

Interactions between endogenous and exogenous attention on cortical visual processing

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Sensory processing is affected by both endogenous and exogenous mechanisms of attention, although how these mechanisms interact in the brain has remained unclear. In the present study, we recorded event-related potentials (ERPs) to investigate how multiple stages of information processing in the brain are affected when endogenous and exogenous mechanisms are concurrently engaged. We found that the earliest stage of cortical visual processing, the striate-cortex-generated C1, was immune to attentional modulation, even when endogenous and exogenous attention converged on a common location. The earliest stage of processing to be affected in this experiment was the late phase of the extrastriate-cortex-generated P1 component, which was dominated by exogenous attention. Processing at this stage was enhanced by exogenous attention, regardless of where endogenous attention had been oriented. Endogenous attention, however, dominated a later, higher-order stage of processing indexed by an enhancement of the P300 that was unaffected by exogenous attention. Critically, between these early and late stages, an interaction was found wherein endogenous and exogenous attention produced distinct, and overlapping, effects on information processing. At the same time that exogenous attention was producing an extended enhancement of the late-P1, endogenous attention was enhancing the occipital–parietal N1 component. These results provide neurophysiological support for theories suggesting that endogenous and exogenous mechanisms represent two attention systems that can affect information processing in the brain in distinct ways. Furthermore, these data provide new evidence regarding the precise stages of neural processing that are, and are not, affected when endogenous and exogenous attentions interact. © 2005 Elsevier Inc. All rights reserved.

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Introduction

Attention mechanisms bias information processing in the brain, leading to a selective perception of a small subset of the vast amount of information continually inundating our senses. Attention is thought to include both endogenous (i.e., voluntary, top-down, internally driven) and exogenous (i.e., involuntary, bottom-up, externally driven) mechanisms. Exogenous mechanisms can be triggered reflexively by a salient sensory event (e.g., a flash in the periphery) whereas endogenous mechanisms involve a more purposeful and effortful orienting process (e.g., orienting to a location based upon instructive information at another location). Behavioral studies have revealed a number of differences between these systems. Exogenous attention is oriented more rapidly, is less susceptible to interference, and does not place the demands on cognitive resources that endogenous attention does (Cheal and Lyon, 1991; Jonides, 1981; Müller and Rabbitt, 1989; Posner et al., 1978). Furthermore, endogenous attention may be maintained at a location for extended periods, whereas the initial facilitation following exogenous orienting is replaced at longer intervals by a slowing of responses to stimuli at the exogenously cued location (an effect termed inhibition of return, “IOR,” by Posner and Cohen, 1984). Despite the fact that it is generally agreed that attention may be oriented in an exogenous or endogenous manner, there is uncertainty regarding whether these mechanisms simply reflect two modes of orienting a unitary focus of attention, or rather represent two distinct attention systems, each capable of biasing neural activity via different mechanisms.

A number of neuroimaging studies have concluded that endogenous and exogenous orienting rely upon largely the same neural architecture (Corbetta et al., 1993; Kim et al., 1999; Nobre et al., 1997; Rosen et al., 1999; Peelen et al., 2004), thereby suggesting a unitary focus of attention that can simply be engaged through somewhat different means. The few differences in neural activity were typically taken as evidence that additional processes may have been engaged exclusively in one condition or the other to orient a common attentional focus (e.g., frontal activity related to maintaining an endogenous attentional set in working memory; temporal–parietal activity related to the disengagement of attention

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necessary after an invalid exogenous cue), and were not usually considered to be an indication of two separate and independent attention systems. A more recent neuroimaging study (Mayer et al., 2004), however, compared exogenous and endogenous orienting using the cue-to-target intervals that would be expected to yield the strongest facilitation effects for each type of attention (i.e., shorter cue–target intervals for exogenous cuing). This critical aspect of the study allowed the authors to find evidence for a greater differentiation between these systems, with much of the typical attentional network (i.e., frontal eye fields, intraparietal sulcus, superior temporal gyrus, temporo-parietal junction) being activated by endogenous attention but not by exogenous attention. In addition, a recent fMRI study of overt attention similarly found distinct differences between the neural systems supporting voluntary vs. reflexive saccades (Mort et al., 2003). Voluntary saccades produced greater activity in the frontal eye fields and intraparietal sulcus, while reflexive saccades produced greater activity in the angular gyrus of the inferior parietal lobe. These recent studies provide new evidence suggesting separable endogenous and exogenous attention systems. If the systems are in fact distinct, however, a question still remains of whether they modulate information processing in the brain in the same way and at the same stages of processing. Further, it is unclear how these systems interact when both are engaged simultaneously. Does one or the other have priority at certain stages of processing, or do they affect distinct stages of processing and therefore modulate processing independently of one another?

Theories proposing that endogenous and exogenous mechanisms simply reflect two modes of orienting a single unitary attention system would predict that, when in competition, the more powerful orienting system at a given moment would control the placement of a single focus of attention. Thereby, the effects on information processing at all stages of analysis should be a function of where that mode of orienting placed attention, with little or no effect of the less powerful orienting system. According to such a model, if a highly salient event triggers an exogenous orienting away from a desired location, all information processing in the brain should be enhanced only for stimuli at the captured location. If one subsequently re-oriens, endogenously, to the desired location, information only at this location would be enhanced. Although this series of events would correspond well to the phenomenological experience of a single focus of attention moving sequentially, the underlying mechanisms that lead to this experience could be more complex. For example, consistent with biased competition accounts of attention (e.g., Desimone and Duncan, 1995), the experience of a unitary focus of attention may be the end result of biased processing at multiple levels within the brain. Accordingly, endogenous and exogenous mechanisms could independently and concurrently affect various stages of processing that precede conscious awareness, with the spatial location or object that receives the greatest amount of overall processing becoming the focus of the mind's eye because it was the beneficiary of greater processing relative to all other stimuli at that time. Bisley and Goldberg (2003) reported activity in the lateral intraparietal area (LIP) that is consistent with the view that endogenous and exogenous mechanisms can be active concurrently and have independent effects. Specifically, they found that endogenous mechanisms modulated activity in cells coding the spatial location of a planned saccade. When an irrelevant abrupt onset distracter appeared and triggered exogenous mechanisms at a different spatial location, activity in the cells coding the spatial

location of that distracter transiently exceeded the activity in the cells coding the endogenously attended location. Critically, however, the appearance of the abrupt distracter did not modulate the activity in the cells coding the endogenously attended location. In other words, the enhancement of activity in LIP neurons by endogenous mechanisms was independent of the effects that exogenous mechanisms had on other LIP neurons coding the location of the distracter stimulus. Although the endogenous effects on LIP activity did not change when exogenous attention was engaged at other locations, at any given moment, the psychophysical benefits of attention were only observed at the spatial location that corresponded to the relatively most active population of LIP neurons. These results highlight how a unitary 'focus of attention' can emerge in overt behavioral measures, even though earlier levels of processing reflect separate and concurrent effects of endogenous and exogenous mechanisms.

Investigations using behavioral measures to examine how exogenous and endogenous systems interact have not provided consistent conclusions. A number of these studies suggested that exogenous and endogenous orienting compete for the control of a unitary focus of attention, although results differed in terms of which type of orienting was dominant. Early studies suggested that exogenous orienting disrupts the focus of endogenous attention, with highly salient visual events automatically capturing attention away from the voluntarily attended location (e.g., Jonides, 1981; Müller and Rabbitt, 1989). Other studies, however, found that exogenous orienting could be prevented if endogenous attention were highly focused on an object or location before the appearance of the potentially distracting stimulus (Yantis and Jonides, 1990). Folk and colleagues (Folk et al., 1992) have suggested that exogenous orienting is actually dependent on top-down control. Specifically, in a number of experiments, nonpredictive peripheral cues only "captured attention" (defined as enhanced reaction times to cued location targets relative to uncued location targets) when those cues shared key attributes with the expected target stimuli. Recent results, however, suggest that exogenous orienting can be automatic and independent of top-down control, at least for certain highly salient stimuli, even though this automatic orienting is sometimes obscured in overt reaction time measures (e.g., Theeuwes et al., 2000). These studies differ in the conclusions regarding the precise mechanisms of interaction between exogenous and endogenous systems, but generally agree in interpreting the results as indexing the locus of a single unitary focus of attention.

Other behavioral research, however, has provided evidence that exogenous and endogenous attention are not simply two modes of orienting a unitary focus of attention, but rather are distinct systems that affect information processing in different ways (e.g., Briand, 1998; Briand and Klein, 1987; Han et al., 2005). Furthermore, recent research suggests that voluntary and involuntary attention mechanisms may be able to produce simultaneous and independent effects (Friesen and Kingstone, 2003; Friesen et al., 2004). In order to better understand the nature of the interaction between endogenous and exogenous attention, it would be desirable to observe the effects of these interacting mechanisms at multiple stages of information processing in the brain.

One useful method for exploring such interactions is scalp-recorded event-related brain potentials (ERPs). ERPs index neural processing with high temporal resolution, and therefore provide a means of investigating the rapid processing and multiple effects of attention that precede, and may go unobserved in some measures

of, overt behavior (e.g., Handy et al., 2001a,b). Previous ERP studies have separately investigated the effects of endogenous and exogenous attention. Endogenous attention alone has been shown to enhance neural activity at multiple stages of information processing (Eason et al., 1969; Van Voorhis and Hillyard, 1977). Numerous studies have found that endogenous attention enhances visual stimulus processing as early as the extrastriate-generated P1 component (e.g., Clark and Hillyard, 1996; Di Russo et al., 2003; Heinze et al., 1994; Mangun and Hillyard, 1991; Mangun et al., 1997; Martinez et al., 1999). The N1 component, a slightly longer latency visual-evoked component, has also been shown to be enhanced at endogenously cued locations (Eason et al., 1969; Van Voorhis and Hillyard, 1977), although the enhancement of this component may depend on the difficulty and type of task being performed (Handy and Mangun, 2000; Mangun and Hillyard, 1991; Luck, 1995; Vogel and Luck, 2000). The P300 component, thought to index higher-order stages of information processing related to working memory updating and decision-making, can also be enhanced by endogenous attention. One critical level of processing that has not been found to be modulated by endogenous attention is the earliest visually evoked cortical component, the C1 (peaking ~70–80 ms, and sometimes referred to as the NP80: negative polarity for upper visual field stimuli, positive polarity for lower visual field stimuli). The neural generator of the C1 has been localized to striate cortex (e.g., Clark et al., 1995; Martinez et al., 2001; Noesselt et al., 2002; Di Russo et al., 2003), and existing evidence suggests that this initial stage of processing in striate cortex is immune to the effects of endogenous attention (e.g., Anllo-Vento et al., 1998; Clark and Hillyard, 1996; Di Russo et al., 2003; Martinez et al., 2001). Striate cortex does, however, appear to be modulated by attention at longer latencies, via later re-entrant processes (e.g., Martinez et al., 1999).

The effects of exogenous attention on stimulus processing have also been investigated with ERPs (e.g., Fu et al., 2001; Hopfinger and Mangun, 1998, 2001; McDonald et al., 1999). Comparing the ERP effects from exogenous attention studies vs. endogenous attention studies, there seem to be similarities and differences between these types of attention. Similar to endogenous attention, exogenous attention has never, to our knowledge, been found to modulate the C1. Exogenous attention has been found to enhance the P1 component (Fu et al., 2001; Hopfinger and Mangun, 1998, 2001; Hopfinger and Ries, 2005), the same early stage of processing enhanced by endogenous attention. Although similar to the effect of endogenous attention on the P1, the enhancement of the P1 by exogenous attention occurs only at very short cue-to-target intervals (~50–300 ms). At the cue-to-target intervals at which endogenous attention produces its strongest effects (over ~500 ms), exogenous attention actually reduces the P1 (Hopfinger and Mangun, 1998, 2001; McDonald et al., 1999; Prime and Ward, 2004), in line with a slowing of reaction times at the cued location at these longer intervals (e.g., Posner and Cohen, 1984). A more subtle difference between the endogenous and exogenous effects on the P1 is that the exogenous effect has been found to sometimes extend beyond the peak of the component (e.g., Hopfinger and Ries, 2005; McDonald et al., 1999), whereas the endogenous effect is typically more tightly focused around the peak processing. At a slightly later stage of processing, the N1 is robustly enhanced by endogenous attention during discrimination tasks, but this component has not been found to be enhanced by reflexive attention, regardless of task (Fu et al., 2005; Hopfinger and Mangun, 1998, 2001). In fact, some studies have reported that the N1 is

significantly reduced to stimuli at the cued location, at short cue to target intervals (Fu et al., 2005), although this may be due to an extended positivity overlapping from the enhancement of the P1 component combined with the lack of modulation of the N1 proper (e.g., Hopfinger and Ries, 2005). Exogenous attention has also been found to enhance the stage of processing indexed by the P300 component, but only when the target stimulus is relevant to the participants' task (e.g., Hopfinger and Mangun, 1998, 2001; Hopfinger and Maxwell, 2005).

The main aim of the present ERP study was to investigate the interaction of endogenous and exogenous attention in the brain. We used nonpredictive peripheral cues to trigger the exogenous system and instructive central cues to engage the endogenous system. The main focus here is on the visually evoked C1, P1, and N1 components, as well as the higher-order P300. As mentioned above, the C1 has never been found to be affected by attention, in studies that tested the separate effects of endogenous and exogenous attention. In the present study, we sought to investigate if this stage of processing would be modulated in possibly the strongest case—when exogenous and endogenous attention converge on a common location. If the C1 is found to be unaffected, this would provide strong support to the hypothesis that this stage of processing is immune to mechanisms of attention. The P1 component has been found to be modulated by endogenous and by exogenous attentions in numerous investigations of the separate effects of each system. Therefore, we expect this stage of processing to be modulated; the critical issue is whether this stage of processing is dominated by one or the other attention system, or whether there are additive effects on the P1 reflecting input from both the exogenous and endogenous systems. The N1 is typically enhanced by endogenous attention when a discrimination of the stimulus is necessary to perform the task, whereas exogenous attention has never been found to enhance this stage of processing. In the present discrimination task, we therefore expect that this stage of processing will be enhanced by endogenous attention, possibly even independently of exogenous attention. Finally, the P300 has been found to be modulated in studies of endogenous and exogenous attention; here, we test how this stage of processing is affected when both endogenous and exogenous mechanisms are engaged simultaneously. In addition to testing these effects on multiple stages of information processing, the present results may also shed light on the issue of whether exogenous and endogenous cuing simply trigger two modes of orienting a unitary focus of attention, or whether they engage two separate attention systems. If the results show that neural activity at all stages of information processing is dominated by one or the other type of cuing, this would suggest that a single focus of attention was under the control of the stronger orienting system. On the other hand, if some stages of processing are affected by exogenous mechanisms, while different stages are being controlled by endogenous mechanisms, this would provide new evidence for at least partially separable attention systems.

Experiment 1

Methods

Participants

Twenty healthy college students participated in this study and were paid \$10 per hour. Participants had 20/20 or corrected-

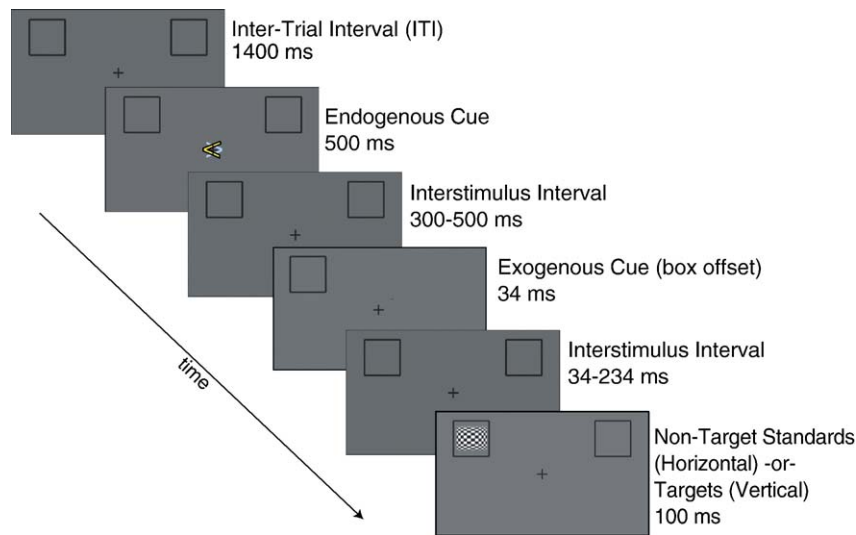


Fig. 1. Trial sequence. Subjects maintained fixation upon a centrally located cross throughout all trials. The endogenous cue consisted of overlapping, equiluminant yellow and cyan arrowheads ('<' and '>') pointing in opposite directions. For illustration purposes only, the yellow arrowhead is outlined in black here. Participants were instructed to direct their attention to the location to which the yellow arrow was pointing and to respond only to targets at that location. The exogenous cue was the disappearance of one of the black square outline boxes for 34 ms. At the end of each trial, a rectangular checkerboard oriented either vertically or horizontally appeared for 100 ms. Targets were vertical checkerboards at the location indicated by the endogenous arrow cue. "Standards" were horizontal checkerboards at either location. Shown here is an endogenously cued location and exogenously uncued location "standard." (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to-20/20 vision and no known neurological problems. Four participants' data were not usable due to errors in data acquisition; therefore, the final analysis included data from 16 participants (ages 19–26, all right-handed, 6 female).

Materials and procedure

Participants viewed a 17-inch computer monitor at a distance of 75 cm while sitting in an electrically shielded, sound-attenuated recording booth. All stimuli were presented on a dark gray background (Fig. 1). Trials were separated by a 1400 ms intertrial interval (ITI). Participants were required to maintain fixation upon a centrally located cross throughout each block of trials. The background display consisted of a central fixation cross and two black square outline boxes ($3.13^\circ \times 3.13^\circ$), located in the upper left and upper right visual fields (25° above the horizontal meridian relative to the fixation cross). Each trial contained an instructive endogenous cue and a nonpredictive peripheral exogenous cue. The endogenous cue consisted of overlapping, equiluminant yellow and cyan arrowheads ('<' and '>') presented for 500 ms, one pointing to the left and the other to the right. Neither arrow was predictive of the likely location of the upcoming stimulus, as each colour pointed to the right on 50% of trials and to the left on the other 50%. However, this central cue provided critical information—participants were instructed to direct their attention to the location to which the yellow arrow was pointing and to respond only to targets at that location, ignoring all stimuli at the opposite location. The exogenous cue, consisting of the disappearance of one of the black square outline boxes for 34 ms, occurred 300–500 ms after the endogenous cue. The exogenous cue was equally likely at the left or right location and was not predictive of where the target or nontarget (i.e., "standards") stimuli would occur. Participants were instructed to ignore these task-irrelevant exogenous cues. Following the exogenous cue by a 34–234 ms interstimulus interval (ISI), a rectangular checkerboard oriented either vertically or horizontally appeared for 100 ms in the upper

right or upper left visual field, within the confines of the black outline background boxes. Participants were required to respond with a button press to vertical checkerboards only, and only when they appeared at the location indicated by the preceding endogenous cue. Fifteen blocks of ninety-six trials were completed. In each of the blocks, only 16 of the 96 trials contained vertical checkerboards. Eight of these were on the endogenously cued side (i.e., targets); eight were at the opposite location. These trials were excluded from the ERP analyses to ensure that the effects we were interested in were not confounded with motor responses. The ERP analyses focus on the nontarget horizontal checkerboard "standards." There were four conditions describing the cuing of the standards: (1) endogenously cued location and exogenously cued location; (2) endogenously cued location and exogenously uncued location; (3) endogenously uncued location and exogenously cued location; (4) endogenously uncued location and exogenously uncued location. Each trial type occurred an equal number of times in each visual field. Note that because we were interested in the possible interaction between these systems, we chose to use different cue-to-target intervals for the endogenous and exogenous cues. Specifically, we used a short cue-to-target interval for the exogenous cue and a longer cue-to-target interval for the endogenous cue because previous research has shown these intervals to be optimal (in terms of maximal facilitation of behavioral performance) for each cue type (e.g., Cheal and Lyon, 1991; Mayer et al., 2004; Müller and Rabbitt, 1989).

Recording and analysis

The electroencephalogram (EEG) was recorded from 96 electrode sites, referenced to the right mastoid, amplified at a bandpass of 0.05–100 Hz and digitized at 250 samples per second. Eye movements were observed throughout all runs via a closed-circuit video camera, and the electro-oculogram was recorded by electrodes located beneath both eyes and lateral to the outer canthi of each eye. All trials containing eye-movements or blinks were rejected

off-line and were not included in the analysis. EEG data were averaged offline to create ERP waveforms, and the data were low-pass filtered (24.06 Hz cutoff) to remove high-frequency noise and high-pass filtered (0.51 Hz cutoff) with a single-pole causal filter to reduce low-frequency drifts across time. Due to the close temporal proximity of the exogenous cues and “standards,” the Adjacent Response (Adjar) technique was used to remove overlapping activity by convolving the initial estimates of the waveforms for the cues and “standards” with previous and subsequent event distributions (Woldorff, 1993). This procedure has previously been shown to be an effective way of estimating and removing overlapping responses from the waveforms of interest (e.g., Hopfinger and Mangun, 1998, 2001; Woldorff, 1993). The Adjar filter was applied to the individual participant averages in order to remove overlapping ERP activity from the exogenous cue and standards. When implemented correctly, the estimates of overlap for the cue and standard waveforms should converge to a stable solution after a number of iterations. Here, 10 iterations were performed for each type of cue and standard for each participant (most achieved stable estimates within the first 6 iterations, but 10 iterations were performed on each participant’s data to ensure stability and consistency). The resulting ERP waveforms were then averaged across participants.

Results

Behavioral results

Although the primary interest of this study was the ERP effects of endogenous and exogenous cues on the neural processing of the “standards,” the overt behavior of participants provided evidence of the effectiveness of the endogenous and exogenous cues. To investigate if the exogenous cues were having significant effects on overt performance, reaction times to the targets were analyzed as a function of whether the target was preceded by an exogenous cue at the same vs. the opposite location. If the instructive endogenous cues were in complete control of a unitary focus of attention, then exogenous cues would not be expected to have any effect on overt performance. On the other hand, if exogenous cues did affect performance, this would suggest that either the exogenous cues grabbed the unitary focus of attention or that exogenous cues may have effects on performance that are independent from those of endogenous cuing. A repeated-measures (across 16 participants) ANOVA was performed on the targets (vertical checkerboards at the endogenously cued location) with the factors of exogenous attention (exogenously cued location vs. exogenously uncued location) and visual field (right vs. left). Targets at the exogenously cued location were responded to significantly faster (566 ms) than targets at the exogenously uncued location (596 ms; $F(1,15) = 9.12$; $P < 0.01$). There was no significant effect of visual field. These behavioral measures thus provide evidence that the peripheral cues were effective in triggering exogenous mechanisms and affecting information processing.

To investigate if participants were utilizing the instructive endogenous cues, accuracy to the targets and standards was analyzed. If participants frequently responded to stimuli at the endogenously uncued location, this would suggest that they were not attending to the side indicated by the instructive cues. On the other hand, if participants only responded to targets and only responded to stimuli at the instructed location, this would provide some evidence that they were utilizing the endogenous cues. Overall accuracy was near perfect (mean accuracy 99.5%, range

97.7%–99.9%). The hit rate to targets (vertical checkerboards at the endogenously cued location) was very high (mean hit rate = 95.0%, range 71.7%–100%), and participants rarely responded to the vertical checkerboards at the endogenously uncued location (mean error rate = 0.09%, range 0%–0.4%). These accuracy measures provide evidence that participants were utilizing the central cues to engage endogenous attention at the location indicated by these instructive cues.

ERP results

ERPs to exogenous cues. Evidence for the allocation of endogenous attention was also tested by investigating the ERP responses to the exogenous cues. Specifically, if participants were voluntarily focusing on the location indicated by the endogenous cue, then the sensory ERP components to the exogenous cues should be enhanced when these occur at the endogenously cued vs. the endogenously uncued location. Analyses were performed on the amplitude of the contralateral P1 (80–120 ms) and N1 (135–175 ms) components evoked by the exogenous cues using a repeated-measures ANOVA. All ERP amplitude measures here refer to mean voltage amplitudes over the latency ranges listed. The factors in the model included endogenous attention (endogenously cued location vs. endogenously uncued location), visual field (right vs. left), electrode (lateral vs. more medial contralateral occipital locations; lateral electrodes were the contralateral T5 and T6 electrodes of the International 10–20 system of electrode placement (Jasper, 1958); the medial electrode locations were the contralateral “Occipital-Left (OL)” and “Occipital-Right (OR)” electrodes; “OL” lies midway between O1 and T5 of the 10–20 system; “OR” lies midway between O2 and T6), and participant ($N = 16$). There was a significant main effect of endogenous attention on the P1, as exogenous cues at the endogenously cued location evoked a significantly larger P1 component (0.49 μ V) than the exogenous cues at the endogenously uncued location (0.02 μ V; $F(1,15) = 39.52$, $P < 0.001$) (see Fig. 2). This provides further evidence that participants were voluntarily allocating attention to the location indicated by the endogenous cue. There were no other significant main effects or interactions during the latency range of the P1. There was a trend for the contralateral N1 component to be larger at the endogenously cued location (−0.54 μ V) vs. the endogenously uncued location (−0.47 μ V), but there were no significant main effects or interactions in the N1 analysis (Fig. 2). This lack of an N1 effect is in concordance with models suggesting that the N1 attention effect reflects a higher-level discrimination process (e.g., Mangun and Hillyard, 1991; Luck, 1995; Vogel and Luck, 2000). The exogenous cues in the present experiment were known to be irrelevant to the participants’ task and no discrimination of the exogenous cues was necessary. Therefore, the lack of an N1 effect may be expected here, even if participants were using the central cues to endogenously orient to the instructed location. Analyses were not conducted during the latency ranges of the C1 and P300 components because these components were not generated robustly to the exogenous cue stimuli. The exogenous cues were subtle and irrelevant to the participants’ task, which can account for the lack of the C1 and P300 components, respectively.

Inspection of the waveforms in Fig. 2 reveals a negative shift in the waveform between 200 and 230 ms, in which the endogenously uncued exogenous cues produced a greater negativity than cued location cues. The timing and shape of this

Effects of Endogenous Cue on Processing of Exogenous Cue

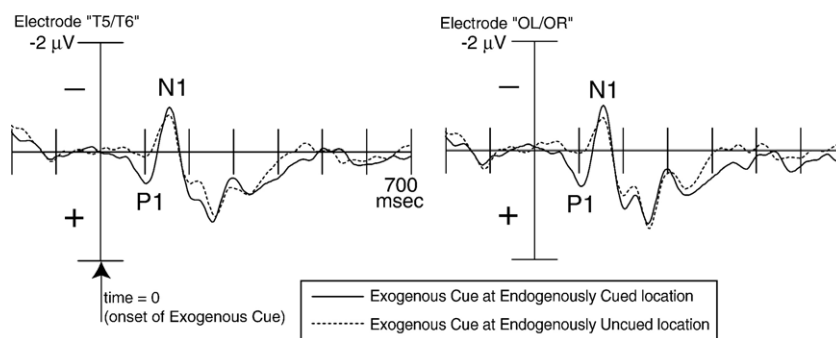


Fig. 2. Event-related potentials (ERPs) evoked by the exogenous cue stimuli (Experiment 1). Data from contralateral occipital scalp sites (right hemisphere electrode locations for left visual field stimuli averaged with left hemisphere location for right visual field stimuli; electrode locations described in text). The visually evoked P1 component was significantly enhanced at the endogenously cued location compared to the endogenously uncued location.

difference resemble the N2pc component, which is thought to index attentional orienting or spatial filtering (Luck and Hillyard, 1994). However, the typical N2pc is observed as a difference between contralateral and ipsilateral scalp sites, with the negativity being greater contralateral to the target item. Critically, the paradigms that elicit the N2pc involve complex displays with multiple items presented bilaterally (e.g., Girelli and Luck, 1997), whereas the current paradigm consisted of one stimuli at a time occurring in one visual field. Luck and Hillyard (1994) found that single item displays did not produce the canonical N2pc, when differences in spatial location of the physical stimuli were controlled for. No clear N2pc can be observed in the comparison of contralateral to ipsilateral scalp sites in the current experiment. Therefore, the effect observed here is unlikely to be the prototypical N2pc component. Nevertheless, there was a trend for the endogenously uncued location exogenous cues to have a greater negativity ($0.63 \mu\text{V}$) than endogenously cued location exogenous cues ($0.90 \mu\text{V}$) over the 200–230 ms latency range at these electrodes. The ANOVA (with the same factors as above) revealed no significant main effect of cuing ($F(1,9) = 2.63$), nor any other main effects or interactions. At slightly more lateral and ventral locations (IN3 and IN4 of the International 10/20 systems, and a neighboring location between IN3/IN4 and T5/T6), however, an ANOVA (with the same factors as above, but with different electrode locations) revealed a significant difference (endogenously uncued cues: $-0.34 \mu\text{V}$; endogenously cued cues: $0.31 \mu\text{V}$; $F(1,9) = 8.04$, $P < 0.05$). This difference indicates that the uncued location stimuli are evoking additional processing compared to the cued location stimuli, and, based on its timing and scalp location, this may be similar to the processing indexed by the N2pc. One possible explanation is that greater resources are needed to process the endogenously uncued location stimulus because it did not benefit from endogenous attention during initial sensory processes. Alternatively, since the N2pc may index the filtering out of distracting information, the present activity may indicate that the endogenously uncued location is being filtered more strongly than the endogenously cued location. This would make sense, as the endogenous cues are 100% instructive and all of the information at that location should be filtered out. Further research may better clarify the relation between the present cued-vs.-uncued difference and the contralateral-vs.-ipsilateral difference indexed by the N2pc.

ERPs to standards (nontargets)

C1. The amplitude of the C1 (60–80 ms) evoked by the standards (nontarget checkerboard stimuli) was investigated using a repeated measures ANOVA with the factors of endogenous attention (endogenously cued location vs. endogenously uncued location), exogenous attention (exogenously cued location vs. exogenously uncued location), visual field (left vs. right), electrode (midline posterior electrodes “Pz” vs. “POz,” of the International 10–20 system), and participant ($N = 16$). There were no main effects, as the amplitude of the C1 was not significantly modulated by endogenous or exogenous attention (Fig. 3). Furthermore, there was no interaction between endogenous and exogenous cuing (Figs. 4 and 5). The only significant interaction was between endogenous attention and electrode ($F(1,15) = 4.62$, $P < 0.05$), as the peak of the C1 was at the slightly more anterior location for endogenously cued location targets than for endogenously uncued location targets.

P1. The amplitude of the peak of the contralateral P1 (80–120 ms) evoked by the standards was investigated using a repeated measures ANOVA with the factors of endogenous attention (endogenously cued location vs. endogenously uncued location), exogenous attention (exogenously cued location vs. exogenously uncued location), visual field (left vs. right), electrode (lateral vs. medial contralateral occipital locations; “OL/OR” and “T5/T6” as described above), and participant ($N = 16$). Unlike previous studies in which endogenous or exogenous cues were both found to enhance the P1 when these attention systems were investigated in isolation, the peak of the P1 in this experiment was not affected by endogenous attention ($F(1,15) = 0.67$, $P = 0.43$; Fig. 3, top, and Fig. 4) or exogenous attention ($F(1,15) = 0.22$, $P = 0.65$) (Figs. 3B and 5). There were no significant main effects or interactions in this analysis.

Late phase of the P1. Although the peak of the P1 was not modulated by endogenous or exogenous cues, inspection of the waveforms reveals that there was a positive shift in the waveform following the peak of the P1 that was exclusive to exogenously cued location stimuli. This positive shift following the peak of the P1 has been observed in a number of previous studies of reflexive attention (e.g., Fu et al., 2005; Hopfinger and Maxwell, 2005; Hopfinger and Ries, 2005; McDonald et al., 1999). Although most previous studies have found that this extended positivity follows an enhancement of the peak of the P1, there is evidence suggesting

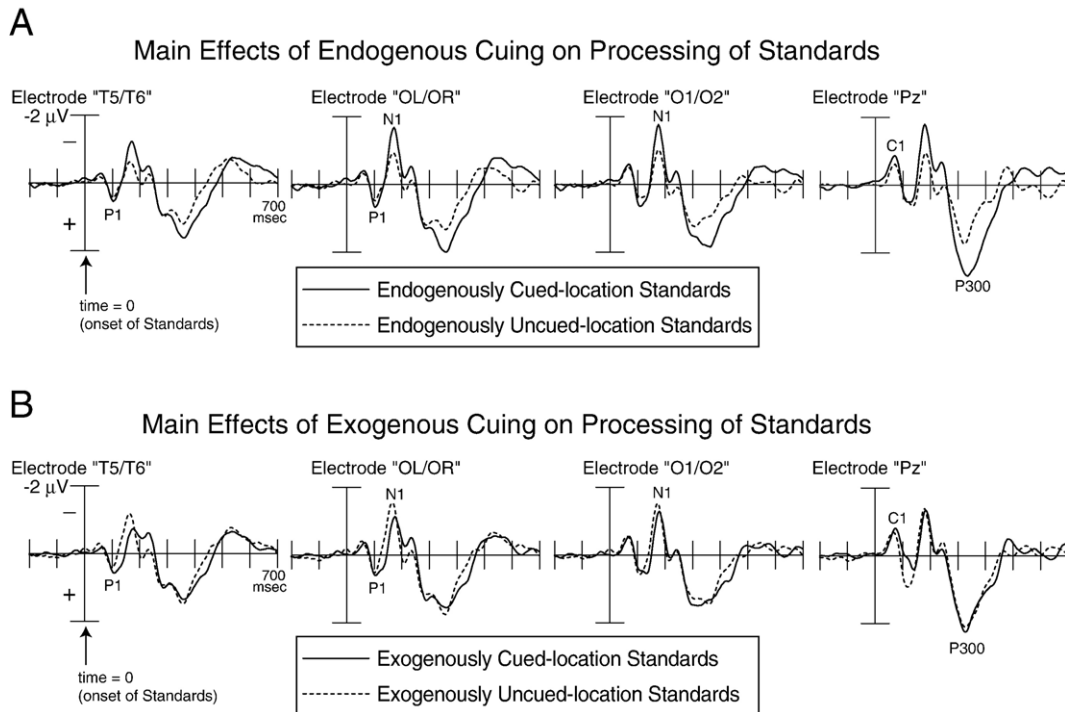


Fig. 3. Event-related potentials (ERPs) to standards (Experiment 1). Data are collapsed over contralateral occipital scalp site (electrode locations described in text). ERP components are labeled on the electrodes at which they were tested. (A) ERPs to standards, as a function of preceding *endogenous* cue location (collapsed over exogenous cue location). Standards occurring at the location indicated by the endogenous cue elicited significantly enhanced N1 and P300 components compared to standards occurring at the endogenously uncued location. (B) ERPs to standards, as a function of preceding *exogenous* cue location (collapsed over endogenous cue location). Standards occurring at the location of the preceding exogenous cue elicited an enhanced positivity during the late-stage of the P1 compared to standards occurring at the opposite location.

that the later portion of the P1 may represent a different neural process than that reflected in the earlier peak of the P1. Specifically, evidence suggests that the exogenous enhancement of the early-P1 is triggered automatically by physical attributes of the cue, regardless of top-down control settings, whereas the duration of this enhanced positivity relates to the congruency between an irrelevant peripheral cue and the expected target type (Hopfinger and Ries, 2005). Furthermore, recent neural modeling of scalp-recorded visual-evoked potentials has suggested that there is a late phase of the P1 generated in fusiform gyrus that is separate from the middle occipital gyrus activity that produces the earlier phase of the P1 (Di Russo et al., 2001, 2003; Martinez et al., 1999, 2001). Therefore, we performed an additional analysis on the amplitude of the late phase of the P1 (120–150 ms), using a repeated measures ANOVA with the factors of endogenous attention (endogenously cued location vs. endogenously uncued location), exogenous attention (exogenously cued location vs. exogenously uncued location), visual field (left vs. right), electrode (lateral vs. medial contralateral occipital locations; "T5/T6" and "OL/OR", respectively), and participant ($N = 16$). This analysis revealed a significant main effect of exogenous cuing, as exogenously cued standards ($0.34 \mu\text{V}$) produced greater positive activity than exogenously uncued location standards ($-0.32 \mu\text{V}$; $F(1,15) = 5.91$, $P < 0.05$) (Fig. 3B). This effect did not interact with endogenous cuing, as the effect of exogenous cuing was present at both endogenously cued locations (Fig. 5A) and endogenously uncued locations (Fig. 5B). The late phase of the P1 was not affected by endogenous cues (Figs. 3A and 4), and there were no interactions in this analysis.

N1. The amplitude of the contralateral N1 (150–180 ms) evoked by the standards was investigated using a repeated measures ANOVA with the factors of endogenous attention (endogenously cued location vs. endogenously uncued location), exogenous attention (exogenously cued location vs. exogenously uncued location), visual field (left vs. right), electrode (lateral vs. medial contralateral occipital locations; "OL/OR" and "O1/O2"), and participant ($N = 16$). In agreement with previous studies in which endogenous attention was investigated in isolation, the N1 was significantly enhanced at the endogenously cued location ($-1.26 \mu\text{V}$) vs. the endogenously uncued location ($-0.68 \mu\text{V}$; $F(1,15) = 15.91$, $P < 0.005$) (Fig. 3). There was also a significant effect of exogenous attention, as the N1 was significantly smaller to exogenously cued location standards ($-0.73 \mu\text{V}$) vs. exogenously uncued location standards ($-1.21 \mu\text{V}$; $F(1,15) = 5.22$, $P < 0.05$). This latter effect, however, may be due in part to overlap from the extended positivity from the late phase of the P1 for exogenously cued location standards, rather than a significant reduction in the processes indexed by the N1. Importantly for the purposes of the current study, there was a significant interaction between endogenous and exogenous cuing ($F(1,15) = 10.74$, $P < 0.01$; Figs. 4 and 5). This suggests that endogenous and exogenous attentions were affecting information processing in different ways during this latency range. We explore this interaction further through the analysis of cued location minus uncued location difference waveforms described in a subsequent section below.

P300. The P300 component (peaking 300–400 ms) was investigated using a repeated measures ANOVA with the factors of endogenous attention (endogenously cued location vs. endoge-

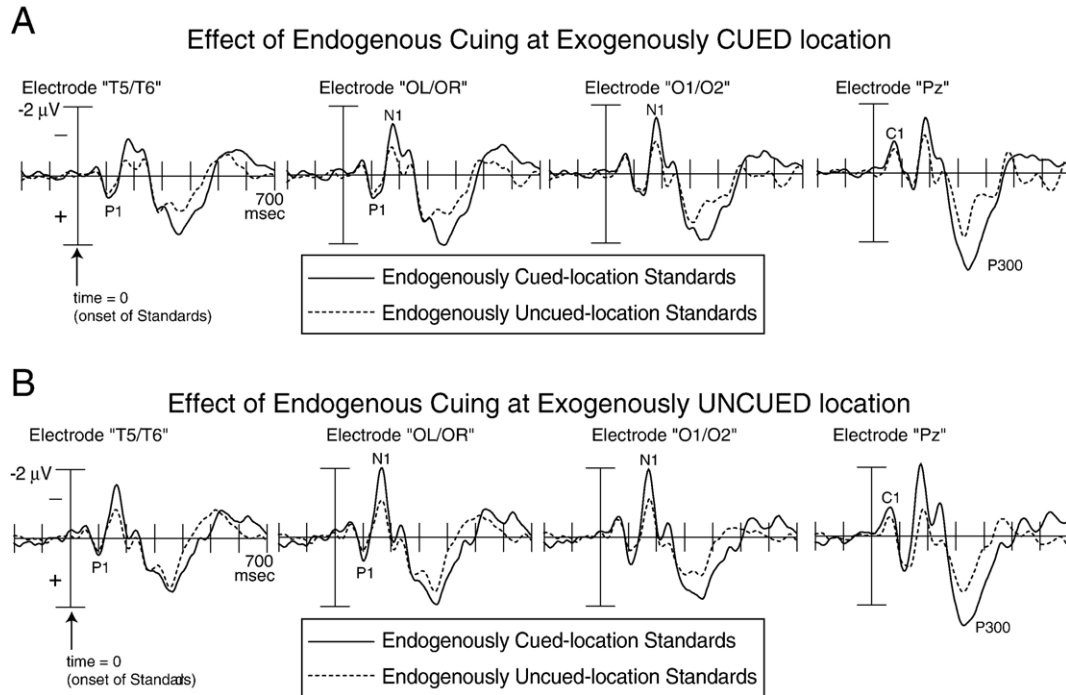


Fig. 4. Event-related potentials (ERPs) to standards (Experiment 1), as in Fig. 3, but separated into (A) the effects of endogenous attention at the exogenously cued location and (B) the effects of endogenous attention at the exogenously uncued location.

nously uncued location), exogenous attention (exogenously cued location vs. exogenously uncued location), visual field (left vs. right), electrode (Pz vs. a central posterior electrode location midway between Pz and Cz of the International 10–20 system), and participant ($N = 16$). This test revealed a significant effect of endogenous attention, as the amplitude was significantly larger to

endogenously cued location standards ($2.32 \mu\text{V}$) vs. endogenously uncued location standards ($1.13 \mu\text{V}$; $F(1,15) = 15.08$, $P < 0.005$) (Fig. 3). There was no effect of exogenous cuing and the interaction of endogenous and exogenous cuing did not approach significance ($F(1,15) = 0.43$, $P = 0.52$; Figs. 4 and 5). As shown in Fig. 4, the P300 was enhanced at endogenously cued locations vs.

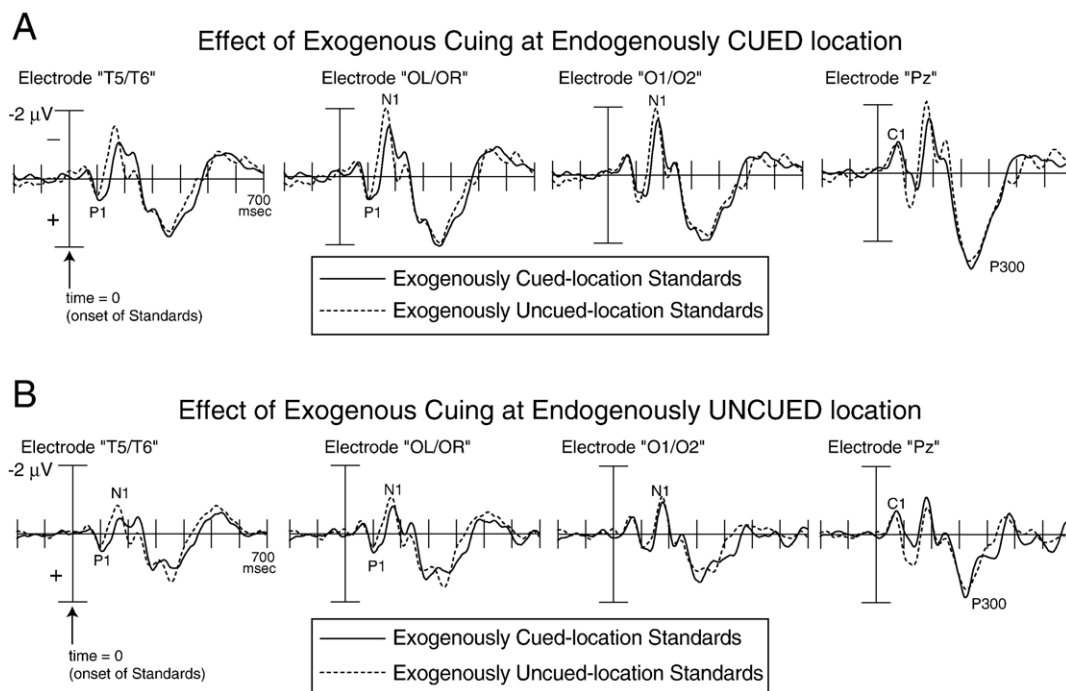


Fig. 5. Event-related potentials (ERPs) to standards (Experiment 1), as in Fig. 3, but separated into (A) the effects of exogenous attention at the endogenously cued location and (B) the effects of exogenous attention at the endogenously uncued location.

endogenously uncued locations, regardless of whether the standard occurred at the exogenously cued location (Fig. 4A) or at the exogenously uncued location (Fig. 4B). There was an interaction between visual field and electrode ($F(1,15) = 5.40$, $P < 0.05$), as the peak of the P300 was slightly more anterior for left visual field targets than right visual field targets. There was a 3-way interaction between endogenous cuing, exogenous cuing, and electrode ($F(1,15) = 5.48$, $P < 0.05$), as the endogenous cuing effect at the exogenous cue location was slightly anterior to the peak of the endogenous effect at the exogenously uncued location. There were no other significant main effects or interactions in this analysis. It should be noted that the high-pass filter that was used here likely reduced the amplitude of the P300 in these data. Duncan-Johnson and Donchin (1979) showed that the amplitude of the P300 could be significantly diminished when activity below 0.5 Hz is filtered out. As the authors note, however, this does not negate the effects found within an experiment, as long as the same filters were used for all conditions. Since the P300 may consist of multiple components, the filter settings used in the present study may have removed some of components of the P300, and highlighted remaining components. Caution must be taken, however, when comparing the P300 amplitudes in this study to studies that use different filter settings.

Difference wave analyses. To further investigate the effects of endogenous and exogenous attention on early visual cortical activity, we calculated difference waves and performed additional analyses on these differences. Specifically, we subtracted the ERPs to the endogenously uncued location standards from the ERPs to the endogenously cued location standards, and we subtracted the ERPs to the exogenously uncued location standards from the exogenously cued location standards. As shown in Fig. 6A, the predominant effects of endogenous and exogenous cuing occurred during overlapping latencies, with exogenous cuing producing an enhanced positivity at a slightly earlier latency than the enhanced negativity produced by endogenous cuing. To investigate the interaction between endogenous and exogenous cuing during these latency ranges, the difference waves were calculated separately for each combination of exogenous and endogenous cuing (Figs. 6B and C). These analyses are described below.

Exogenous effects. The predominant effect of exogenous attention (exogenously cued location standards minus exogenously uncued location standards) was an enhanced positivity peaking around 150 ms (Figs. 6A and B). We performed analyses to investigate whether this exogenous attention effect interacted with endogenous attention. The amplitude of this exogenous effect was investigated using a repeated measures ANOVA over the latency range of 125–175 ms, with the factors of endogenous attention (endogenously cued location vs. endogenously uncued location), visual field (left vs. right), electrode (lateral vs. medial contralateral occipital locations; “T5/T6” and “OL/OR”, respectively), and participant ($N = 16$). This analysis revealed an effect of endogenous attention, as the exogenous attention effect was significantly larger at the endogenously cued location (0.86 μ V) compared to the exogenous attention effect at the endogenously uncued location (0.41 μ V; $F(1,15) = 6.21$, $P < 0.05$). There were no other significant effects or interactions. The latency of the peak of this exogenous effect was similarly analyzed as a function of endogenous attention, using an ANOVA with the same factors as above. There were no main effects, and the latency of the

difference wave did not differ between endogenously cued locations (149.5 ms) and endogenously uncued locations (150.6 ms; $F(1,15) = 0.11$; $P = 0.75$). Therefore, endogenous attention was found to modulate the amplitude, but not the latency, of the exogenous attention effect at this stage of processing.

Endogenous effects. The predominant effect of endogenous cuing was an enhanced negativity that corresponded with the peak of the N1 (Figs. 6A and C). We performed analyses to investigate whether exogenous attention had any effect on the amplitude or latency of this endogenous attention effect. The amplitude of this endogenous effect was investigated using a repeated measures ANOVA, over the latency range of 150–210 ms, with the factors of exogenous attention (exogenously cued location vs. exogenously uncued location), visual field (left vs. right), electrode (lateral vs. medial contralateral occipital locations; “OL/OR” and “O1/O2”, respectively), and participant ($N = 16$). There were no main effects or interactions, and the trend for the amplitude of the difference wave to be larger at the exogenously uncued location (−0.63) vs. the exogenously cued location (−0.46) did not approach significance ($F(1,15) = 0.51$; $P = 0.48$). The latency of the peak of the endogenous effect was analyzed using an ANOVA with the same factors as above. The latency of the endogenous effect was significantly earlier at exogenously uncued locations (177.0 ms) compared to exogenously cued locations (186.4 ms; $F(1,15) = 5.01$, $P < 0.05$; Fig. 6, top left). There were no other significant main effects or interactions. Therefore, exogenous attention was found to modulate the latency, but not the amplitude, of the endogenous attention effect at this stage of processing.

Discussion

In this experiment, we investigated the influence of endogenous and exogenous attention on neural processing when these systems are concurrently engaged. The ERPs evoked by the nontarget “standards” revealed that neither exogenous nor endogenous attention significantly modulated the earliest stage of visual cortical processing. Specifically, the striate-generated C1 was not modulated by attention in this experiment, in agreement with numerous previous studies that examined exogenous and endogenous mechanisms separately. The lack of an effect in this experiment is noteworthy; however, as here, we were able to examine the condition wherein exogenous and endogenous attentions converge on a common location, which may have been expected to have the greatest chance of causing a modulation of this earliest stage of cortical processing. Our results provide evidence that even in this optimal situation, mechanisms of attention are unable to affect this initial activity in striate visual cortex.

In studies investigating the isolated effects of endogenous cuing (e.g., Clark and Hillyard, 1996; Di Russo et al., 2003; Handy and Mangun, 2000; Heinze et al., 1994; Mangun and Hillyard, 1991; Mangun et al., 1997; Martinez et al., 1999) and exogenous cuing (Fu et al., 2001; Hopfinger and Mangun, 1998, 2001), both types of attention have been shown to modulate sensory visual processing as early as ~90 ms latency (i.e., the “early” phase of the P1; Di Russo et al., 2001; Martinez et al., 1999). Therefore, we predicted that this stage of processing should either reveal that one system is stronger and dominates this processing independent of the other system, or that there would be additive effects of exogenous and endogenous attention. However, this early phase of the P1 was unaffected in this experiment, whether endogenous and exogenous attention were working in concert or in competition. Why this stage of processing

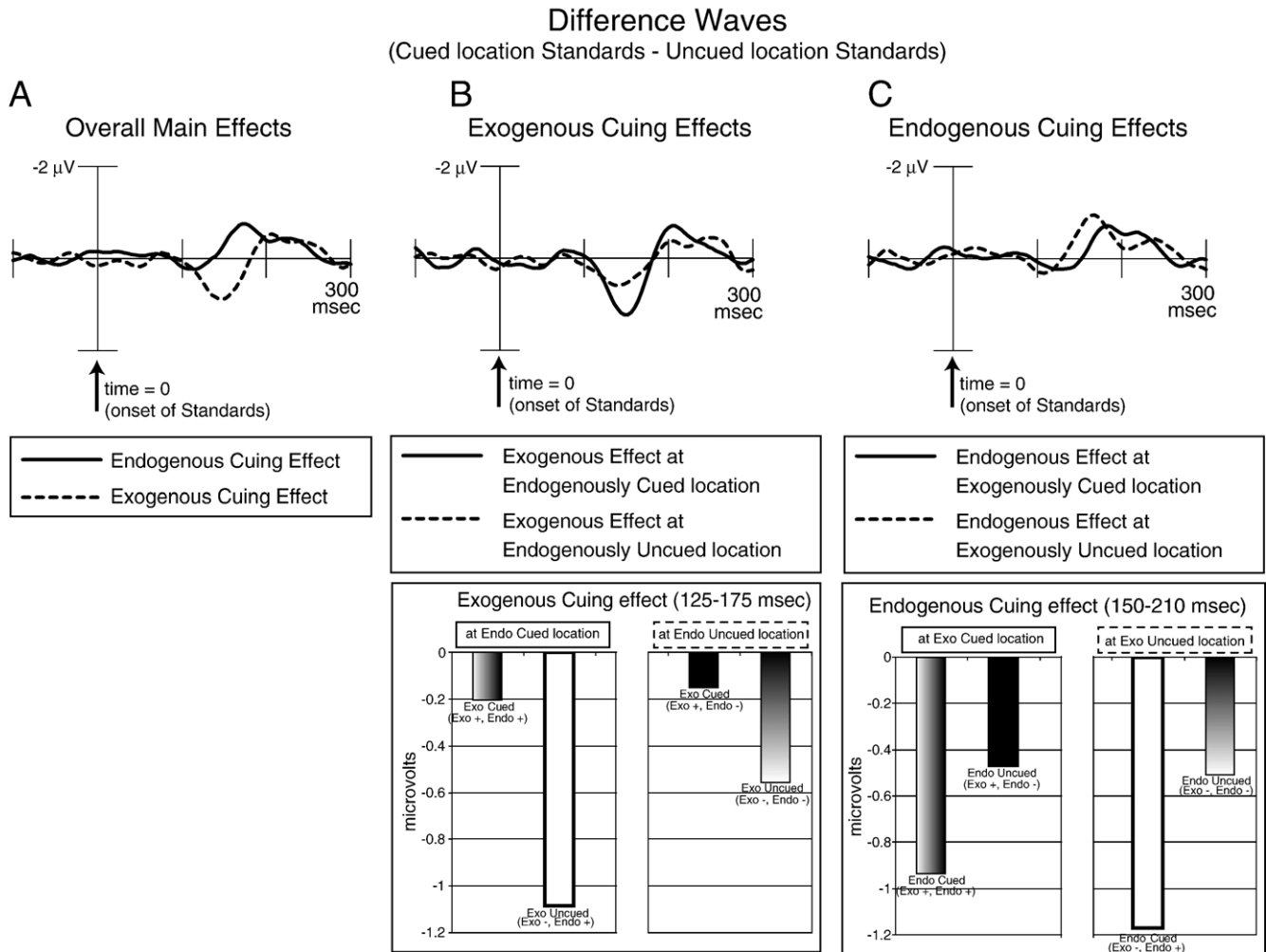


Fig. 6. Difference waves (Experiment 1). The “endogenous effect” difference wave was calculated by subtracting the endogenously uncued location standards from the endogenously cued location standards; the “exogenous effect” was calculated by subtracting the exogenously uncued location standards from the exogenously cued location standards. Electrode shown is contralateral “OL/OR” location. Note that the time scale covers a shorter period here than in previous figures, to magnify the latency range of the difference wave effects. (A) Main effects of endogenous cuing and exogenous cuing. (B) Effect of exogenous cuing, separated into the exogenous effect at the endogenously cued location vs. the exogenous effect at the endogenously uncued location. The graph shows the mean amplitude in the latency window of the exogenous cuing effect (125–175 ms) within each condition. Note that the positive shift due to exogenous cues is occurring as the larger N1 component is beginning to dominate the raw waveform; therefore, less negative voltage in the graph indicates the positive shift associated with exogenously cued locations. (C) Effect of endogenous cuing, separated into the endogenous effect at the exogenously cued location vs. the endogenous effect at the exogenously uncued location. Graph shows the mean amplitude in the latency window of the endogenous cuing effect (150–210 ms) within each condition. Note that the negative shift due to endogenous cues is occurring during the N1 component; therefore, greater negative voltage in the graph indicates the negative shift associated with endogenously cued locations.

was unaffected by attention in this experiment is unclear. The behavioral responses and ERPs to the exogenous cues provided evidence that both endogenous and exogenous attentions were engaged in this task; therefore, the lack of a P1 attention effect does not seem due to the lack of attentional engagement. Furthermore, the lack of a P1 attention effect was not simply due to the two systems canceling each other out when at competing locations, because there was no enhancement even when exogenous and endogenous attention converged at a single location. Rather, it may be that the present paradigm presents a more complex situation than most previous ERP studies of covert attention. In this experiment, the stage of processing indexed by the early-P1 would receive multiple and often conflicting inputs from the exogenous and endogenous system. In effect, the brain’s response to this frequent

conflict may be to simply delay the filtering of information to a slightly later stage, allowing for more processing of stimuli to be performed before any information is filtered out. However, another possibility is that the lack of an early-P1 attention effect is simply due to the stimuli and task used here. Although previous studies have found exogenous and endogenous effects on the early-P1, research has shown that attention effects on the P1 and N1 can be dependent on perceptual and cognitive load (e.g., [Handy and Mangun, 2000](#); [Handy et al., 2001a,b](#)). In order to further explore the lack of an early-P1 in the current experiment, we conducted a control experiment to investigate whether the absence of this attention effect is simply due to the specific stimuli and task used in the current experiment. That control experiment is described in a subsequent section, as Experiment 2.

The earliest stage of visual processing modulated in the current experiment was the late phase of the P1 component, as exogenous cuing significantly enhanced processing at this stage. This enhancement by exogenous attention occurred even at the endogenously uncued location, despite the fact that participants were to completely ignore that location. Though previous behavioral studies have suggested that highly focused voluntary attention can prevent a reflexive orienting to an abrupt exogenous event (Yantis and Jonides, 1990), the present results provide evidence that salient transients in the visual scene trigger exogenous attention effects at relatively early stages of processing, regardless of the location being voluntarily attended. Indeed, our findings suggest that when both endogenous and exogenous systems are engaged, the earliest modulation of processing is dominated by exogenous attention.

Immediately following this processing, however, we found a significant interaction between endogenous and exogenous attention. Endogenous attention was found to significantly enhance the N1, in agreement with numerous previous ERP studies of voluntary attention, while exogenous attention produced a significantly smaller N1. As revealed by analysis of the difference waves, however, the reduced N1 at exogenously cued vs. exogenously uncued locations appears to be a consequence of the overlapping positivity from the exogenous enhancement of the late-P1. The critical point here is that the interaction during this latency range highlights that endogenous and exogenous attention were producing different effects almost simultaneously. If endogenous and exogenous attention simply described two modes of orienting a common and unitary “attentional focus,” then attention should only be at one location at a time. In contrast, we find different effects of exogenous and endogenous attention occurring at the same time. Therefore, these data provide neurophysiological support for the view that the exogenous and endogenous systems can have distinct effects on information processing (Briand, 1998; Briand and Klein, 1987; Friesen et al., 2004; Han et al., 2005; Klein, 1994). The present results provide new evidence regarding the stages of neural processing at which these attention systems have separable and interacting effects.

Although exogenous and endogenous attention were found to have differing effects on neural processing that overlapped in time, the analysis of the difference waves revealed that the two systems were not acting completely independently. Interestingly, endogenous attention had an effect on the amplitude, but not latency, of the exogenous cuing effect, whereas amplitude but not attention affected the latency, but not amplitude, of the endogenous cuing effect. This pattern provides further evidence that exogenous and endogenous cues engage somewhat different systems. The enhancement of the exogenous cuing effect by endogenous attention suggests that even though endogenous cuing did not directly modulate this stage of processing, it influenced the degree to which exogenous attention modulated this processing. Further research is necessary, but this may be due in part to the salience of the exogenous cue being enhanced at the endogenously attended vs. endogenously ignored location. Another possibility is that this relates to the hypothesis that some forms of reflexive orienting are contingent upon top-down control (e.g., Folk et al., 1992). Indeed, recent research has indicated that the duration of the enhanced positivity following exogenous cuing is partially dependant on top-down settings (Hopfinger and Ries, 2005). The finding that exogenous cuing affected the latency of the endogenous attention effect is more difficult to explain, but is consistent with previous reports of

exogenous cuing affecting the latency of the N1 component (Fu et al., 2005).

Finally, our results suggest that, at the later stage of processing indexed by the P300 component, endogenous attention is dominant. Although previous studies have shown that exogenous attention can enhance the P300 (e.g., Hopfinger and Mangun, 1998, 2001), these effects are typically smaller than the modulations of the P300 produced by endogenous attention. Here, we find that when both systems are activated, endogenous attention controls this stage of processing. Of course, in the current design, endogenous attention provided specific instructive information that determined whether or not a stimulus needed to be processed at the levels indexed by the P300 (e.g., decision making regarding a possible target). Specifically, all stimuli at the endogenously uncued location could be completely ignored, creating a clear and simple distinction from endogenously cued location stimuli. Exogenous cuing, on the other hand, was meaningless in terms of providing information regarding the relevance of the upcoming stimuli. Nevertheless, such exogenous cues had significantly enhanced the P300 in other studies wherein endogenous attention was not focused on a particular location. Thus, the present results suggest that endogenous attention overrides the influence of exogenous attention on the processes indexed by the P300.

The present results provide new evidence regarding how endogenous and exogenous attention systems affect information processing in the brain. These data suggest that the interaction of endogenous and exogenous attention cannot be accounted for simply as the sum of the separate effects of each type of attention, nor as the stronger system dominating all levels of processing. In this experiment, exogenous attention was found to have the stronger influence over early stages of visual processing, enhancing the late phase of the P1 (120–150 ms latency) regardless of where endogenous attention was focused. Endogenous attention did, however, affect the magnitude of the exogenous cuing effect on the late-P1. Endogenous attention also dominated later higher order processing, enhancing the P300 (300–400 ms latency) regardless of exogenous attention. In between these stages of processing, however, exogenous and endogenous attention interacted in unique ways, with endogenous attention affecting the amplitude of the exogenous attention effect, and exogenous attention affecting the latency of the endogenous effect.

A remaining question, however, is why there was no attentional modulation of the early-P1 by either type of attention. Both endogenous and exogenous attentions have previously been shown to enhance visual processing as early as 90 ms latency, when tested separately. The lack of modulation in the current experiment could suggest that when exogenous and endogenous attentions are in frequent competition, selective biasing in the brain may be delayed to a slightly later stage. Alternatively, it could simply be that the early-P1 is not affected because of some specific aspect of the current stimuli, task, or methodology. To investigate this issue, we conducted the following control experiment.

Experiment 2

The finding from Experiment 1 that the early-P1 was unaffected by endogenous and exogenous attention is at odds with previous studies that have found that the early-P1 is enhanced by endogenous attention (e.g., Di Russo et al., 2003)

and exogenous attention (e.g., Hopfinger and Mangun, 1998) when these systems are tested separately. Previous studies have shown, however, that task and stimulus parameters (specifically cognitive and perceptual load) can determine whether the P1 and N1 show modulation by attention (e.g., Handy and Mangun, 2000; Handy et al., 2001a,b). Therefore, we conducted a control experiment to determine whether the typical P1 and N1 attention effects could be observed with the present stimuli and task, if endogenous and exogenous attention were not concurrently triggered.

Methods

Participants

Twelve healthy college students participated in this study and were paid \$10 per hour. Participants had 20/20 or corrected-to-20/20 vision and no known neurological problems. Two participants' data were not used due to excessive alpha activity in the raw EEG; therefore, the final analysis included data from 10 participants (ages 18–21; 9 right-handed, 1 ambidextrous; 6 female).

Materials and procedure

The materials and procedures were identical to the first experiment, except for the following differences. Participants completed two different types of blocks: seven blocks of endogenous-only-cuing and seven blocks of exogenous-only-cuing. The exogenous blocks were always run first, so that the central cues would be meaningless to participants. Specifically, the stimuli and timing of these exogenous blocks were identical to the first experiment. Here, however, participants were told that the overlapping yellow and blue arrows were completely irrelevant and should be ignored. Participants were instructed to respond to the vertical checkerboards, regardless of which hemifield they occurred in. These blocks thus allowed us to investigate the effects of exogenous cuing with the same stimuli as in Experiment 1, but in the absence of endogenous orienting. In order to investigate endogenous orienting in the absence of exogenous attention, we conducted a second set of blocks. In these blocks, there was no exogenous cue, and participants were told to orient their attention to the location indicated by the yellow arrow and only respond to target stimuli at that location.

Recording and analysis

The electroencephalogram (EEG) was recorded from 96 electrode sites, referenced to the right mastoid, amplified at a bandpass of 0.05–100 Hz and digitized at 250 samples per second. Eye movements were observed throughout all runs via a closed-circuit video camera, and the electro-oculogram was recorded by electrodes located beneath both eyes and lateral to the outer canthi of each eye. All trials containing eye-movements or blinks were rejected off-line and were not included in the analysis. EEG data were averaged offline to create ERP waveforms, and the data were low-pass filtered (24.06 Hz cutoff) to remove high frequency noise and high-pass filtered (0.51 Hz cutoff) with a single-pole causal filter to reduce low-frequency drifts across time. Due to the close temporal proximity of the exogenous cues and “standards,” the Adjacent Response (Adjar) technique was used to remove overlapping activity in the exogenous cuing blocks as in the first experiment. Ten iterations were performed for each type of cue and standard for each participant. The resulting ERP waveforms were then averaged across participants.

Results

Behavioral results

In the endogenous blocks, participants only responded to targets at the cued location; therefore, endogenous cuing effects on behavior cannot be calculated. In the exogenous blocks, however, participants responded to targets at either location, so the effects of exogenous cuing on reaction times to the targets could be analyzed. A *t* test revealed that targets at the exogenously cued location were responded to significantly faster than targets at the exogenously uncued location (cued: 494.6 ms; uncued: 506.0 ms; $t(1,9) = 4.18$, $P < 0.005$).

Overall accuracy was near perfect in both the endogenous blocks (mean accuracy 99.6%, range 98.7%–100%) and exogenous blocks (mean accuracy 99.6%, range 98.8%–100%). In the endogenous blocks, the hit rate to targets (vertical checkerboards at the endogenously cued location) was very high (mean hit rate = 96.8%, range 89.3%–100%), participants rarely incorrectly responded to the horizontal checkerboards (mean error rate = 0.13%, range 0%–0.54%), and participants rarely incorrectly responded to vertical nontargets (vertical checkerboards on the uncued side; mean error rate = 0.54%, range 0%–3.6%). In the exogenous blocks, the hit rate to targets (vertical checkerboards on either side) was very high (mean hit rate = 98.8%, range 95.5%–100%), and the error rate was low (mean rate of responding incorrectly to horizontal standards = 0.18%, range 0%–0.71%).

ERP results

Endogenous cuing blocks. The mean amplitude of the peak of the contralateral early-P1 (90–110 ms) evoked by the standards was investigated using a repeated measures ANOVA with the factors of endogenous attention (endogenously cued location vs. endogenously uncued location), visual field (left vs. right), electrode (lateral vs. medial contralateral occipital locations; “OL/OR” and “T5/T6” as described earlier), and participant ($N = 10$). Similar to previous studies that investigated endogenous attention alone, the P1 was significantly enhanced at the cued location (1.44 μ V) vs. the uncued location (1.03 μ V; $F(1,9) = 14.35$, $P < 0.005$; Fig. 7, left column). There were no significant interactions with cuing, and there were no other main effects.

The mean amplitude of the contralateral N1 (140–170 ms) evoked by the standards was investigated using a repeated measures ANOVA with the factors listed above. In agreement with previous studies in which endogenous attention was investigated in isolation, the N1 was significantly enhanced at the endogenously cued location (−0.96 μ V) vs. the endogenously uncued location (0.09 μ V; $F(1,9) = 14.12$, $P < 0.005$; Fig. 7, left column; note more negative indicates a stronger N1). There were no other significant main effects or interactions.

Exogenous cuing blocks. The mean amplitude of the peak of the early-P1 (90–110 ms) evoked by the standards in the exogenous cuing blocks was investigated using a repeated measures ANOVA with the same factors as above, except with the factor of endogenous attention replaced with exogenous attention (exogenously cued location vs. exogenously uncued location). In contrast to previous studies, this early phase of the P1 was not significantly modulated by exogenous attention, although there was a trend for the P1 to be slightly larger at the cued location (0.78 μ V) vs. the

Experiment 2

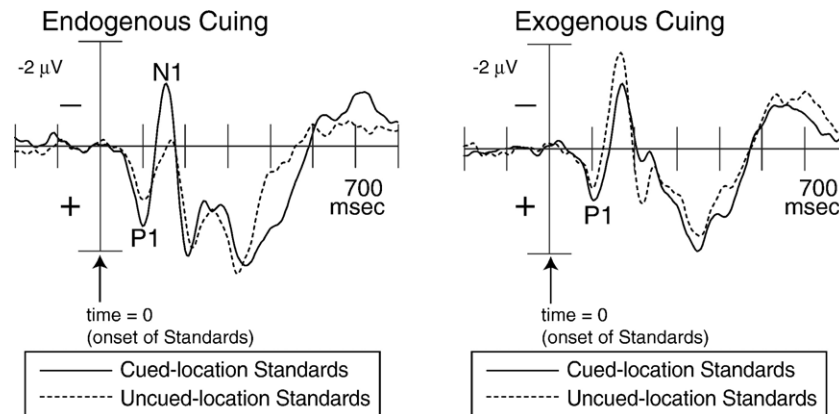


Fig. 7. Event-related potentials (ERPs) to standards in Experiment 2. Data are collapsed over contralateral occipital scalp sites OL and OR. (A) ERPs to standards in the endogenous cuing blocks, as a function of preceding *endogenous* cue location. Standards occurring at the location indicated by the endogenous cue elicited significantly enhanced P1 and N1 components compared to standards occurring at the endogenously uncued location. (B) ERPs to standards in the exogenous cuing blocks, as a function of preceding *exogenous* cue location. Standards occurring at the location of the exogenous cue elicited a significant positive shift that began during the period of the late-P1 and continued through the N1 latency range.

uncued location ($0.66 \mu\text{V}$; $F(1,9) = 0.29$, $P = 0.6$; Fig. 7, right column). There were no significant interactions with cuing.

The mean amplitude of the contralateral late-P1 (120–150 ms) evoked by the standards in the exogenous cuing blocks was investigated using a repeated measures ANOVA with the same factors as above. In agreement with previous studies, this stage of processing was significantly modulated by exogenous attention, as cued location standards ($0.31 \mu\text{V}$) were significantly more positive compared to uncued location standards ($-0.34 \mu\text{V}$; $F(1,9) = 8.04$, $P < 0.05$; Fig. 7, right column). There were no other significant main effects or interactions in this analysis.

The mean amplitude during the peak of the contralateral N1 (160–190 ms) evoked by the standards was investigated using a repeated measures ANOVA with the factors listed above. In agreement with previous studies in which exogenous attention was investigated in isolation, the N1 appears to be reduced at the exogenously cued location ($-1.13 \mu\text{V}$) vs. the endogenously uncued location ($-1.70 \mu\text{V}$), although this difference was not quite significant ($F(1,9) = 4.82$, $P = 0.056$; Fig. 7). This reduced N1 likely reflects the positive shift for cued location stimuli overlapping in time with the activity producing the typical N1. There was a significant main effect of electrode, as the N1 was greater at the more medial location ($-1.13 \mu\text{V}$) vs. the more lateral location ($-1.52 \mu\text{V}$; $F(1,9) = 5.15$, $P < 0.05$). There was also a significant interaction between electrode and cuing, as the cuing difference (cued–uncued) was larger at the more medial location ($0.69 \mu\text{V}$) vs. the more lateral location ($0.45 \mu\text{V}$; $F = 6.44$, $P < 0.05$). There were no other significant main effects or interactions.

Discussion

In Experiment 2, we investigated whether the typical cuing effects of endogenous and exogenous attention could be found using the present stimuli and task parameters. This experiment revealed that endogenous attention, when not triggered concurrently with exogenous attention, significantly enhanced both the early-P1 and the N1 components. Exogenous attention, when not triggered concurrently with endogenous attention, did not produce

a significant modulation of the early-P1, although it did produce the typical positive shift during the latency range of the late-P1.

The results of Experiment 1 must be reinterpreted in light of these new findings. Specifically, the lack of an exogenous effect on the early-P1 in Experiment 1 is unlikely to be due to endogenous attention being concurrently active. Rather, the present stimuli and design are simply not optimal for inducing an exogenous effect at that early stage. Indeed, recent data have shown that the early-P1 exogenous attention effect is more sensitive to physical attributes of the stimuli, whereas the late-P1 is more sensitive to the congruency between features of the cue stimuli and expected target stimuli (Hopfinger and Ries, 2005). In contrast, the lack of an endogenous effect on the P1 in Experiment 1 is likely due to exogenous attention, because in the absence of exogenous attention being concurrently triggered, endogenous attention does produce an enhancement of the P1 with this task and stimuli.

To further investigate these effects, we calculated difference waves for the results from Experiment 2 by subtracting the ERPs to the uncued location standards from the ERPs to the cued location standards (separately for the endogenous and exogenous blocks). For comparison with Experiment 1, Fig. 8 shows the difference waves from Experiment 2 plotted over the difference waves from Fig. 6 (Experiment 1). Although a direct statistical comparison of the effects across the two experiments would be problematic (because the experiments used different participants, a different number of participants, and a different number of trials), a visual inspection of the waveforms reveals some interesting trends. The predominant effect of exogenous attention was an enhanced positivity peaking around 150 ms (Figs. 8A and B). The exogenous attention effect occurred regardless of endogenous attention, but the magnitude of the effect appears to depend on endogenous attention. Specifically, the exogenous cuing effect is largest when endogenous attention is focused on the same location and smallest when endogenous attention is focused elsewhere. The data from Experiment 2 suggest that when endogenous attention is not highly engaged at a specific location, the magnitude of the exogenous attention effect is between these two extremes. The latency of the peak of this exogenous effect seems to be unaffected

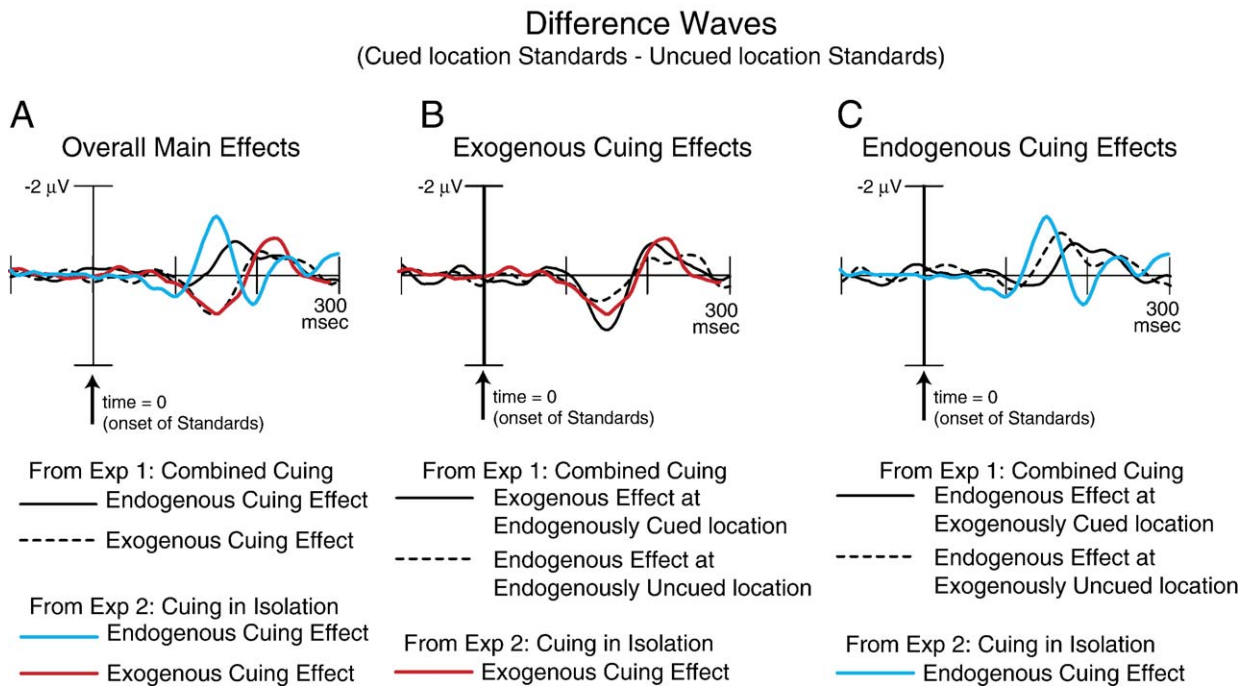


Fig. 8. Difference waves from Experiments 1 and 2 combined. The difference waves were calculated as described in Fig. 6. Electrode shown is contralateral “OL/OR” location. (A) Main effects of endogenous cuing and exogenous cuing from Experiments 1 and 2. (B) Effect of exogenous cuing in Experiment 2, and this effect from Experiment 1 separated into the exogenous effect at the endogenously cued location vs. the exogenous effect at the endogenously uncued location. (C) Effect of endogenous cuing in Experiment 2, and this cuing effect from Experiment 1, separated into the endogenous effect at the exogenously cued location vs. the endogenous effect at the exogenously uncued location.

by endogenous attention, as in Experiment 1. These data provide further support for our earlier suggestion that at the stage of processing indexed by the late-P1, endogenous attention modulates the amplitude, but not the latency, of the exogenous attention effect.

The effects of endogenous attention reveal a different pattern of interaction. The difference wave from the endogenous blocks of Experiment 2 illustrates the enhancement of the early P1 (~90–110 ms; Fig. 8A). Comparing this result to the difference waves from Experiment 1 (Fig. 8C) highlights that this early-P1 enhancement was absent when exogenous attention was concurrently active, regardless of whether exogenous attention had been triggered at the same vs. an opposite location. Therefore, exogenous attention interferes with the ability of endogenous attention to enhance this particular early stage of processing. As in Experiment 1, endogenous attention significantly enhanced the N1 component in Experiment 2. Endogenous effects on the N1 were not eliminated by exogenous attention, although the latency of the endogenous effect was affected by exogenous attention. Specifically, the endogenous enhancement of the N1 peaks earliest when exogenous attention is not triggered at all (Experiment 2), slightly later when exogenous attention is engaged at a different location, and latest when exogenous attention is engaged at the same location. In other words, the less exogenous attention is affecting stimuli at that location, the sooner endogenous attention can enhance processing there.

In summary, we investigated the influence of endogenous and exogenous attention on neural processing when these systems are active in isolation (Experiment 2) and when they are concurrently engaged (Experiment 1). The results indicate that neither exogenous nor endogenous attention significantly modulates the earliest stage of visual cortical processing, the striate-generated C1, even

when these systems converge on a common location. Shortly after this stage of processing, however, the systems begin to show interactive effects. The early-P1 component was significantly enhanced in the present experiments only at the endogenously cued location, and only when exogenous attention was not engaged at all (Experiment 2). When exogenous and endogenous attention were concurrently engaged, the early-P1 was not modulated by endogenous attention. The late-P1 was enhanced by exogenous attention, regardless of endogenous attention, although the magnitude of the effect was affected by the locus of endogenous attention. Exogenous attention thus appears to be dominant at the earliest stages of processing, although not completely independently of endogenous attention. In contrast, the N1 component was enhanced only by endogenous attention, and it did so regardless of where exogenous attention was triggered. Again, however, there was an interaction between the systems at this stage of processing, as the endogenous N1 effect was delayed at the exogenously cued relative to uncued location. At the later stages of processing indexed by the P300, endogenous attention dominated processing, without influence from exogenous attention. In conclusion, the present results provide evidence that endogenous and exogenous cuing trigger two partially separate but interacting attention systems, and that these systems can be active concurrently and affect overlapping stages of information processing in the brain.

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