to a behavioral response, demonstrating that early visual-cortical processing is enhanced at the attended location. Furthermore, the type of cue used as a neutral baseline condition may also play a role. The central sound used in our study was matched to the peripheral cues with regards to its low-level features (i.e., amplitude, frequency spectrum) and provided the same temporal—but not spatial—information about the visual targets. This means that the central and peripheral cues presumably had equivalent processing demands, served as equivalent alerting signals, and required roughly equivalent encoding times²⁶. This is supported by our behavioral data in which we see a decrement of similar magnitude in each cue condition at the long vs. short SOA, indicating that there are no large differences in the (non-spatial) alerting signal triggered by the central and peripheral cues. Furthermore, the frontal ERP index of attentional shifting showed significantly different neural activity for peripheral relative to central cues. Thus, we think the central cue in our study acts as a valid baseline relative to the peripheral cues, as it differs only in the main dimension of interest: shifting attention to a new location vs. not.

In the present study we used auditory cues to orient spatial attention, which allowed us to examine cue-related activity over occipital cortex without the contamination of visual-evoked responses that are necessarily triggered when using visual peripheral cues. Previous work has shown that salient but uninformative peripheral sounds result in enhancements in the detection²¹, discrimination^{18,20}, apparent contrast^{17,19} and even perceived latency³⁵ of visual stimuli at the location of the sound in a diverse range of cross-modal cueing paradigms. Electrophysiological studies on the topic suggested that these changes in behavior are the result of enhanced early responses to the visual targets themselves when presented at the same location as the auditory cues, such as increases in the visually-evoked P1 amplitude^{17,19,35}. However, later work demonstrated that visual-cortical processing is also altered following peripheral auditory sounds even in the absence of visual targets, as indexed by both a lateralized positive ERP (i.e., ACOP^{10,18,20}), and lateralized decreases in the power of alpha-frequency oscillations^{18,36,37}. The present study extends these findings by demonstrating that the lateralized changes in visual-cortical processing that follow the salient cue are representative of facilitated processing at the location of the cue rather than suppression of the uncued area, using a novel auditory no-shift cue that served as a baseline and a cost-benefit analysis approach.

Though our attention is often captured by auditory and not only visual stimuli in the real world, one question that may arise is whether our cross-modal findings can be generalized to intra-modal studies of attention. Critically, several cross-modal attention paradigms have found effects similar to visual-only attention paradigms (for a review, see¹¹), and a recent experiment directly comparing ERP activity triggered by peripheral visual and auditory cues found similar lateralized biasing signals over parietal-occipital cortex as here (Störmer, McDonald, & Hillyard, 2019). This suggests that the present results would hold for visual cues as well. Thus, the present paradigm extends previous work on visual and audiovisual attentional cueing, demonstrating that exogenous attention effectively operates across modalities, in support of a supra-modal account of spatial attention³⁸. Furthermore, in our study none of the sounds were predictive of target location, target timing, or even the occurrence of a target, eliminating the possibility that the observed effects are due to endogenous components of attention or expectations (e.g., signal probability) about the audio-visual stimuli, which are also known to interact across sensory modalities (for recent reviews, see^{39,40}).

While we interpret this occipital activity as being the result of a supra-modal attentional system, it should be noted that non-human primate work indicates that there are direct connections between auditory and visual sensory cortices that may allow for bottom-up stimulation of visual cortex by auditory stimuli⁴¹. However, the time course of the positivity that we observe over occipital cortex argues against this hypothesis, as one would expect this activity to emerge much more quickly if it were the result of direct connections between the sensory cortices. Indeed, human imaging work has demonstrated that audiovisual interactions, in which the neural response to the simultaneous presentation of an auditory and visual stimulus is greater than the sum of responses to each stimulus individually, emerge in visual cortex as early as 45–73 ms after the onset of the stimuli^{42–45}; for a review, see⁴⁶. The much later onset of the positivity in the present study (~250 ms) therefore suggests that more elaborate processing occurs between the sensory processing of the auditory cue and the activation of visual cortex, perhaps in higher-level multisensory or attentional areas¹⁰. Supporting this argument, prior human ECoG work has found that peripheral auditory tones result in separate early (<100 ms post-tone) and later (>200 ms post-tone) activation of visual cortex⁴⁷. This suggests that an earlier cross-modal activation of visual cortex, which may represent activity resulting from direct connections between the areas, is separable from the later and presumably attention-related activity that we observe in the present study.

The present findings implicate a difference in the neural mechanisms engaged by exogenous and endogenous attention, as prior research has shown that endogenous attention results in both costs and benefits in behavior^{48,49} and facilitation and suppression of neural activity^{50,51}. That is, the present results indicate that exogenous attention only facilitates processing of information at the location of a salient cue, whereas endogenous attention seems to additionally involve suppressive attentional mechanisms that possibly emerge later in time. This conclusion contrasts with recent work proposing that the lateralized positivity observed over parietal-occipital cortex following peripheral auditory stimuli (i.e., ACOP) is instead representative of the suppression of unattended locations⁵². In this study, it was demonstrated that the same peripheral sounds that elicit an ACOP during a spatial localization task may not elicit an ACOP during non-spatial tasks, such as pitch discrimination. Additionally, the study compared visual-cortical activity in each hemisphere in the localization task that elicited an ACOP to activity in tasks that did not elicit a reliable ACOP. When making this comparison, they found an ipsilateral decrease in the localization task relative to both ipsilateral and contralateral activity across all other tasks. This was interpreted

as evidence that the ACOP reflects suppression of the unattended location. However, it is unclear whether the ACOP-absent trials in the aforementioned study served as an effective baseline in the same way that a central no-shift cue does. Given that processing demands varied between the tasks that did and did not elicit an ACOP, and subjects performed these tasks in separate blocks, it is difficult to directly and clearly interpret differences in neural data elicited by the sounds in the separate tasks. Additionally, the sounds were still presented peripherally in the tasks that did not elicit an ACOP, and thus may have engaged spatial exogenous attention to some extent. Further supporting the present study's conclusion, the facilitation-only account of exogenous attention comports well with other recent evidence demonstrating that lateralized occipital activity predicts behavioral performance only on validly but not invalidly cued trials^{20,36}. This suggests that only neural activity at the location of a cue (presumably reflecting the facilitative effects of attention) is related to behavioral performance in exogenous cueing tasks. However, it is important to note that these studies, including ours, only investigated the first ~600 ms of cue-elicited neural activity, in line with the rapid time course of exogenous attention. Accordingly, it is possible that there is a later, suppressive component of attention that only emerges at longer timescales—and thus would likely only be engaged during endogenous attention due to its relatively sluggish response. Indeed, prior research measuring alpha frequency oscillatory activity following informative central cues suggests that suppression may emerge on a later timescale than facilitation⁶. Thus, it might also be the case that separate neural measures (e.g., ERPs and oscillatory activity) reveal different patterns of hemisphere-specific neural processing in response to peripheral cues. This is an important question for future research, as in the present study we did not observe reliable lateralized alpha activity in response to the cues. The present data also demonstrate a novel similarity between the exogenous and endogenous orienting of attention, as we find that exogenous cues elicit a Shift-Related Positivity over frontal areas that has previously only been demonstrated in response to endogenous cues^{17,19}. Taken together, these findings suggest that the shifting of exogenous and endogenous attention may be mediated by similar control processes in frontal areas, but that these shifts result in different effects in posterior cortex.

Overall, our data demonstrate that the exogenous orienting of spatial attention results in visual-cortical enhancement at the location of a salient cue but does not result in spatially specific suppression of visual processing at uncued locations (i.e., opposite hemisphere). Broadly, these findings suggest that exogenous and endogenous spatial attention differ in how they bias visual-cortical processing to support effective stimulus selection.

Data availability

Preprocessed data and MATLAB scripts re-creating the analyses of main effects in the data are available at https://osf.io/unsqh/?view_only=2f7fef4c4db747d487179a7359f8cb88. Raw data will be available upon reasonable request, made via email to the corresponding author.

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Author contributions

J.M.K. and V.S.S. developed the study concept. All authors contributed to the study design. Testing and data collection were performed by E.P. and J.M.K. J.M.K. and V.S.S. performed the data analysis and interpretation. J.M.K. drafted the initial manuscript, and J.M.K. and V.S.S. revised the manuscript together. All authors approved the final version of the manuscript for submission.

Competing interests

The authors declare no competing interests.

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Chapter 3:

Exogenous attention operates independently of endogenous task goals

Jonathan M. Keefe & Viola S. Störmer

(Manuscript in preparation)

Abstract

Spatial attention can be oriented exogenously by salient events or endogenously based on goals. A critical distinction between exogenous and endogenous attention lies upon the control that individuals have over these processes. Whereas endogenous attention is theorized to be a controlled process and determined by volitional control of an observer, exogenous attention is presumed to operate reflexively and largely independently of task goals. To test whether exogenous attention is indeed insensitive to task goals and thus as reflexive as often presumed, we ran three online experiments utilizing both a typical exogenous cueing paradigm where a visual cue briefly preceded a masked target at a random and non-predictive location (left or right; Non-Predictive Task) and a nearly identical task in which the salient cue was counter-predictive of the target's location (Counter-Predictive Task). This counter-predictive cue appeared on the opposite side of where the subsequent target would be presented on 80% of trials, such that subjects were incentivized to attend to the opposite location of the cue. We expected to see higher d' and faster response times (RT) for same-location trials relative to different-location trials in the Non-Predictive Task, replicating previous work. The main question of interest was whether this pattern would change in the Counter-Predictive Task. If subjects have control over their exogenous attention, then we expected to see the opposite pattern, with lower d' and higher RTs on same-location trials relative to different-locations trials. Instead, we found that d' remained higher for targets presented at the same physical location of the counter-predictive cue, indicating that attention was exogenously oriented to the location of the cue regardless of whether it was counter-predictive. Overall, these studies suggest that exogenous attention indeed operates outside of individuals' control and represents a highly reflexive attention system.

Introduction

To deal with the surfeit of information presented to our sensory systems in every moment, we must attend to relevant features or spatial locations while attempting to ignore the irrelevant, which can be accomplished via selective attention. According to classic theories of selective spatial attention, attention can be deployed endogenously (i.e., voluntarily) following the goals of an observer or exogenously (i.e., involuntarily) through capture by a sudden event in the environment (Reynolds and Chelazzi, 2004; Wright and Ward, 2008). While each of these types of attention results in improved performance in discrimination or detection tasks (Posner, 1980; Posner and Cohen, 1984), these benefits demonstrate different time courses depending on how attention is deployed. Exogenous attentional benefits emerge quickly but transiently, while endogenous attentional benefits emerge more slowly and may sustain indefinitely based upon task demands (Müller and Rabbitt, 1989; Nakayama and Mackeben, 1989; Cheal & Lyon, 1991). In addition to the differences in temporal profiles, clear differences also exist in how each type of attention affects visual processing, including contrast sensitivity (Jigo & Carrasco, 2020), texture sensitivity (Barbot, Landy, & Carrasco, 2012), and spatial resolution (Yeshurun & Carrasco, 1998; Barbot & Carrasco, 2017; Fernandez, Okun, & Carrasco, 2021; Jigo, Heeger, & Carrasco, 2021), further differentiating between the two types of attention.

The distinction between exogenous and endogenous attention rests critically upon the control that individuals are theorized to have over these processes. Endogenous attention is characterized as emerging from the task goals of an individual and thus is under their volitional control. Conversely, exogenous attention is considered to deploy reflexively or even “automatically”, such that individuals lack control over exogenous attention and therefore cannot volitionally resist its deployment to salient events. Indeed, there is a great deal of evidence for

the reflexiveness of exogenous attention. A large body of literature has demonstrated that spatial attention is exogenously deployed even when a salient event is irrelevant and when attending to it is detrimental to task performance (Yeshurun & Carrasco, 1998; Yeshurun & Levy, 2003; Carrasco, Loula, & Ho, 2006; Yeshurun, Montagna, & Carrasco, 2008). Furthermore, the magnitude of exogenous attentional benefits does not vary based upon the cue's predictive value (Giordano, McElree, & Carrasco, 2009; Keefe & Störmer, 2021) or the reward/punishment information conveyed by the cue (Bucker & Theeuwes, 2014; Bucker & Theeuwes, 2016). These benefits occur both in the periphery and the foveola (Zhang, Shelsckova, Ezzo, & Poletti, 2021); and even salient events at completely irrelevant spatial locations can capture attention (Folk, Leber, & Egeth, 2002; Prasad, Mishra, & Klein, 2021). Further, these exogenous attentional benefits can emerge even when the cue and target are presented in separate sensory modalities (Spence & Driver, 1997; McDonald, Teder-Sälejärvi, & Hillyard, 2000; Störmer, McDonald, & Hillyard, 2009; Keefe & Störmer, 2021). Therefore, the orienting of exogenous attention to a new location is often presumed to operate like a reflex, outside of an individual's control.

In some ways, this claim may seem to contrast with other literature suggesting that salient stimuli fail to exogenously orient spatial attention when presented outside the focus of endogenous attention (Yantis & Jonides, 1990; Belopolsky et al., 2007; Ishigami, Klein, & Christie, 2009; Belopolsky & Theeuwes, 2010; Ruthruff & Gaspelin, 2018). Each of these studies manipulated the distribution of endogenous attention by providing an informative central cue, varying the likelihood of targets appearing at certain locations, or changing the spatial spread of a task; and each of these studies found that salient peripheral events presented outside the focus of endogenous attention captured attention less readily than those within. Indeed, it may at first glance seem that these findings argue for individuals having some control over

exogenous attentional capture. However, this line of research is more informative regarding interactions between the two types of attention given that they manipulate the endogenous distribution of spatial attention prior to a salient cue and measure how that modulates the exogenous attentional response to that cue (Yantis, 1993). That is, while these studies do suggest that exogenous attentional capture can be lessened by endogenously orienting attention elsewhere, they do not answer the question of whether it is possible to exert control over exogenous attentional orienting itself independently of manipulations to endogenous spatial attention. A promising approach to resolving this question is to design a cueing task in which subjects are incentivized to resist or even re-map their spatial orienting response to a salient cue by manipulating the information conveyed by the cue. Previous studies adopting this approach have attempted to do this by making the cue *counter-predictive* as to where a target would appear after a variable stimulus-onset asynchrony (i.e., SOA; Lambert, Spencer, & Mohindra, 1987; Warner, Juola, & Koshino, 1990; Tepin & Dark, 1992). However, the results from each of the studies were equivocal, with one study suggesting that subjects are unable to overcome attentional capture by the salient cue (Lambert, Spencer, & Mohindra, 1987) and the others indicating that it is possible following minimal (Tepin & Dark, 1992) or extensive training (Warner et al., 1990). Furthermore, each of these studies was limited given that they used reaction time (RT) alone to address this question, which may lack the specificity to measure the effects of attention upon perception given that it neglects errors and is susceptible to changes in other cognitive processes (e.g., response selection; Santee & Egeth, 1982) or states (e.g., arousal level; Freeman, 1933; Eason, Harter, & White, 1969).

Accordingly, we sought to extend this approach to test whether it is possible to exert control over exogenous attentional orienting. Leveraging the ability to perform large online

studies, we collected data from 200 subjects across 3 experiments utilizing two variants of a classic attentional cueing paradigm. We used a typical exogenous cueing paradigm where a visual cue is briefly presented at a random, non-predictive location prior to a visual target (i.e., Non-Predictive Task) and another stimulus-matched task in which the salient cue was now predictive (80% valid) of where the target would *not* appear (i.e., Counter-Predictive Task). In addition to RT, we measured the impact of the exogenous cue upon visual discrimination performance using d' – providing a direct measure how cues affect visual processing per se. By comparing each of these measures following the cues of the Non-Predictive and Counter-Predictive Tasks, we investigated whether subjects could resist or even re-map exogenous attentional orienting if given sufficient instruction and incentive.

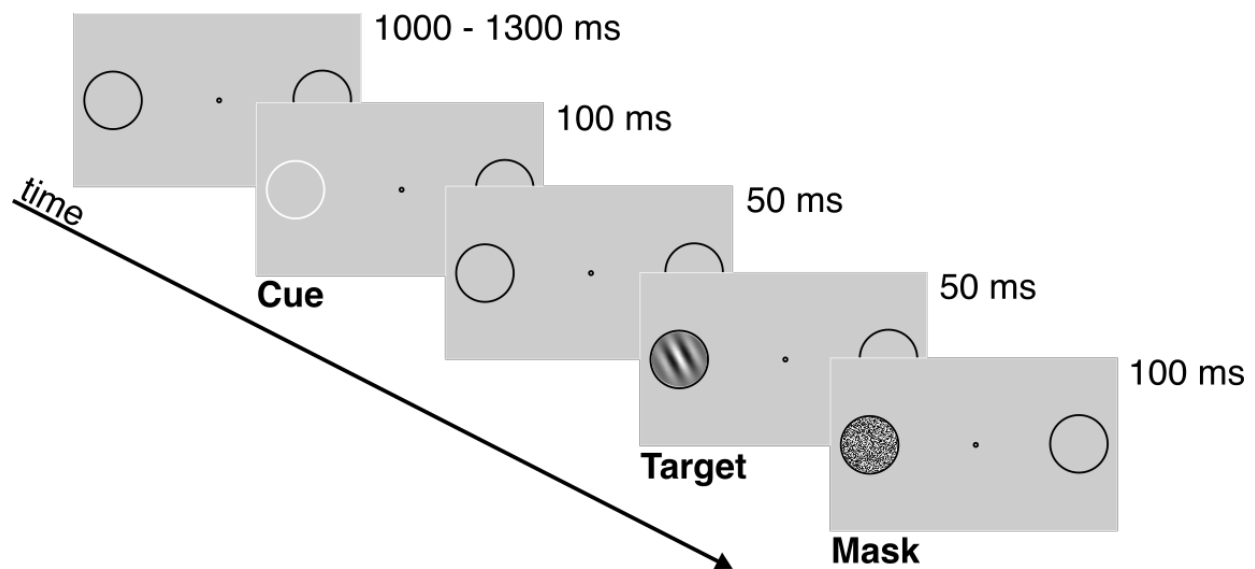


Figure 3.1. General task design. Participants discriminated the direction of rotation (clockwise or counterclockwise) of a masked Gabor patch target. Prior to the appearance of the target, participants were presented with a visual cue that was either presented randomly 150 ms prior to the target (50% valid; Non-Predictive task) or informative as to where the future target would not appear (80% valid; Counter-Predictive Task). This cue involved one of the possible placeholders flashing white for 100 ms.

Experiment 1

In Experiment 1, we sought to replicate the classic exogenous cueing effect to get an estimate of the size and consistency of the effect in our online population.

Method

Participants

Fifty participants from the UCSD community were included in the final sample of Experiment 1, which was performed online. All participants gave informed consent in accordance with the IRB guidelines of the Human Research Protections Program of the University of California, San Diego and received course credit for their participation (1 credit/hr). All participants were over 18 years old and reported having normal or corrected-to-normal vision and normal hearing. Participants were excluded if their d' across all conditions was less than 0.5, if their median RT was more than 2 standard deviations above the sample mean, or if they reported performing the task incorrectly in a subsequent survey (e.g., monitoring only one target location). 26 participants were excluded based upon these criteria. All results hold when including all subjects with $d' > 0$.

Stimuli

A small black fixation circle with a diameter of 12 pixels was always present in the center of the experiment window (1000 x 700 pixels), which was centered on the screen and uniformly gray (RGB: 150, 150, 150). The target was presented in one of two peripheral locations indicated by black circles with a diameter of 100 pixels, centered 300 pixels to the left and right of fixation. The target was a Gabor patch with a spatial frequency of 0.3 cycles/pixel, turned either -

30° or 30° from vertical. The contrast of the Gabor patch was determined for each participant in a calibration task prior to the main experiment (see below). Each target was immediately followed by a visual noise mask of the same size.

Procedures

All experimental procedures were approved by and conducted in accordance with the guidelines and regulations of the University of California, San Diego Institutional Review Board. An example of a full trial presentation is outlined in Figure 1. Participants were asked to keep their eyes on the central fixation dot throughout each experimental block. Following an ITI of 1,000 – 1,300 ms, one of the two placeholders (circles) that indicated the two possible target positions flashed white for 100 ms, acting as an exogenous attention cue. This cue occurred randomly at either the left or right target location and was not predictive of the spatial location of the visual target. Consequently, participants were instructed to ignore the cues because they would not be informative to the task. Following the cue at an SOA of 150 ms, the target Gabor patch was presented at one of the two peripheral locations for 50 ms. The target 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 offset of the noise mask at an interstimulus interval (ISI) of 300 ms, the central fixation dot turned red, 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. Following this response, participants also rated how vivid the target appeared, using the Perceptual Awareness Scale (PAS; Ramsøy & Overgaard, 2004), which entails the choice of one of four levels of awareness:

1. No experience. No impression of the stimulus is experienced. All answers are experienced as mere guessing.
2. Brief glimpse. A feeling that something was present, even though content cannot be specified any further.
3. Almost clear experience. Feeling of having seen the stimulus but being only somewhat sure about it.
4. Clear experience. Nonambiguous experience of the stimulus.

Subjects performed 8 blocks of 48 trials each over the course of the half-hour experiment. 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 using a 1-up, 2-down procedure (Levitt, 1971). In this thresholding task, participants discriminated the direction of the 30°-oriented Gabor patch in the absence of any attention cues. Each participant performed 64 trials of the thresholding task and the individual contrast thresholds were used for the main experiment.

Statistical Analyses

Behavior was analyzed by comparing d' in the Gabor discrimination task separately for when the cue and target were presented at the same location (i.e., “Same Loc”) vs. when they were presented at opposite locations (i.e., “Opp Loc”). D' is a Signal Detection Theory-based and bias-free measure of task performance that considers both hits and false alarms when assessing behavior (Green & Swets, 1966; Macmillan & Creelman, 2004). Perfect hit rates or false alarm rates were adjusted according to the (1/2N) rule (Macmillan & Kaplan, 1985). In

addition to d' , we also analyzed reaction time (i.e., RT) to investigate the possibility of cue-related benefits in target processing. RT was quantified as milliseconds (ms) from the onset of the response probe, which appeared at a fixed interval from the target (450 ms SOA). Only RTs from trials in which a correct response was given to the target were analyzed. To offset the characteristically skewed distribution of RTs, median RT values were analyzed. Vividness ratings were collected as an exploratory measure of task performance and are not analyzed in the present manuscript. Behavioral data were statistically analyzed using repeated-measures ANOVAs and paired t-tests ($\alpha = 0.05$) using R (R Core Team, 2019). Error bars in all figures represent 1 within-subjects standard error of the mean (SEM; Cousineau, 2005).

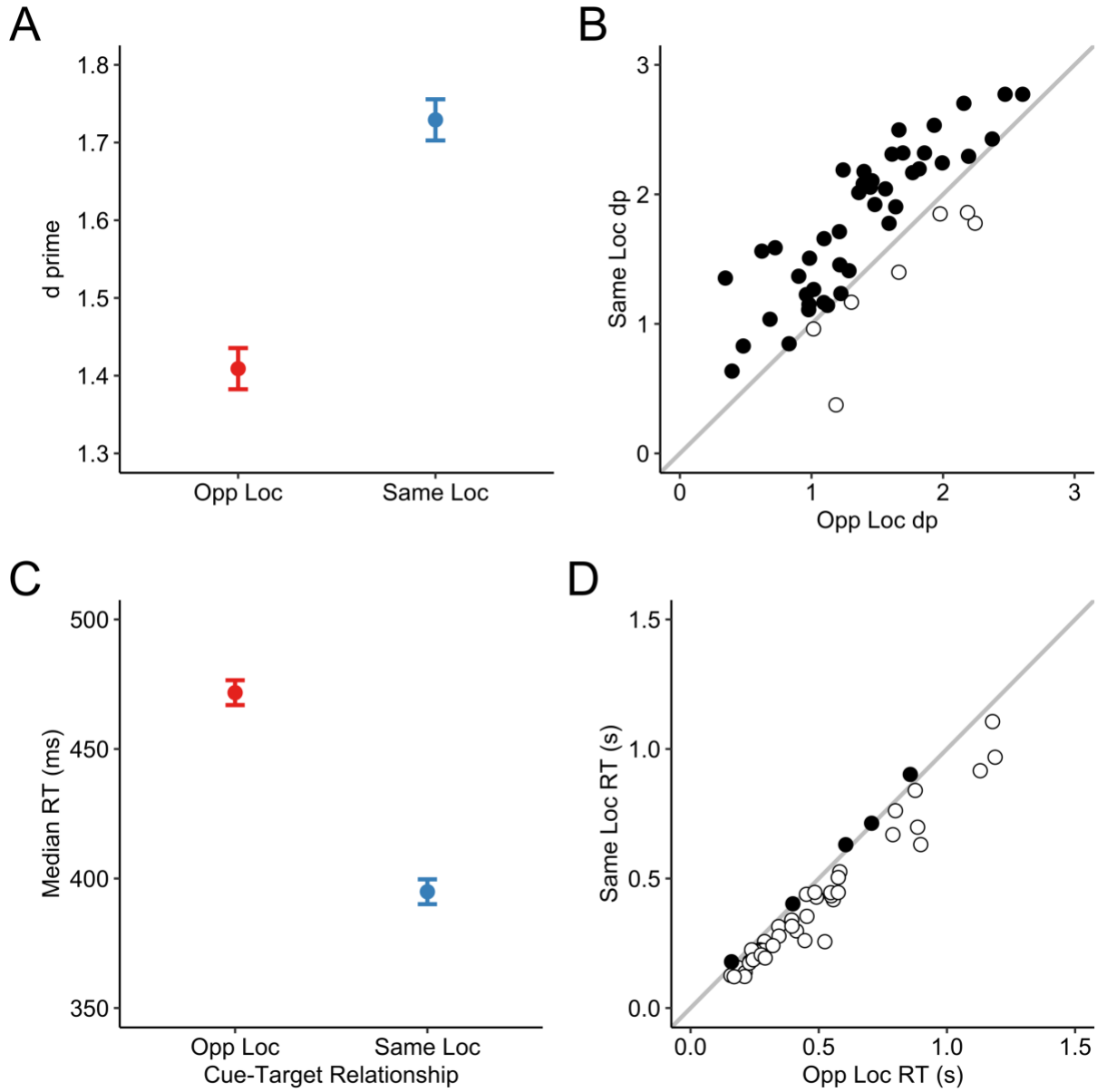


Figure 3.2. Target discrimination performance and RT in Experiment 1. D' is plotted as a function of cue-target relationship at the group-average (A) and individual level (B); and RT is similarly plotted as a function of cue-target relationship at the group-average (C) and individual level (D). Black dots in (B) and (D) indicate subjects that had higher d' or RT in the Same Location condition, whereas white dots indicate subjects that had higher d' or RT in the Opposite Location condition. Error bars represent ± 1 standard error of the mean.

Results and Discussion

Discrimination performance and RT in each condition of the target discrimination task is plotted in Fig. 2. To test for the presence of a behavioral cueing effect, we performed a paired-samples t-test comparing d' in the same location and opposite location conditions. This analysis revealed that d' was significantly higher when the target appeared at the same location as the cue vs. when each were presented at opposite locations, $t(49) = 6.04$, $p < .001$, $d = 0.57$. This indicates that attention was indeed drawn to the location of the salient but uninformative visual cue, leading to improved visual discrimination ability at the location of the cue.

To further investigate whether there was a cue-related benefit in target processing, we additionally performed a paired-samples t-test comparing RT in the same location and opposite location conditions. This analysis revealed that RT was significantly faster when the target appeared at the same location as the cue vs. when each were presented at opposite locations, $t(49) = 8.02$, $p < .001$, $d = 0.29$. These findings demonstrate that higher d' in the same location vs. opposite location condition cannot be explained by a trade-off between speed and accuracy and instead suggests that target processing was improved at the location of the cue. Overall, Experiment 1 demonstrates that exogenous cueing effects are not only replicable in online studies, but also remarkably consistent across subjects (see Fig. 2, B & D).

Experiment 2

In Experiment 2, we had subjects perform both the Non-Predictive Task outlined in Experiment 1 and a Counter-Predictive Task in which the cue indicated with 80% validity where the target would **not** appear. If subjects can exercise control over their reflexive responses to the salient cue, then we expected to see the pattern of better d' and RT in the same vs. opposite

location of the Non-Predictive Task diminish in magnitude, disappear, or even reverse in the Counter-Predictive Task. Conversely, if subjects are not able to exercise control over exogenous attentional orienting, then we expected to see a similar pattern of d' and RT across both tasks.

Method

Participants

Fifty participants from the UCSD community were included in the final sample of Experiment 2, which was performed online. All participants gave informed consent in accordance with the IRB guidelines of the Human Research Protections Program of the University of California, San Diego and received course credit for their participation (1 credit/hr). All participants were over 18 years old and reported having normal or corrected-to-normal vision and normal hearing. Participants were excluded if their d' across all conditions was less than 0.5, if their median RT was more than 2 standard deviations above the sample mean, or if they reported performing the task incorrectly (e.g., monitoring only one target location). 34 participants were excluded based upon these criteria, with 2 subjects reporting ignoring the cue in the Counter-Predictive Task and 7 subjects demonstrating a large negative d' ($d' < -1$) suggestive of a flipped stimulus-response mapping. All results hold when including all subjects with $d' > 0$.

Stimuli and Procedures

All stimuli and procedures were identical to Experiment 1 except as follows. On half of the blocks in Experiment 2, subjects performed the same exogenous cueing task as in Experiment 1 (Non-Predictive Task), where an uninformative cue at a randomly chosen target

location shortly preceded the Gabor patch target. However, for the other half of blocks in Experiment 2, this cue was now informative as to where the target would appear (Counter-Predictive Task). In this task, the spatial location of the cue indicated with 80% validity where the target would *not* appear. For example, if the cue was presented at the left target location, then this indicated that the target was very likely to appear at the right target location. All other aspects of this task were the same. Subjects were explicitly informed about this cue-target relationship and instructed to attempt to shift their attention as quickly as possible to the likely target location while maintaining fixation on the central fixation dot. The target appeared at the same latency from the cue with equal probability at each location across the block and was always followed by a mask at the same location.

Subjects performed 6 blocks of 40 trials of each task (12 blocks total) over the course of the one-hour experiment. Subjects performed 6 consecutive blocks of each task, with task order counterbalanced across subjects. Prior to the experimental tasks, task difficulty was adjusted for each participant according to the same procedure as in Experiment 1.

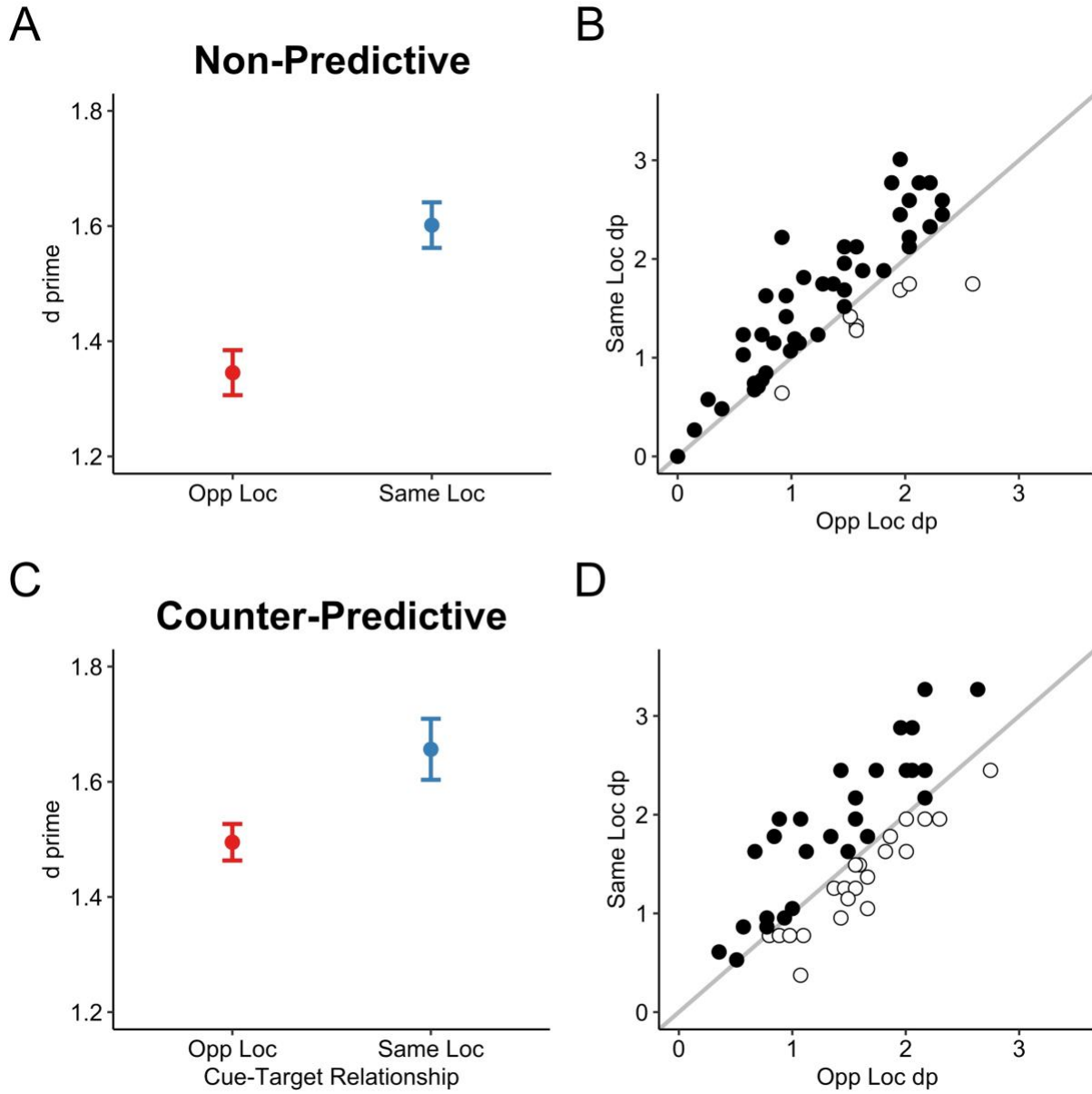


Figure 3.3. Target discrimination performance in both tasks of Experiment 2. D' is plotted as a function of cue-target relationship at the group-average (A) and individual level (B) in the Non-Predictive Task; and plotted as a function of cue-target relationship at the group-average (C) and individual level (D) in the Counter-Predictive Task. Black dots in (B) and (D) indicate subjects that had higher d' in the Same Location condition, whereas white dots indicate subjects that had higher d' in the Opposite Location condition. Error bars represent ± 1 standard error of the mean.

Results and Discussion

Discrimination performance and RT in each condition of each target discrimination task are plotted in Figures 3 and 4, respectively. To test for the presence of a behavioral cueing benefit in each task, we performed a two-way repeated-measures ANOVA with factors of cue-target relationship (Same Location, Opposite Location) and task (Non-Predictive, Counter-Predictive). This analysis revealed a significant main effect of cue validity, $F(1, 49) = 19.38, p < 0.001, \eta_p^2 = 0.28$, indicating that discrimination performance was better in the Same Location vs. Opposite Location condition. Additionally, there was a trend towards a main effect of task, $F(1, 49) = 3.28, p = 0.08, \eta_p^2 = 0.06$, suggesting that performance was overall better in the Counter-Predictive vs. Non-Predictive task. Critically, there was not a significant interaction between cue validity and task, $F(1, 49) = 1.53, p = 0.22, \eta_p^2 = 0.03$, indicating that there was no clear difference in the magnitude of the cueing effect between the Counter-Predictive and Non-Predictive tasks. As indicated by the lack of a significant interaction, follow-up t-tests revealed that there was an effect of cue-target relationship in the Non-Predictive task, $t(49) = 4.68, p < 0.001, d = 0.37$, and in the Counter-Predictive task, $t(49) = 2.42, p = 0.02, d = 0.24$.

To investigate whether this pattern was mirrored in the RT data, we performed a two-way repeated-measures ANOVA with factors of cue-target relationship (Same Location, Opposite Location) and task (Non-Predictive, Counter-Predictive). This analysis indicated that there was neither a main effect of cue-target relationship, $F(1, 49) = 2.46, p = 0.12, \eta_p^2 = 0.05$, nor a main effect of task, $F(1, 49) = 0.03, p = 0.86, \eta_p^2 = 0.001$, indicating that RT did not generally vary between cue conditions or tasks. Critically, however, there was a significant interaction between cue validity and task, $F(1, 49) = 12.81, p = 0.001, \eta_p^2 = 0.21$. This indicates that the pattern of RT

to same-location and different-location cues differed between the two tasks, with RTs being faster in the same-location condition of the Non-Predictive task, $t(49) = 4.20, p < 0.001, d = 0.16$, and not differing between conditions in the Counter-Predictive task, $t(49) = 1.00, p = 0.32, d = 0.06$.

Overall, these results demonstrate a novel dissociation between our measures of target processing in the Counter-Predictive Task: while subjects demonstrate the ability to resist attentional capture in our RT measure, there is still a cueing effect in d' as was observed in the Non-Predictive Task. This result suggests that subjects are indeed sensitive to the information conveyed by the cues of the Counter-Predictive task, as they no longer responded more quickly to targets at the same location as the cue. However, despite this sensitivity, subjects still demonstrated better discrimination performance in the same location condition. Therefore, we find some preliminary but mixed evidence that subjects can exert some control over their exogenous attentional orienting. The results of Warner et al. (1990, Experiment 2) suggest that this effect may emerge more clearly with greater practice, however, so in Experiment 3 we tested this possibility.

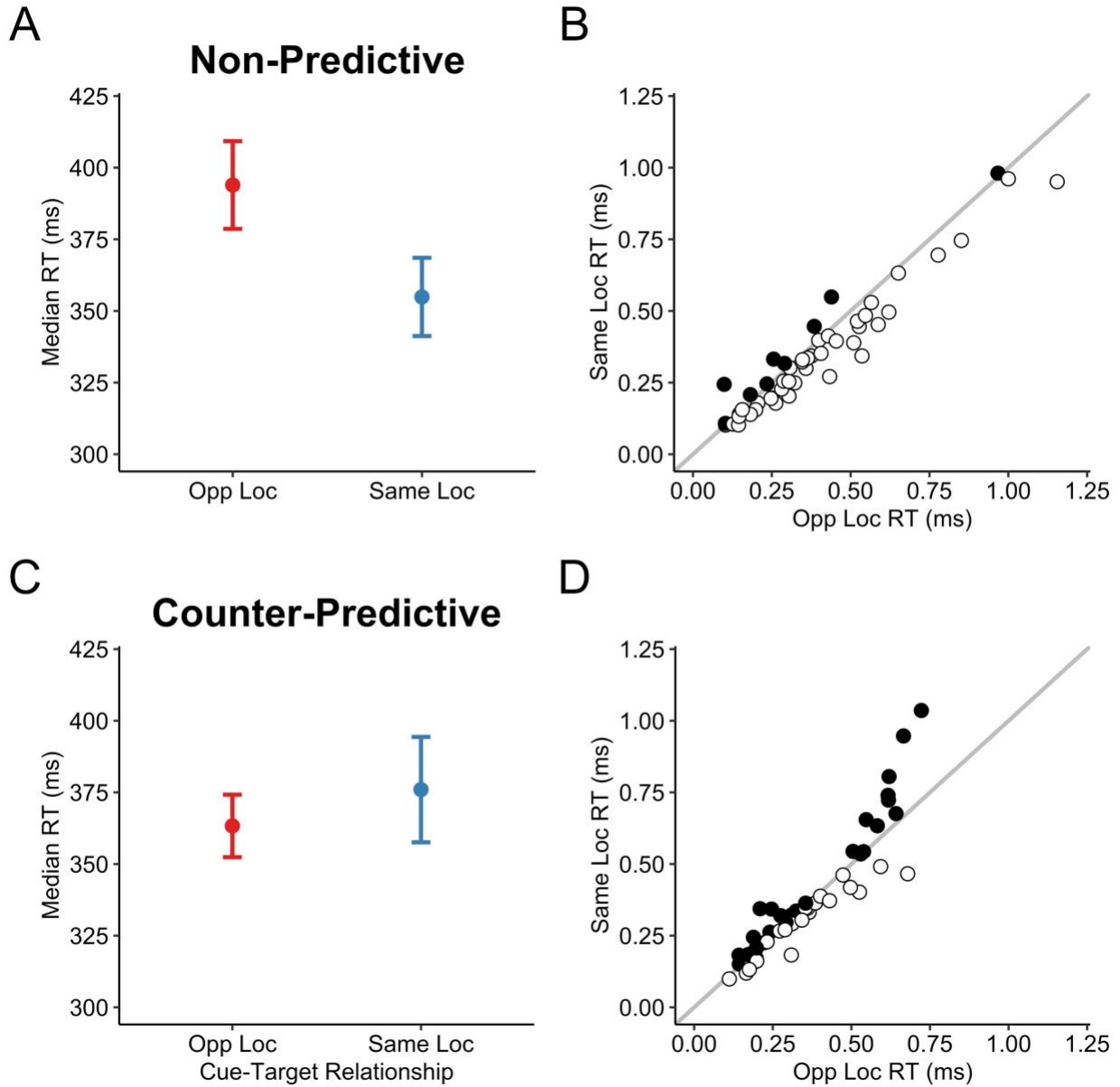


Figure 3.4. RT in both tasks of Experiment 2. RT is plotted as a function of cue-target relationship at the group-average (A) and individual level (B) in the Non-Predictive Task; and plotted as a function of cue-target relationship at the group-average (C) and individual level (D) in the Counter-Predictive Task. Black dots in (B) and (D) indicate subjects that had higher RT in the Same Location condition, whereas white dots indicate subjects that had higher RT in the Opposite Location condition. Error bars represent ± 1 standard error of the mean.

Experiment 3

In Experiment 3, we sought to replicate the results of the Counter-Predictive Task in Experiment 2 as well as test whether more experience in the task may modulate the extent to which subjects can resist or re-map their orienting response to the cue. Accordingly, subjects performed twice as many blocks of the Counter-Predictive Task as in Experiment 2 and only performed this task. This allowed us to investigate whether the changes in RT found in the previous experiment are the result of learning/practice over the course of many trials, as suggested by Warner et al. (1990), and test whether a similar pattern may emerge in d' .

Method

Participants

One hundred participants from the UCSD community were included in the final sample of Experiment 3, which was performed online. Sample size was doubled in this experiment vs. previous experiments to increase statistical power and allow for post-hoc investigations of individual differences if appropriate. All participants gave informed consent in accordance with the IRB guidelines of the Human Research Protections Program of the University of California, San Diego and received course credit for their participation (1 credit/hr). All participants were over 18 years old and reported having normal or corrected-to-normal vision and normal hearing. As in the first two experiments, participants were excluded if their d' across all conditions was less than 0.5, if their median RT was more than 2 standard deviations above the sample mean, or if they reported performing the task incorrectly (e.g., monitoring only one target location or ignoring the cue). 73 participants were excluded based upon these criteria, with 8 of these participants reporting that they did not utilize the cue and 4 subjects demonstrating a large

negative d' ($d' < -1$) suggestive of a flipped stimulus-response mapping. The results of the d' analysis below hold when including all subjects with $d' > 0$. The results of the RT analysis seem to indicate a flipped RT cueing effect when applying the same loosened inclusion criterion, but further inspection demonstrates that this is the result of including a few RT outliers that demonstrated tremendously slower RT in the same location vs. opposite location condition (~200 – 300 ms difference).

Stimuli and Procedures

In Experiment 3, subjects performed only the Counter-Predictive cueing task described in Experiment 2. Subjects performed 12 blocks of 40 trials over the course of the one-hour experiment. In this experiment, subjects were not asked to provide a vividness rating following their target response. Prior to the experimental task, task difficulty was adjusted for each participant according to the same procedure as in Experiment 1.

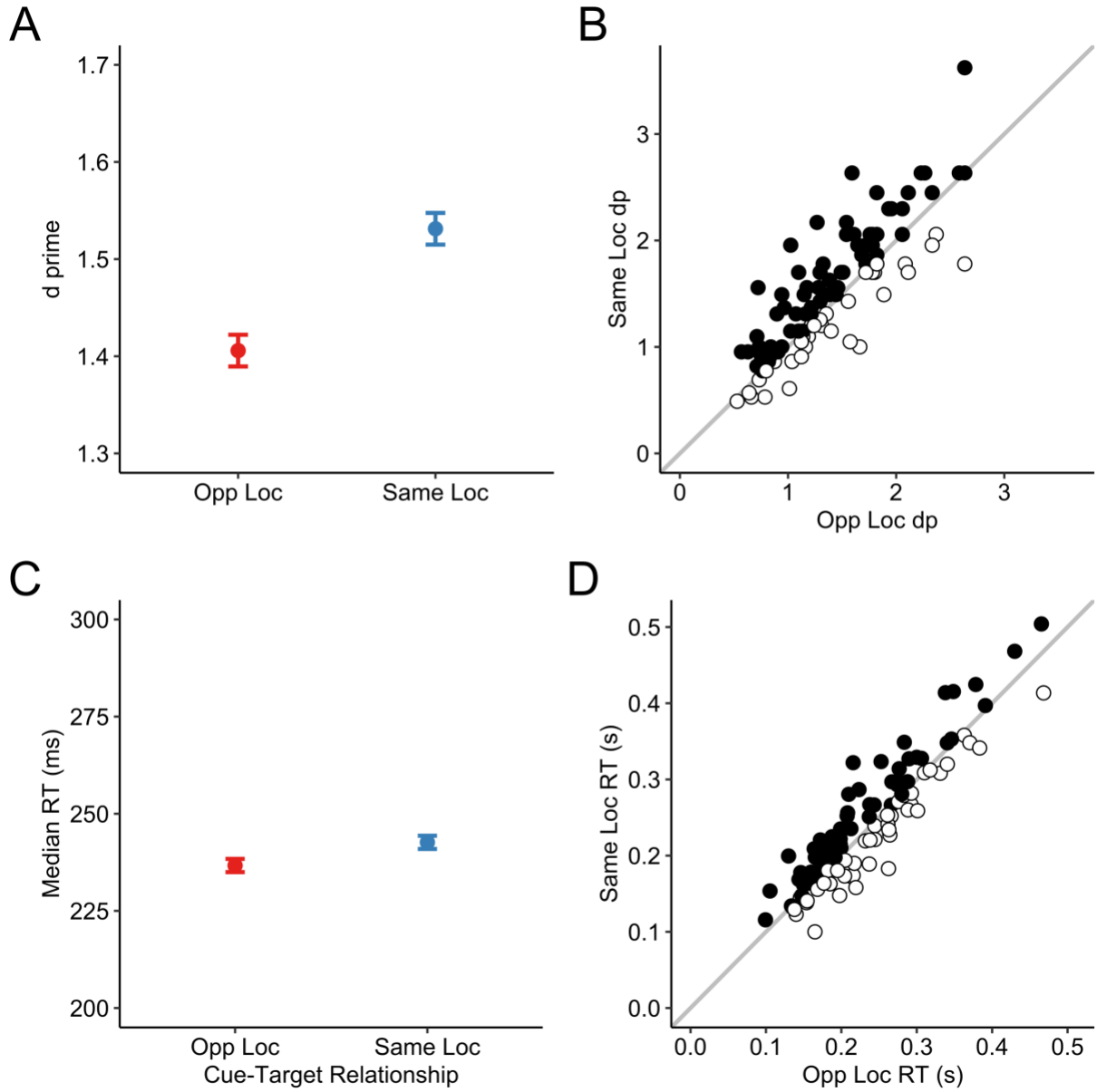


Figure 3.5. Target discrimination performance and RT in Experiment 3. D' is plotted as a function of cue-target relationship at the group-average (A) and individual level (B); and RT is similarly plotted as a function of cue-target relationship at the group-average (C) and individual level (D). Black dots in (B) and (D) indicate subjects that had higher d' or RT in the Same Location condition, whereas white dots indicate subjects that had higher d' or RT in the Opposite Location condition. Each of these metrics clearly reveals a benefit in target processing at the same vs. opposite location condition. Error bars represent ± 1 standard error of the mean.

Results and Discussion

Discrimination performance and RT in each condition of the target discrimination task is plotted in Fig. 5. To test for the presence of a behavioral cueing benefit, we performed a paired-samples t-test comparing d' in the same location and opposite location conditions. This analysis revealed that d' was significantly higher when the target appeared at the same location as the cue vs. when each were presented at opposite locations, $t(99) = 3.84, p < 0.001, d = 0.22$. This indicates that attention was still drawn to the location of the salient visual cue, leading to improved visual discrimination ability at the location of the cue despite the target being likely to appear in the opposite location. As in the Counter-Predictive Task of Experiment 2, this effect was smaller than in the Non-Predictive Tasks of the first two experiments though indeed still substantial in size.

To investigate whether there was still a cue-related benefit in RT, we performed a paired-samples t-test comparing RT in the same location and opposite location conditions. This analysis revealed that RT was not significantly different in the same vs. opposite location conditions, $t(99) = 1.75, p = 0.08, d = 0.07$. A follow-up Bayesian statistical analysis utilizing a Scaled Jeffrey-Zellner-Siow prior distribution indicated that the null hypothesis (i.e., no effect of the cue) was nearly three times as likely as the alternative hypothesis (i.e., cue-related differences in RT; $BF_{01} = 2.84$), providing further evidence that there was no difference between the conditions. These findings demonstrate that higher d' in the same location vs. opposite location condition cannot be explained by a trade-off between speed and accuracy, but that there was no benefit in RT to targets in the opposite vs. same location condition as might have been expected based on other experiments both here and in previous studies. Overall, these results replicate the

dissociation between our measures of target processing in the Counter-Predictive Task, with nearly identical effect sizes across the two studies.

In a follow-up analysis, we explored whether the decreased effect sizes in d' and lack of RT effect in Experiment 3 emerged gradually over the course of the experiment, as could be anticipated based upon Warner et al. (1990). To do this, we split each subject's data into quarters, consisting of 3 blocks each in their order of performance. The results of this qualitative analysis are plotted in Figure 6, which plots d' and RT for each cue condition over the quarters of the experiment. It is clear from this analysis that subjects demonstrate very different patterns of d' and RT, neither of which support the idea that these effects are the result of learning/practice over time. As indexed by d' , target discrimination performance is consistently better in the same vs. opposite location condition, and the size of this benefit remains constant throughout the experiment. This suggests that subjects' inability to resist capture in Experiment 2 as indexed by d' is not the result of insufficient training or practice. Conversely, as indexed by RT, the speed of target discrimination started out faster in the opposite vs. same location condition, but this difference quickly became negligible by the second quarter of the experiment. Overall, this analysis reveals a striking dissociation between the d' and RT measures and suggests that practice was not a significant factor in subjects' inability to resist attending to the location of the cue in the present results.

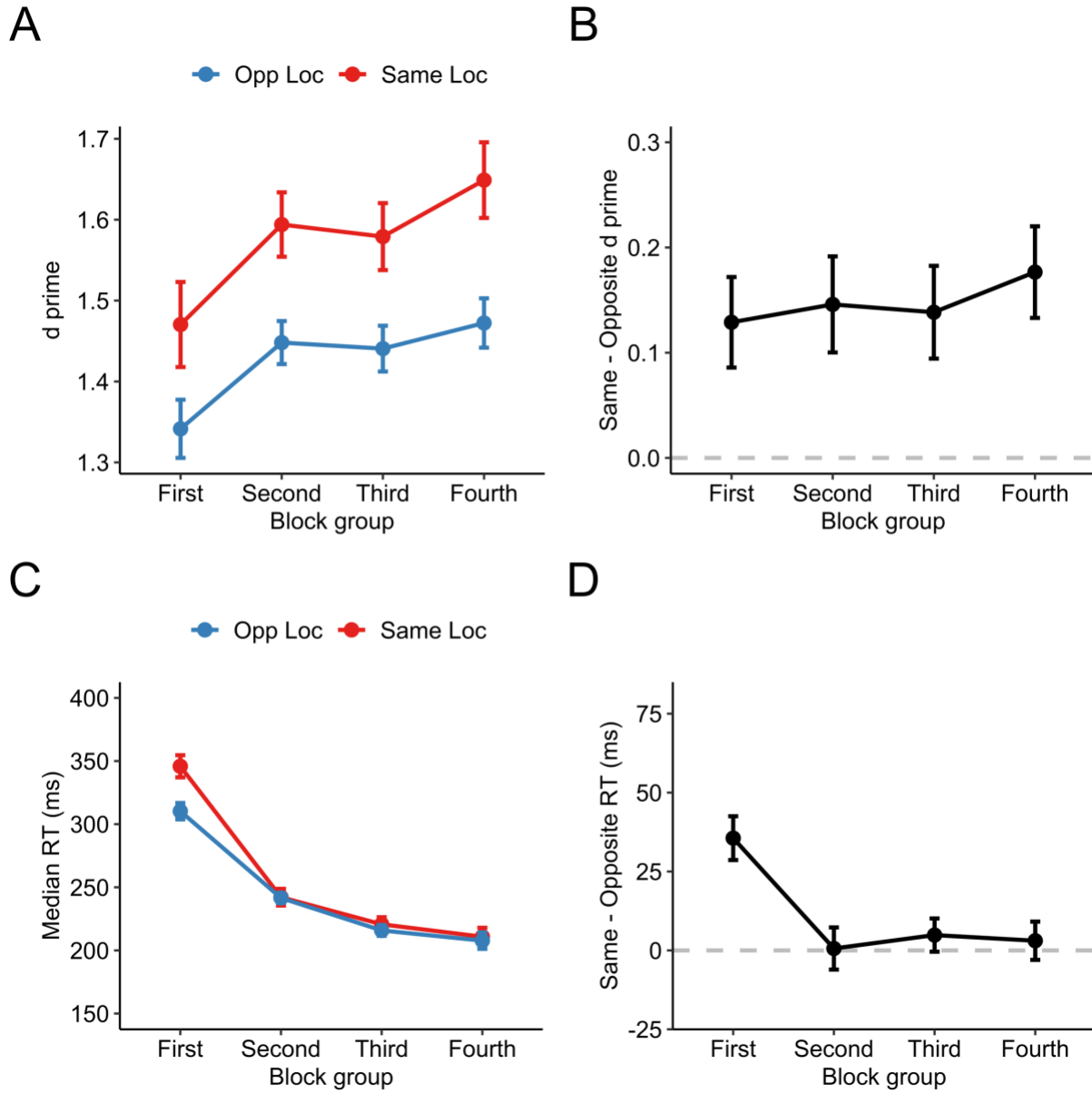


Figure 3.6. Target discrimination performance and RT in Experiment 3, split by quarter of experiment. D' is plotted as a function of experiment quarter for both cueing conditions (A), with the same – opposite difference in d' plotted alongside (B). RT is similarly plotted as a function of experiment quarter for both cueing conditions (C), with the same – opposite difference in RT plotted alongside (D). Error bars represent ± 1 standard error of the mean.

General Discussion

Classic experiments and theories of spatial attention suggest that attention can be oriented exogenously through capture by a salient event or endogenously based upon task goals (for a review, see Carrasco, 2011). One critical distinction between these two types of attention rests in how much control individuals have over each process: whereas exogenous attention is presumed to act reflexively and without volitional control, endogenous attention is presumed to depend critically upon an individual's goals and is thus deployed voluntarily. However, surprisingly little research has attempted to directly test to what degree exogenous attention can be modulated by the information conveyed by the cue and related task goals. In fact, the studies that have tested this have yielded equivocal findings reliant upon interpreting RT alone (Lambert, Spencer, & Mohindra, 1987; Warner et al., 1990; Tepin & Dark, 1992). Therefore, we attempted to test this presumption across 3 large online studies measuring both d' and RT in both a typical exogenous cueing paradigm (i.e., Non-Predictive Task) and another stimulus-matched paradigm in which the cue was counter-predictive as to where a target would appear. As expected, we found that subjects were more accurate and responded more quickly to targets at the location of the cue in the Non-Predictive Tasks of Experiment 1 and 2. If subjects can exercise control over their exogenous attentional orienting, then we expected to see this pattern of better d' and RT at the location of the cue disappear or even reverse following the cues of the Counter-Predictive Task. Indeed, we found that RT did not differ when the cue and target appeared at the same vs. opposite locations. Critically, however, we found that d' continued to be higher when the cue and target appeared at the same vs. opposite locations – despite the cue indicating that the target was likely to appear at the opposite location. This continued to hold true even when subjects performed twice as many trials, with follow-up analyses demonstrating no evidence of changes

to this pattern over the course of nearly 500 trials. Broadly, this finding suggests that individuals are not able to exert control over their exogenous attentional orienting – at least not within an experimental session of nearly 500 trials.

One surprising result of the present study is the striking dissociation between the d' and RT measures of the Counter-Predictive task. Indeed, based upon the RT measure alone one might conclude that subjects were able to resist or re-map their reflexive response to the salient cues to some extent, as was found in previous studies employing similar paradigms (Warner et al., 1990; Tepin & Dark, 1992). However, we find that these effects are not mirrored in d' – our bias-free measure of perceptual sensitivity – which continues to demonstrate same-location benefits regardless of cue predictability. Why would d' and RT differ in their pattern across the two tasks? One possible explanation is that RT is a more sensitive measure in this context, and that subjects could also show effects in d' given more time to practice with the counter-predictive cues. However, this seems unlikely given that subjects do not demonstrate any improvements in their ability to ignore the cue over the course of Experiment 3 as indexed by d' or RT. Instead, it seems to be the case that the RT differences do not index the effects of attention at all. As depicted in Fig. 6, RT differences are only reliably observed at the beginning of the experiment. As subjects grew accustomed to the cueing contingencies over the first quarter of the experiment, this RT difference disappeared – as indicated by the lack of RT effects in the final $\frac{3}{4}$ of the study. This suggests that differences in RT seen at the beginning of the experiment simply reflect delayed responses when subjects are surprised by infrequent violations of the cue contingencies in the same location condition of the Counter-Predictive Task; and as subjects grew accustomed to the less frequent “same location” trials, this effect disappeared. Therefore, the most parsimonious account of this data is that subjects are sensitive to the information

conveyed by the cue, as demonstrated by the RT measure, but that they are unable to overcome the exogenous orienting of attention to the location of the cue, as indexed by consistently higher d' at the location of the cue. This supports the idea that RT is an indirect measure of the quality of target processing, as it is susceptible to biases and changes in several cognitive and motor processes. In contrast, d' provides a bias free and direct measure of the representational quality of the target, which did not reliably change over the course of the experiment.

In some ways, our task resembles an antisaccade task, in which subjects are presented with a cue at one location indicating that they must plan and execute an eye movement to the opposite side of a visual display. Relevant to the present study, research utilizing this paradigm indicates that subjects often perform errant saccades to the location of a cue and typically take ~100 – 150 ms longer to effectively perform an antisaccade away from a cue than a prosaccade towards a cue (Walker et al., 2000; Munoz & Everling, 2004). While the extremely short SOA (150 ms) of the present study means that eye movements were not possible given that they require ~200 ms to plan and execute (Munoz & Everling, 2004), it is possible that the successful control of exogenous attention similarly requires a greater amount of time. However, the parallels between the antisaccade task and our Counter-Predictive Task raise an important question about how this re-mapping would be interpreted. In the antisaccade task, a successful antisaccade is assumed to be the result of both inhibiting a reflexive saccade to the location of the cue and then executing a volitional saccade to the opposite location (Hutton & Ettinger, 2006). This idea is mirrored in visual search literature suggesting that exogenous attention acts reflexively but can be suppressed by endogenous attentional mechanisms to effectively orient attention within a display (Gaspelin & Luck, 2018). However, as laid out in the introduction, the focus of the present study is whether exogenous attention can be placed under volitional control,

not the interplay between exogenous and endogenous attention. Therefore, should the pattern of better d' at the cued location flip when subjects are afforded more time between the counter-predictive cue and target, it is important to distinguish whether this is the result of endogenously suppressing reflexive attentional orienting or the re-mapping of exogenous attention itself.

Neuroimaging may prove particularly useful in distinguishing between these possibilities. Previous research has demonstrated that exogenous cues elicit increased activity in visual cortex following both salient visual stimuli (Störmer, McDonald, & Hillyard, 2019) and auditory stimuli (Störmer, McDonald, & Hillyard, 2009; Feng et al., 2014; Keefe & Störmer, 2021; Keefe, Pokta, & Störmer, 2021). Critically, this increased activity is localized to the hemisphere of visual cortex that is responsible for processing the cued location and is consequently interpreted as reflecting the effects of attention upon visual cortical processing (Keefe & Störmer, 2021). Therefore, measuring this activity following a counter-predictive cue can provide additional evidence as to whether attention is reflexively oriented to the location of the cue and then suppressed or is instead reflexively oriented to the opposite location. Given the present behavioral findings, we predict that we would see the previously demonstrated pattern of increased activity in the hemisphere responsible for processing the cued location. However, it would be particularly interesting to examine the exact time course of these effects to see whether the initial enhancement of processing at the location of the cue sustains or possibly reverses and flips to the opposite location; and relating the temporal dynamics of this neural activity to behavior should prove especially useful.

Overall, our data demonstrate that subjects are unable to exercise control over the exogenous orienting of attention to the location of salient stimuli. While this finding is in line with existing conceptions of exogenous attention, the experiments presented here offer a novel

and critical test of this presumption by including both d' and RT measures in a task that heavily incentivizes resisting attention to the cue. Altogether, the present study indicates that there is indeed a clear divide between the control that individuals can exert over exogenous and endogenous attention, with subjects having control over only the latter.

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Chapter 3, in full, is being prepared for submission for publication of the material. Keefe, Jonathan M.; Störmer, Viola S. The dissertation author was the primary investigator and author of this paper.

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CONCLUSION

The present dissertation sought to examine and more fully characterize exogenous attention and its relationship to endogenous attention. Across three chapters, I uncovered both striking similarities and differences between the two types of attention. Chapter 1 indicates that exogenous and endogenous attentional orienting result in common changes of neural activity in visual cortex, though they do indeed vary in time course. Chapter 2 suggests that exogenous attention uniquely operates by facilitating visual processing at attended locations and not by suppressing processing at unattended locations, suggesting that only endogenous attention results in suppression. Further delineating between these two types of attention, Chapter 3 demonstrates that exogenous attention is not modulated by task goals (i.e., informativity of the cue), and thus appears to operate outside of one's volitional control. Broadly, these findings suggest that many of the distinctions drawn between the two types of attention are justified, and that this dichotomy is often accurate in describing the characteristics of attention.

At the same time, the results of this dissertation demonstrate that the explanatory power of this dichotomy can be extremely limited. Take, for example, the Hybrid Task utilized in Chapter 1, where a peripheral cue indicated where a target was likely to occur. We found that attention-mediated neural activity following the informative, peripheral cue emerged quickly and sustained throughout the entire cue-target interval. While one could interpret this finding as evidence that separate attentional systems can work together to involuntarily orient and voluntarily sustain attention to a location, a researcher naïve to existing models of attention may instead have concluded that there is only a single attentional system involved in this process. Indeed, this conclusion seems increasingly favorable when considering Occam's razor. Along the same lines, the lack of attentional suppression following the salient cues of Chapter 2 may

not be an indicator of different mechanisms underlying each type of attention. Instead, this finding may simply reflect the fact that a single attentional system is responsible for both facilitating and suppressing processing at spatial locations, but that facilitation simply emerges more quickly than suppression when deploying in response to a cue.

Therefore, it seems appropriate to consider the dichotomous model of attention as being an effective framework for *describing* the effects of attention but perhaps not as a comprehensive model of its causes and effects. The strength of this model is that it has allowed researchers to characterize the mechanisms, time courses, and neural correlates of attention. However, these characteristics do not clearly necessitate a dichotomous model of attention. As an example of how these mechanisms may be incorporated into a non-dichotomous model, I propose a speculative but plausible descriptive model of attention based upon these findings and key literature. In this model, attention is deployed to behaviorally relevant information in the environment thanks to activity in a singular but disparate network of areas in the brain. This network is comprised of both frontal areas, presumably responsible for monitoring ongoing goals and states of the world, and the parieto-occipital areas associated with deploying attention to a location and exerting its effects. The time course of these effects varies based upon the salience and interpretability of the behaviorally relevant information in the environment. While attention acts nearly instantly when a location is easy to pick out and orient to, thanks perhaps to a salient stimulus being presented there, it may deploy more slowly when it takes longer to map information or goals to a relevant location. Importantly, the time course of this process is not dichotomous and can vary continuously based upon these factors. The results of this deployment are both facilitation of processing at the attended location and suppression of processing at unattended locations, though the active vs. passive nature of this suppression is up for debate.

Importantly, facilitation emerges more quickly than suppression, as the location of this information is typically more readily identified. For example, a target must be identified for prioritization before other stimuli can be labeled as distractors for suppression. This exercise reveals that it is not difficult to accommodate what is known about attention in a model where there is no dichotomy, and many of the findings outlined in the present dissertation argue that it is useful to think of attention in this manner.

Considering these findings and others as part of a more comprehensive framework will undoubtedly be integral to understanding attention in the real world, where bottom-up and top-down factors are constantly interacting. For example, as pointed out in the discussion of Chapter 1, salient events in the real world that involuntarily orient attention are often indicative of behaviorally relevant information that individuals are voluntarily searching for. Though this observation is trivial, dichotomous models must invoke neural mechanisms for coordinating the interactions between the two attentional systems to explain how humans can navigate even the most basic real-world environment. Still, resolving this issue is not as simple as dropping the dichotomy. There are several findings not accommodated by the purposefully simplistic model outlined above, including the different neural networks that appear to be engaged in response to central and peripheral cues. However, the results of this dissertation and their implications suggest that the characteristics of attention as described by dichotomous models of attention can and should be re-evaluated from a critical and novel perspective to advance our understanding of selective attention beyond the confines of our current paradigms.