Selective attention: Electrophysiological and neuromagnetic studies.

Joseph B. Hopfinger[1], Steven J. Luck[2], & Steven A. Hillyard[3]

[1]Department of Psychology, University of North Carolina at Chapel Hill
[2]Department of Psychology, University of Iowa
[3] Department of Neuroscience, University of California, San Diego

Corresponding author:
Joseph B. Hopfinger
Department of Psychology
CB 3270, Davie Hall
University of North Carolina at Chapel Hill
Chapel Hill, NC 27599-3270
office: (919) 962-5085
FAX: (919) 962-2537
email: hopfinger@unc.edu

Introduction

Most visual scenes contain more information than can be assimilated at a single glance. To manage the intake of information from the intricate scenes of the natural world, the human visual system employs an array of attentional mechanisms capable of selecting relevant information at multiple stages of processing. Much has been learned in recent years about the neural operations that mediate stimulus selection at different levels of the visual pathways, and these data have informed theoretical accounts of visual attention (Luck & Hillyard 2000). In humans, studies using hemodynamic neuroimaging techniques (PET and fMRI) have identified specific anatomical areas and pathways that participate in different aspects of visual attention, while electrophysiological and neuromagnetic recordings have revealed the timing and sequencing of stimulus selection processes within those pathways (for reviews see Kanwisher & Wojciulik 2000; Martinez et al. 2001)

The present chapter considers recent visual attention experiments in which noninvasive recordings of brain activity have clarified the nature of the underlying mechanisms of selection. The emphasis is on showing how recordings of event-related brain potentials (ERPs) and event-related magnetic fields (ERFs) provide timing information that is critical for understanding the dynamic operation of different attentional processes. In some cases, these ERP and ERF recordings have been combined with parallel neuroimaging studies to yield a more complete spatio-temporal picture of the attentional operations under study. These approaches have shed light on the mechanisms underlying spatial attention, visual search, the automatic capture of attention, post-perceptual selection, and the voluntary control of attention.

Visual-Spatial Attention

Psychophysical studies have shown that allocating visual attention to a selected region of the visual field may enhance the perception of stimuli at that location (Luck, Hillyard, Mouloua, & Hawkins, 1996; Luck et al., 1994; Yeshurun & Carrasco, 1998). The neural basis of this perceptual facilitation has been investigated extensively in both animal and human studies. Considerable progress has been made in identifying the specific cortical areas where spatial attention influences visual processing and in specifying the timing of those selection processes. This research has also led to new proposals about the controversial role of the primary visual cortex (area V1) in attention.

Multiple visual-cortical areas are influenced by visual-spatial attention

Recordings of single-unit activity in monkeys have shown that neural responses evoked by attended-location stimuli are enhanced in extrastriate visual areas V2, V3a, V4, and MT, as well as in higher areas in inferotemporal cortex and the posterior parietal lobe (Maunsell & McAdams 2000; Reynolds & Desimone 2001). There is also evidence that spatial attention can modulate neural activity in the primary visual cortex (area V1) under certain conditions, such as when multiple, competing stimuli are presented (Motter 1993; Roelfsema et al. 1998; Vidyasagar 1999). These attention-related changes in V1 activity were often found to be delayed well beyond the initial geniculo-striate evoked response in V1, however, which suggests that they may be mediated by delayed feedback projections from higher visual areas (Vidyasagar 1999; Schroeder et al. 2001).

Neuroimaging studies have confirmed the participation of both striate and extrastriate visual areas in spatial attention in humans. Using fMRI, it was found that directing attention to a stimulus position results in increased neural activity in circumscribed zones of visual areas V1, V2, V3, V3a, and V4 that correspond to the retinotopic projection of the attended location (Tootell et al. 1998; reviewed in Martinez et al.1999; 2001). Given the limited temporal resolution of fMRI, however, it has been difficult to determine whether these attention-related increases in activity represent an enhancement of early sensory-evoked responses, a delayed modulation of activity due to feedback from higher areas, or a sustained increase in activity associated with the spatial focusing of attention.

The time course of attentional modulation

The time course of these spatial attention effects in humans has been clarified by recordings of ERPs and ERFs. In the typical experimental design, stimuli are presented in randomized sequences to two (or more) locations in the visual field while the subject pays attention to only one location at a time (Figure 1). Numerous studies of this type over the past 25 years have shown that stimuli at attended locations typically elicit enlarged positive (P1 at 80-130 ms) and negative (N1 at 150-200 ms) components over the posterior scalp relative to stimuli at unattended locations (reviewed in Hillyard & Anllo-Vento 1998; Luck & Hillyard 2000). As illustrated in Figure 1, these amplitude modulations of the P1 and N1 components usually occur with little or no change in component latencies or scalp distributions (Mangun 1995; Di Russo et al. 2003), suggesting that the voluntary focusing of attention involves a gain control or amplification mechanism within the early visual pathways (Hillyard et al 1998). The general idea of a gain control mechanism has also been supported by single-unit studies (Reynolds, Chelazzi, & Desimone, 1999) and psychophysical studies (Lu & Dosher, 1998). Increasing the sensory gain at a given location may enhance perception by increasing the size of small sensory signals relative to the brain's internal noise (Hawkins et al., 1990) or by giving the attended location a competitive advantage over ignored locations (Desimone & Duncan, 1995).

The neural generators of the attention-sensitive P1 and N1 components have been localized through dipole source modeling and co-registration with PET and fMRI activations to specific zones of extrastriate visual-cortical areas (Figures 1b, 1c and Figure 2; Heinze et al. 1994; Mangun et al. 1997; Martinez et al. 1999; 2001; Di Russo et al. 2001, 2003). As illustrated in Figure 2, the initial phase of the P1 (at 80-100 ms) appears to originate from mid-occipital regions in or near areas V3/V3a and the immediately anterior middle occipital gyrus, while the later phase of the P1 (at 100-130 ms) appears to arise from ventral occipital cortex in or near area V4 and the adjacent fusiform gyrus (DiRusso et al. 2001). The N1 was also found to arise from multiple generators, including an early posterior parietal phase (140-160 ms) and a later ventral occipital-temporal phase (160-200 ms). Thus, the earliest modulations of visual-evoked neural activity by the spatial focusing of attention were found to occur at multiple sites along the extrastriate visual pathways.

The Role of Primary Visual Cortex

ERP and ERF recordings have been informative about the way in which spatial attention influences neural activity in area V1. There is good evidence that the earliest visual ERP component (the C1 wave, ca. 50-60 ms; Figure1) represents the initial stimulus-evoked response in area V1 (Figure 2). In particular, the C1 wave inverts in polarity for stimuli in the upper versus lower visual fields, in accordance with the retinotopic organization of area V1 within the calcarine fissure, and dipole modeling has been consistent with a calcarine generator site (Martinez et al 2001; Noesselt et al 2002; Di Russo et al 2003). In studies to date the C1 has been found to be unaffected by spatial attention (reviewed in Di Russo et al. 2003) or by attention to other visual features such as spatial frequency (Martinez et al. 2001) or color (Anllo-Vento et al 1998). These findings support the view that the initial feedforward geniculostriate response in area V1 is not subject to attentional control. Dipole modeling studies, however, have provided evidence of a delayed modulation of V1 activity during spatial attention that begins at around 130-160 ms after stimulus onset (Martinez et al. 2001; Noesselt et al. 2002; Di Russo et al. 2003). This suggests a mechanism whereby selection of attended-location stimuli first occurs in extrastriate cortical areas at a latency of 80-100 ms, as described above, and delayed feedback from these higher areas then modulates neural activity in V1. Support for such attention-related feedback signals comes from neurophysiological studies in monkeys (Schroeder et al. 2001; Lamme & Spekreijse 2000), and it has been proposed that delayed, re-entrant activity in area V1 may improve figure/ground segregation and enhance the salience of stimuli at attended locations (Lamme et al. 2000).

Dissociable mechanisms of visual-spatial attention

Although the P1 and N1 waves occur in close temporal proximity and are both affected by spatial attention, there are clear indications that these components reflect different aspects of spatial selection. In particular, dissociations between the P1 and N1 components have been observed in trial-by-trial cuing experiments. In these experiments, a symbolic cue at the beginning of each trial directs the subject to attend preferentially to the indicated location for that trial. Mangun & Hillyard (1991) found that the N1 component was enhanced for valid targets, relative to invalid targets, only when a discrimination of the target's features was required, whereas the P1 component exhibited a robust attention effect (valid greater than invalid) regardless of whether subjects were performing a simple detection or more difficult discrimination task. A dissociation between the P1 and N1 was also obtained by Luck et al. (1994), who isolated facilitatory and inhibitory effects by comparing ERPs from stimuli at attended and ignored locations with ERPs from those stimuli on neutral (baseline) trials in which attention was diffusely distributed. Compared to baseline trials, the P1 was found to be suppressed at the ignored location but was not relatively enhanced at the attended location. In contrast, the N1 was enhanced at the attended location but not suppressed at the ignored location relative to the baseline trials. To account for these effects, Luck (1995) proposed that the P1 effect reflects an early sensory gain control mechanism that suppresses noise at ignored locations, whereas the N1 effect reflects the application of a limited-capacity discriminative process at the attended location. Subsequent studies have confirmed that the N1 wave, but not the P1 wave, is enhanced when subjects perform discrimination tasks on a stimulus compared to when they make simple detection responses (Vogel &

Luck, 2000; for a similar dissociation see Handy & Mangun 2000). A recent MEG study (Hopf, Vogel, Woodman, Heinze & Luck 2002) provided evidence that the discriminative processing associated with the N1 component takes place in inferior occipito-temporal cortex of the ventral stream beginning approximately 150 ms after stimulus onset.

Visual Search

In the studies described above, attention was directed to specific locations by explicit verbal instructions or symbolic cues. To study how attention operates when the target location is unknown, attention researchers have used visual search tasks in which subjects try to find a predefined target stimulus within an array of distractors. When the target contains a distinctive feature, it can be detected rapidly, even if many distractors are present. When the target does not contain a distinctive feature, however, search may be slow and effortful, and reaction times may increase as the number of distractors increases. In such cases, some researchers have proposed that attention shifts from object to object until the target is detected (Treisman & Gelade, 1980; Wolfe, 1994). ERP studies of visual search have sought to answer two major questions. First, are the attentional mechanisms that were described in the previous section also used when attention is focused onto an object during visual search? Second, does attention indeed shift serially from object to object in difficult search tasks?

To determine whether sensory processing is enhanced at the attended location in visual search, Luck, Fan and Hillyard (1993) used visual search arrays containing 14 red items, one blue item, and one green item. Subjects were required to discriminate the form of either the blue item or the green item. To measure sensory processing at the attended location, a task-irrelevant probe square was flashed at the location of either the blue item or the green item shortly (250 ms) after the onset of the search array. By the time of the probe flash, subjects should have localized and focused attention onto the target item. The probe stimulus elicited larger P1 and N1 waves when it was presented at the location of the target item than when it was presented at the location of the nontarget item, just as stimuli presented at explicitly cued locations elicit larger P1 and N1 waves than stimuli presented at uncued locations. Moreover, a follow-up study showed that the P1 effect in visual search reflects suppressed processing at the nontarget location, whereas the N1 effect reflects enhanced processing at the target location (Luck & Hillyard, 1995), in line with the P1/N1 dissociation described above. These results suggest that the mechanisms of attention used spontaneously during visual search are basically the same as the mechanisms used when attention is directed by explicit instructions.

The allocation of attention during visual search may also be investigated by examining the ERP waveform elicited by the search array itself. In particular, when attention is directed to an item in a search array, a negative-going ERP component is elicited over the contralateral visual cortex. This ERP component is labeled “N2pc” (N2-posterior-contralateral) to indicate that it usually occurs in the time range of the N2 family of components (ca. 200-300 ms after the onset of the search array), with a posterior, contralateral scalp distribution. A typical paradigm for eliciting the N2pc component is shown in Figure 3-A. Each search array consisted of 15 black distractor items and a white target item in either the left visual field (LVF) or the right visual field (RVF). Subjects make a button-press response to indicate whether the target item is an upright T or an inverted T. This paradigm is designed to allow subjects to shift attention to the target with minimal trial-by-trial variability in latency, which is important when stimulus-locked ERP averages are examined. The N2pc can be visualized by comparing the averaged waveforms calculated for contralateral targets (i.e., left hemisphere/right target waveforms averaged with right hemisphere/left target waveforms) and for ipsilateral targets (i.e., left hemisphere/left target waveforms averaged with right hemisphere/right target waveforms). This comparison is shown in Figure 3-B.

Several pieces of evidence indicate that the N2pc component reflects the allocation of attention (see Luck, Girelli, McDermott, & Ford, 1997; Luck & Hillyard, 1994). The N2pc may be a human ERP homologue of single-unit attention effects from area V4 and inferotemporal cortex that have been observed in monkeys performing visual search tasks (Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993, 2001); it has the same timing, and it is similarly influenced by factors such as target type and distractor density (Luck et al., 1997). Consistent with this proposal, a recent MEG study indicated that the N2pc component is generated primarily in occipital-temporal cortex, with a small contribution from posterior parietal cortex (Hopf et al., 2000).

Two major conclusions have emerged from studies of the N2pc component in visual search. First, consistent with Treisman's (1988) feature integration theory, these ERP studies have indicated that greater allocation of attention is required for targets defined by conjunctions of features than for single-feature targets. This conclusion was based on studies showing that the N2pc component was significantly larger in a variety of task situations when subjects perform conjunction discriminations than when they discriminate the presence or absence of a single feature (Luck et al., 1997; Luck & Hillyard, 1995; Luck & Ford 1998).

The second major conclusion arising from studies of the N2pc component during visual search is that attention does indeed shift serially from object to object during some difficult search tasks. This was inferred from experiments in which the N2pc was found to switch from one hemisphere to the other as attention switched from one visual hemifield to the other (Woodman & Luck, 1999, 2003). The design of these experiments took advantage of the fact that subjects spontaneously tend to search items near fixation before searching items far from fixation, even when the objects are scaled according to the cortical magnification factor (Carrasco, Evert, Change, & Katz, 1995; Wolfe, O'Neill, & Bennett, 1998). Figure 4-A illustrates one of these experiments, in which two red potential target items were presented among many distractor items; one of the red items was near fixation and the other was far from fixation, and they were equally likely to be the target (a square with a gap on the left). When the two items were in opposite hemifields, subjects should search the near item first and then the far item. Consistent with this, the N2pc was first negative contralateral to the near item, and then it became negative contralateral to the far item (see Figure 4-B). Thus, attention first switched to the near item at approximately 200 ms poststimulus and then switched to the far item approximately 100 ms later.

This experiment measured the relative allocation to the near and far items within a single set of ipsilateral and contralateral waveforms; it is therefore possible that subjects actually attended to both the near and far items at the same time, shifting only the relative allocation of attention over time. However, a follow-up study used a slightly different method that allowed the N2pc to be measured separately for the near and far items, and this study demonstrated that the allocation of attention was truly serial: only the near item was attended initially, and after a brief transition period, only the far item was attended (Woodman & Luck, 2003).

Automatic Capture of Attention

Behavioral research has long made a distinction between voluntary and automatic or reflexive attention systems (e.g., Jonides, 1981; Posner et al, 1978). Voluntary attention refers to the effortful, top-down controlled process wherein one decides where to attend. Reflexive attention, on the other hand, refers to a bottom-up mechanism wherein attention is *captured* —in a rapid and involuntary fashion—by an object or location that has just undergone a salient change. Behavioral data has shown that reflexive attention is more resistant to interference and is engaged more rapidly than is voluntary attention. Whereas voluntary attention may be sustained for an indefinite amount of time, reflexive attention dissipates quickly. Furthermore, reflexive attention produces a unique biphasic effect on reaction times. Specifically, attention-capturing cues initially result in faster and more accurate responses to stimuli at the captured location, but at slightly longer intervals between the capturing event and subsequent target, subjects are actually slower to respond to stimuli at the attended location. This phenomenon has been termed *inhibition of return* (IOR; Posner and Cohen, 1984), as attention appears to be inhibited from returning to the location that it was previously engaged at (see Klein, 2000 for comprehensive review). Despite this behavioral evidence for the distinction between these systems, studies of the neural mechanisms of attention have focused predominately on the voluntary system.

Recently, however, ERPs have been used to investigate the mechanisms of reflexive attention. In studies of reflexive attention, the “cue” is typically an abrupt flash or change in the visual scene that is not predictive of the location or type of target stimulus that follows. At short cue-to-target intervals, Hopfinger and colleagues found that these nonpredictive abrupt reflexive cues result in enhanced cortical visual processing for subsequent stimuli that occur at the cued location relative to stimuli at uncued locations. Specifically, the P1 component was significantly larger for cued location targets (Figure 5a). Furthermore, the enhancement of the P1 component occurred whether subjects were performing a difficult discrimination task (Hopfinger & Mangun, 1998), were engaged in a simple detection task (Hopfinger & Mangun, 2001), or were simply viewing task-irrelevant stimuli (Hopfinger et al., 2000b). This pattern of results, combined with the fact that the cue stimuli were completely nonpredictive of target location or target type, suggests that the P1 effect here is due to truly reflexive mechanisms. These results suggest that voluntary and reflexive attention may be able to affect processing at a similar neural locus. However, unlike voluntary attention, reflexive attention has not been found to affect the process indexed by the N1 component, even in a difficult discrimination task.

Although the facilitatory effects of reflexive orienting on visual processing at short cue-to-target intervals appear to be robust across different task parameters, the conclusions are not yet as clear for the effects at longer ISIs when inhibitory processes (IOR) typically dominate the behavioral responses. Several studies have found that the P1 amplitude may be reduced to stimuli at cued versus uncued locations at long ISIs (Figure 5b), but this IOR-like pattern has not always been associated with the strongest behavioral evidence for IOR (Hopfinger & Mangun 1998, 2001; McDonald, Ward & Kiehl 1999). These studies suggest that an early sensory modulation may not fully explain the IOR phenomenon, which may consist of a combination of sensory and response-related factors (see also Kingstone & Pratt, 1999). The results from ERP experiments, however, do suggest a specific perceptual-level locus at which the inhibitory effects may be manifest.

Cross-modal Capture of Attention

In addition to the effects that visual transients have on subsequent visual processing, recent studies have demonstrated that visual processing can also be affected by attentional capture in other sensory modalities. Spence & Driver (1997) provided behavioral evidence for a cross-modal link in auditory and visual attention, finding that a non-predictive auditory "cue" resulted in faster response times to a visual target stimulus that occurred at the same location as the auditory cue. More recent studies have shown that non-predictive auditory events can enhance the perceptibility of a visual stimulus presented at the same location (Dufor, 1999; McDonald & Ward, 2000). ERP recordings have shown that this cross- modal effect on visual perception was associated with an enhanced negativity in the interval from 120-180 ms following the visual target (McDonald et al., 2003). The early phase of this negativity (at 120-140 ms) was localized by dipole modeling to the multimodal region of the superior temporal cortex, while the later phase (at 140-180 ms) was attributed to generators in the ventral occipital cortex of the fusiform gyrus. These results provide support for proposals that cross-modal influences on visual perception are mediated by feedback influences from multimodal areas (such as the superior temporal cortex) to unimodal visual cortex of the ventral processing stream (Driver & Spence 1998; Macaluso et al 2000; McDonald & Ward 2000).

A non-predictive tactile stimulus can also facilitate the processing of a subsequent visual stimulus presented at the same location (Spence, Nicholls, Gillespie & Driver 1998). In an fMRI study of this effect, Macaluso et al. (2000) found that flash-evoked activity in the visual cortex of the lingual gyrus was enhanced by a preceding irrelevant tactile event. A subsequent ERP study (Kennet et al., 2001) showed that the tactile cue produced enhancement of visual-evoked negativity in the 110-200 ms range that included a lateral-occipital N1 component. This crossmodal facilitation was shown to depend on a common spatial location of the tactile and visual stimuli, when conditions of crossed and uncrossed arms were compared. Taken together these studies show that abruptly onsetting stimuli in different modalities (visual, auditory, or tactile) can capture attention automatically and facilitate the processing of co-localized visual targets at an early stage of the extrastriate cortical pathways.

Postperceptual Attention Mechanisms

A great deal of research has been devoted to understanding the role of attention in perception, but attention also has large effects on postperceptual processes such as working memory encoding and response selection[1]. ERPs have been very useful in isolating the specific postperceptual processes that are influenced by attention in a variety of paradigms. Here, we will focus on the attentional blink paradigm, which has been the focus of intense study over the past decade.

Potter (1976) showed observers rapid sequences of photographs of complex scenes, and she found that the observers could identify the photographs at very high presentation rates (e.g., 8/sec) but could not store them in working memory at these high rates. This result implies that we can perceive much more than we can store in working memory. More recent studies using rapid sequences of simpler stimuli have shown that detecting one target (called T1) leads to a period of approximately 500 ms during which a second target (called T2) is not detected. If, however, subjects ignore T1, they can accurately detect T2. This pattern of results, shown in Figure 6, is called the *attentional blink*, because detecting T1 leads to a *blink* of attention during which T2 is not detected. Because Potter (1976) demonstrated that observers can perceive information at the high rates used in these experiments, it seems plausible that T2 is perceived during this blink of attention. However, the process of transforming a perceptual representation into a durable working memory representation may be slower than the process of forming a perceptual representation. Thus, during the period in which T1 is being consolidated into working memory, T2 may fail to be consolidated, and this may explain failures to detect T2 (see Shapiro, Arnell, & Raymond, 1997).

According to this explanation of the attentional blink, the detection of T1 does not impair perceptual processing of T2 but leads to a failure of working memory encoding. This hypothesis was tested in a series of ERP experiments (Luck, Vogel, & Shapiro, 1996b; Vogel & Luck, 2002; Vogel, Luck, & Shapiro, 1998). One of these experiments examined the P1 and N1 waves elicited by a probe stimulus presented at various times following T1(Vogel et al., 1998, Experiment 1). In contrast to the spatial attention experiments described above, in which the P1 and N1 waves were found to be suppressed for ignored stimuli compared to attended stimuli, there was no suppression of the P1 and N1 waves during the attention blink period.

A second experiment used words as the target stimuli and examined the N400 component (Luck et al., 1996b), which is elicited when a word mismatches a previously established semantic context. In this experiment, a semantic context was established at the beginning of each trial, and the T2 word either matched or mismatched this context. Before a mismatching word can elicit an N400 component, the word must be identified and compared with the semantic context. Thus, the presence of a larger N400 for mismatching words than for matching words provides strong evidence that the words were identified to a lexical or semantic level. In this experiment, the N400 was indeed larger for mismatching words than for matching words, and this effect was not reduced during the attentional blink period. This experiment thus provides strong evidence that the failure to detect T2 during the attentional blink period reflects an impairment in postperceptual processing.

A subsequent experiment examined the P3 wave (Vogel et al., 1998, Experiment 4), which is thought to reflect processes associated with working memory encoding (Donchin, 1981; Donchin & Coles, 1988). Unlike the P1, N1, and N400 components, the P3 wave was completely eliminated when T2 was presented during the attentional blink period. This finding supports the hypothesis that the attentional blink occurs because of a failure to encode the perceptual representation of T2 into working memory.

Additional predictions can be made when T2 is the last item in the sequence. In this case, the perceptual representation of T2 will not be masked by a subsequent item and may persist for a few hundred milliseconds. This fading perceptual representation may still be available when the consolidation of T1 has been completed, allowing T2 to be consolidated and thus available for report. Indeed, Giesbrecht and Di Lollo (1998) found that the attentional blink was eliminated when T2 was the last item in the sequence, even if T2 perceptibility was reduced by adding simultaneous masking noise. In an ERP study of this, Vogel and Luck (2002) found that the P3 wave was not eliminated when T2 was the last item in the sequence; instead, the P3 wave was delayed. This result supports the hypothesis that the processing of T1 leads to a delay in the consolidation of T2. When T2 is followed by another item, the following item masks T2 before it has been consolidated, impairing T2 detection performance and eliminating the T2-elicited P3 wave. When T2 is the final item, consolidation is delayed, leading to a delayed P3 wave but accurate T2 detection.

Attentional Control

The preceding sections have described the effects that attention has on perceptual and post-perceptual levels of processing, after attention has been concentrated at a specific location or on a specific object. In addition to delineating the effects of attention on subsequent processing, another important area of research concerns attentional control - the neural mechanisms that account for the movement and focusing of attentional resources. Recent hemodynamic neuroimaging and ERP studies have provided new insights into the neural structures and dynamics underlying attentional control processes.

In trial-by-trial cuing paradigms, it is possible to investigate not only the effects of attention on target processing but also the neural processes that occur in response to instructions (e.g., the cue) to orient attention to a specific location, before the target stimulus appears. In an ERP study of spatial cuing, Harter and colleagues (e.g., Harter et al., 1989) found that instructive cue stimuli produced two prominent components that were largest over the scalp contralateral to the attended visual hemifield. The first component was termed the "early directing attention negativity" (EDAN), a posterior parietal negativity occurring from approximately 200-400 ms after the instructive central cue. Following this component, at latencies of 500-700 ms after the cue, a positivity termed the "late directing attention positivity" (LDAP) was found over occipital scalp sites. The EDAN was interpreted as indexing a control process that acts upon sensory areas to modulate the excitability of neurons representing attended regions of space. It was proposed that this latter modulation of excitability was reflected in the LDAP component.

Hopf and Mangun (2000) conducted a similar experiment and used a higher-density montage of recording sites to provide a more precise localization of the processes underlying attentional control. The results replicated the basic EDAN and LDAP findings described above. However, Hopf and Mangun also found an additional effect occurring in the time interval between the EDAN and the LDAP, that was maximal over frontal regions. Contrary to theories of attention that postulate that regions of the frontal lobe initiate attentional control mechanisms (e.g., Posner & Peterson, 1990; LaBerge, 1997), these findings provide new data suggesting that attentional control activity in parietal regions may actually precede the activity in frontal cortex. Finally, another important result from this study was that the topography of the LDAP effect was highly similar to the topography of the P1 attention effect that was found to the subsequent target stimuli.

This provides support for the hypothesis that attention acts to prime sensory processing regions, and specifically that the LDAP reflects a biasing of neural activity in visual regions that may be responsible for the later selective processing of stimuli occurring at attended locations.

Recent neuroimaging results are providing new evidence regarding the neural structures underlying some of these attentional control processes. Earlier neuroimaging and neuropsychological studies provided evidence that a widespread network of brain regions underlie attention mechanisms, including regions of posterior parietal cortex (Posner et al., 1984; Corbetta et al., 1993; Gitelman et al., 1999; Mesulam, 1981), thalamus (Heinze et al., 1994; LaBerge, 1997; Petersen et al., 1987), superior temporal sulcus (Nobre et al., 1997; Watson et al., 1994), and regions of frontal cortex (Corbetta, 1998; Henik et al., 1994). A limitation in many early neuroimaging studies, however, was that the analysis methods required the tasks to be ‘blocked’ over many seconds or minutes. Therefore, these analyses were not well suited for separating control processes of attention from the selective processing of target stimuli that occur later.

More recently however, the introduction of event-related fMRI analysis techniques (e.g., Buckner et al., 1996; Josephs et al., 1997; McCarthy et al., 1997) has allowed researchers to analyze attentional control and preparatory processes separately from the subsequent effects of attention on the processing of target stimuli (Corbetta et al. 2000; Hopfinger et al., 2000a; Kastner et al., 1999). In the Hopfinger et al. (2000a) study, a color-coded cue appearing at fixation directed the subject to attend to the left or right side of a subsequent target stimulus, which was a bilateral, contrast reversing black and white checkerboard pattern. The results revealed a dissociation between the brain regions active in response to the instructive cue versus those brain regions active in response to the subsequent target stimuli. For instance, the intraparietal sulcus was found to be active in response to the instructive cue stimuli, but not to the target stimuli, consistent with a role in controlling shifts of spatial attention. The superior temporal cortex, regions of the frontal lobe near the frontal eye fields (FEF), and regions of the superior frontal gyrus anterior to the FEF also showed activity specific to processing of the instructive cue stimuli, suggesting that these regions are specifically involved in an aspect of attentional control, as opposed to being involved in later aspects of selective target processing. Target stimuli evoked activity in a highly distinct set of brain regions, including bilateral regions of the supplementary motor area, extending into the mid-cingulate gyrus, bilateral ventrolateral prefrontal regions, bilateral visual cortex, and the precentral and postcentral gyri. Geisbrecht and colleagues (Geisbrecht et al., in press) recently expanded upon these results, finding that portions of the attentional control network (including inferior and medial frontal gyri and posterior parietal regions) were common to both space and feature based attentional control (see also Shulman et al., 2002; Wojciulik & Kanwisher, et al. 1999). However, this study also revealed specificity in parts of the control network, as activity in more superior frontal regions and superior parietal cortex were significantly more involved in spatial shifts of attention compared to feature based attention.

As described in the above ERP studies of attentional control, the LDAP component is thought to index a priming of visual processing regions in response to instructive cues that precedes and is highly similar in scalp distribution to the attention effects (e.g., P1) on target processing. Event-related fMRI techniques are now providing converging evidence. In the Hopfinger et al (2000a) study, enhanced activity in response to the target stimuli was found contralateral to the attended hemifield in two visual processing regions, a ventral region within the lingual/fusiform gyri and a more dorsal region in the cuneus. This finding of an effect of selective spatial attention in extrastriate regions is in agreement with numerous previous studies (e.g., Heinze et al., 1994; Mangun et al., 1997; Woldorff et al., 1997). However, by separating the cue-related activity from the target-related activity, this study was able to isolate the processing in this region that occurred before the target stimuli appeared. The comparison between cues directing attention to the left versus right revealed relative increases in activity in the visual cortex of the hemisphere contralateral to the attended hemifield. Importantly, these regions overlapped with the regions where attention effects were subsequently found in response to the target stimuli (Figure 7). Because this differential activity was found in response to the cue and before target processing, it provides further support for models of attention that posit a preset gain-control mechanism that enhances the excitability of visual cortical neurons coding the attended regions of space (e.g., Hillyard and Mangun, 1986; Chawla, et al., 1999; Kastner et al, 1999). Woldorff and colleagues (Woldorff et al, in press) have recently performed a rapid-event-related fMRI investigation of these mechanisms of attention. By applying techniques initially used for dissociating overlapping ERP components (e.g., Woldorff, 1993; Burock et al, 1998), they have shown that it is possible to analyze fMRI activity for events occurring in relatively close succession (~500ms). This is an important step in relating fMRI findings to the vast behavioral and ERP literature of attention studies that used much shorter intervals between cues and targets than have typically been used in neuroimaging studies. Importantly, their rapid-event-related fMRI study found a biasing in extrastriate regions in response to the cue stimuli, before the appearance of target stimuli, confirming previous results. While these analysis techniques are providing new possibilities for dissociating the sub-component processes of attention, fMRI techniques cannot alone provide the temporal resolution necessary to fully characterize the dynamics of attention processes in the brain. Combining these approaches with ERP and neuromagnetic measures of mental function, however, promises to provide exciting results that should significantly expand our understanding of the mechanisms and processes of attention.

Conclusion

In this chapter, we have reviewed electrophysiological, neuromagnetic, and neuroimaging studies that are informing theories of selective attention mechanisms and the neural underpinnings of these processes. These studies have provided evidence that attention affects visual processing at both perceptual and post-perceptual levels. Perceptual level processing has been found to be enhanced as early as 80-130 ms latency (i.e., the P1 component), and the studies reviewed here show that this effect can be generated either by explicit instructions, visual search processes, or by the involuntary capture of attention. The effects of attention on perceptual level processing include longer latency effects as well (the N1, 140-200 ms), and this slightly later attention effect has been dissociated from the earlier attention effect in a number of the studies reviewed here. Electrophysiological indices of post-perceptual processing (e.g., the P3 component) provide further evidence that attention can act at multiple levels of processing. Finally, ERP and event-related fMRI studies are beginning to identify the neural systems and dynamic processes that underlie attentional control processes. These studies are providing converging evidence for the roles of frontal and parietal regions in the biasing of sensory processing regions that occurs prior to the selective processing of subsequent stimuli. Future studies aimed at further dissociating the subcomponent processes of attention promise to provide even greater precision in identifying the neural dynamics of selective attention.

Notes

1. We are using the terms perceptual and postperceptual to distinguish between the processes that transform sensory inputs into abstract, amodal representations of object identities (perceptual processes) and the processes that that store, manipulate, and respond to these representations (postperceptual processes). The term perception is not meant to imply awareness or phenomenological experience (which would obviate concepts such as "perception without awareness").

References

Anllo-Vento, L., Luck, S.J., & Hillyard, S.A. (1998). Spatio-temporal dynamics of attention to color: Evidence from human electrophysiology. *Human Brain Mapping, 6*, 216-238.

Burock, M. A., Buckner, R. L., Woldorff, M. G., Rosen, B. R. & Dale, A. M. (1998). Randomized event-related experimental designs allow for extremely rapid presentation rates using functional MRI. *Neuroreport, 9*, 3735-3739.

Carrasco, M., Evert, D. L., Change, I., & Katz, S. M. (1995). The eccentricity effect: Target eccentricity affects performance on conjunction searches. *Perception & Psychophysics, 57*, 1241-1261.

Chawla, D., Rees, G. & Friston, K.J. (1999). The physiological basis of attentional modulation in extrastriate visual areas. *Nature Neuroscience, 2*, 671-676.

Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *Journal of Neurophysiology, 80*, 2918-2940.

Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature, 363*, 345-347.

Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (2001). Responses of neurons in macaque area V4 during memory-guided visual search. *Cerebral Cortex, 11*, 761-772.

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., Linenweber, M. R., Petersen, S. E., Raichle, M. E., Van Essen, D. C., & Shulman, G. L. (1998). A common network of functional areas for attention and eye movements. *Neuron, 21*, 761-73.

Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience, 3*, 292-297.

Corbetta, M., Miezin, F., Shulman, G. L., & Petersen, S. E., (1993). A PET study of visuospatial attention. *Journal of Neuroscience, 13*, 1202-1226.

D'Esposito, M., Ballard, D., Aguirre, G. K. & Zarahn, E. (1998). Human prefrontal cortex is not specific for working memory: A functional MRI study. *Neuroimage, 8*, 274-282.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193-222.

Di Russo, F., Martinez, A., Sereno, M., Pitzalis, S. & Hillyard, S.A. (2001). The cortical sources of the early components of the visual evoked potential. *Human Brain Mapping, 15*, 95-111.

Di Russo, F., Martinez, A. & Hillyard, S.A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebral Cortex, 13*, 486-499.

Donchin, E. (1981). Surprise!...Surprise? *Psychophysiology, 18*, 493-513.

Donchin, E., & Coles, M. G. H. (1988). Is the P300 component a manifestation of context updating. *Behavioral Brain Science, 11*, 357-374.

Driver, J., & Spence, C. (1998). Attention and the crossmodal construction of space. *Trends in Cognitive Sciences, 2*, 254-262.

Dufour, A. (1999). Importance of attentional mechanisms in audiovisual links. *Experimental Brain Research, 126*, 215-222.

Eimer, M. (1994). "Sensory gating" as a mechanism for visuospatial orienting: Electrophysiological evidence from trial-by-trial cuing experiments. *Perception & Psychophysics, 55*, 667-675.

Giesbrecht, B. L., & Di Lollo, V. (1998). Beyond the attentional blink: Visual masking by object substitution. *Journal of Experimental Psychology: Human Perception & Performance, 24*, 1454-1466.

Giesbrecht, B. L., Woldorff, M. G., Song, A. W., & Mangun, G. R. (in press). Neural mechanisms of top-down control during spatial and feature attention. *NeuroImage.*

Handy, T. C. & Mangun, G. R. (2000). Attention and spatial selection: Electrophysiological evidence for modulation by perceptual load. *Perception & Psychophysics, 62*, 175-186.

Harter, M. R., Miller, S. L., Price, N. J., LaLonde, M. E. & Keyes, A. L. (1989). Neural processes involved in directing attention. *Journal of Cognitive Neuroscience, 1,* 223-237.

Hawkins, H. L., Hillyard, S. A., Luck, S. J., Mouloua, M., Downing, C. J., & Woodward, D. P. (1990). Visual attention modulates signal detectability. *Journal of Experimental Psychology: Human Perception and Performance, 16*, 802-811.

Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Sholz, M., Munte, T. F., Gos, A., Scherg, M., Johannes, S., Hundeshagen, H., Gazzaniga, M. S., & Hillyard, S. A. (1994). Combined spatial and temporal imaging of brain activity during selective attention in humans. *Nature, 372*, 543-546.

Henik, A. Rafal, R., & Rhodes, D. (1994). Endogenously generated and visually guided saccades after lesions of the human frontal eye fields. *Journal of Cognitive Neuroscience, 6*, 400-411.

Hillyard, S.A. & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences, 95*, 781-787.

Hillyard, S.A. & Mangun, G.R. (1986). The neural basis of visual selective attention: A commentary on Harter and Aine. *Biological Psychology, 23*, 265-270.

Hillyard, S.A., Vogel, E.K. & Luck, S.J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: Electrophysiological and neuroimaging evidence. *Philosophical Transactions of the Royal Society: Biological Sciences 353*, 1257-1270.

Hopf, J.-M., Luck, S. J., Girelli, M., Hagner, T., & Mangun, G. R., Scheich, H., & Heinze, H. J. (2000). Neural sources of focused attention in visual search. *Cerebral Cortex, 10*, 1233-1241.

Hopf, J.-M. & Mangun, G. R. (2000). Shifting visual attention in space: An electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology, 111,* 1241-1257.

Hopf, J.-M., Vogel, E. K., Woodman, G. F., Heinze, H.-J., & Luck, S. J. (2002). Localizing visual discrimination processes in time and space. *Journal of Neurophysiology, 88*, 2088-2095.

Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000a). The neural mechanisms of top-down attentional control. *Nature Neuroscience, 3*, 284-291.

Hopfinger, J. B. & Mangun, G. R. (1998). Reflexive attention modulates processing of visual stimuli in human extrastriate cortex. *Psychological Science, 9,* 441-447.

Hopfinger, J. B. & Mangun, G. R. (2001). Tracking the influence of reflexive attention on sensory and cognitive processing. *Cognitive, Affective, & Behavioral Neuroscience, 1*, 56-65.

Hopfinger, J. B., Maxwell, J., & Mangun, G. R. (2000b, April). *Reflexive attention captured by the irrelevant appearance or disappearance of visual objects modulates early visual processing.* Poster presented at the 7th annual meeting of the Cognitive Neuroscience Society, San Francisco, CA.

Jasper, H. (1958). The ten twenty electrode system of the International Federation. *Electroencephalography and Clinical Neurophysiology, 10,* 371-375.

Jonides, J. (1981). Voluntary versus automatic control over the mind's eye movement. In: J. B. Long &A. D. Baddeley (Eds.), *Attention & Performance IX* (pp. 187-203). Hillsdale, N.J.: Erlbaum.

Jonides, J., Smith, E. E., Koeppe, R. A., Awh, E., Minoshima, S., & Mintun, M. A. (1993). Spatial working memory in humans as revealed by PET. *Nature, 363,* 623-625.

Kanwisher, N. & Wojciulik, E. (2000). Visual attention: insights from brain imaging. *Nature Reviews Neuroscienc,e 1*, 91-100.

Karnath, H. O., Ferber, S., & Himmelbach, M. (2001). Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature, 411*, 951-953.

Kastner, S., Pinsk, M.A., De Weerd, P., Desimone, R. & Ungerleider, L.G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron, 22*, 751-761.

Kennett, S., Eimer, M., Spence, C., & Driver, J. (2001). Tactile-visual links in exogenous spatial attention under different postures: Convergent evidence from psychophysics and ERPs. *Journal of Cognitive Neuroscience, 13*, 462-478.

Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Science, 4,*138-147.

Kingstone, A. & Pratt, J. (1999). Inhibition of return is composed of attentional and oculomotor processes. *Perception & Psychophysics, 61,* 1046-1054.

Kojima, S. & Goldman-Rakic, P. S. (1982). Delay-Related Activity of Prefrontal Neurons in Rhesus Monkeys Performing Delayed Response. *Brain Research, 248,* 43-50.

LaBerge, D. (1997). Attention, awareness, and the triangular circuit. *Consciousness and Cognition, 6,*149-181.

Lamme, V. A. F. & Spekreijse, H. (2000). Contextual modulation in primary visual cortex and scene perception. In M. S. Gazzaniga (Ed.), *The New Cognitive Neurosciences* (pp. 279-290). Cambridge, MA: M.I.T. Press.

Lamme, V.A., Super, H., Landman, R., Roelfsema, P.R. & Spekreijse, H. (2000). The role of primary visual cortex (V1) in visual awareness. *Vision Research, 40*, 1507-1521.

Lu, Z. & Dosher, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research, 38*, 1183-1198.

Luck, S. J. (1995). Multiple mechanisms of visual-spatial attention: Recent evidence from human electrophysiology. *Behavioural Brain Research, 71*, 113-123.

Luck, S. J., Fan, S., & Hillyard, S. A. (1993). Attention-related modulation of sensory-evoked brain activity in a visual search task. *Journal of Cognitive Neuroscience, 5*, 188-195.

Luck, S. J., & Ford, M. A. (1998). On the role of selective attention in visual perception. *Proceedings of the National Academy of Sciences, U.S.A., 95*, 825-830.

Luck, S. J., Girelli, M., McDermott, M. T., & Ford, M. A. (1997). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cognitive Psychology, 33*, 64-87.

Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 1000-1014.

Luck, S. J., & Hillyard, S. A. (1995). The role of attention in feature detection and conjunction discrimination: An electrophysiological analysis. *International Journal of Neuroscience, 80*, 281-297.

Luck, S.J. & Hillyard, S.A. (2000). The operation of selective attention at multiple stages of processing: Evidence from human and monkey electrophysiology. In M. S. Gazzaniga (Ed.), *The New Cognitive Neurosciences* (pp. 687-700). Cambridge, MA: M.I.T. Press.

Luck, S. J., Hillyard, S. A., Mouloua, M., & Hawkins, H. L. (1996a). Mechanisms of visual-spatial attention: Resource allocation or uncertainty reduction? *Journal of Experimental Psychology: Human Perception and Performance, 22*, 725-737.

Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P., & Hawkins, H. L. (1994). Effects of spatial cuing on luminance detectability: Psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 887-904.

Luck, S. J., Vogel, E. K., & Shapiro, K. L. (1996b). Word meanings can be accessed but not reported during the attentional blink. *Nature, 382*, 616-618.

Macaluso, E., Frith, C., & Driver, J. (2000). Modulation of human visual cortex by crossmodal spatial attention*.* *Science, 289*, 1206-1208.

Mangun, G. R. (1995). Neural mechanisms of visual selective attention. *Psychophysiology, 32*, 4-18.

Mangun, G. R., & Hillyard, S. A. (1991). Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception & Performance, 17*, 1057-1074.

Mangun, G.R., Hopfinger, J.B., Kussmaul, C., Fletcher, E. & Heinze, H.J. (1997). Covariations in PET and ERP measures of spatial selective attention in human extrastriate visual cortex. *Human Brain Mapping 5*, 1-7.

Martinez, A., Anllo-Vento, L., Sereno, M.I., Frank, L.R., Buxton, R.B., Dubowitz, D.J., Wong, E.C., Heinze, H.J. & Hillyard, S.A. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience, 2*, 364-369.

Martinez, A., F. DiRusso, L. Anllo-Vento, M.I. Sereno, R.B. Buxton & S.A. Hillyard. (2001). Putting spatial attention on the map: Timing and localization of stimulus selection processes in striate and extrastriate visual areas. *Vision Research, 41*, 1437-1457.

Maunsell, J. H. R., & McAdams, C. J. (2000). Effects of attention on neuronal response properties in visual cerebral cortex. In M. S. Gazzaniga (Ed.), *The New Cognitive Neurosciences* (pp. 290-305). Cambridge, MA: M.I.T. Press.

McDonald, J. J. & Ward, L. M. (2000). Involuntary listening aids seeing: Evidence from human electrophysiology. *Psychological-Science, 11,* 167-171.

McDonald, J.J., Teder-Sälejärvi, W.A., DiRusso, F. & Hillyard, S.A. (2003). Neural substrates of perceptual enhancement by crossmodal spatial attention. *Journal of Cognitive Neuroscience, 15*, 1-10.

McDonald, J. J., Ward, L. M., & Kiehl, K. A. (1999). An event-related brain potential study of inhibition of return. *Perception & Psychophysics, 61*, 1411-1423.

Motter BC (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2 and V4 in the presence of competing stimuli. *Journal of Neurophysiology 70*, 909–919.

Nobre, A. C., Sebestyen, G. N., Gitelman, D. R., Mesulam, M. M., Frackowiak, R. S., & Frith, C. D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain, 120*, 515-533.

Noesselt, T., Hillyard, S.A., Woldorff, M.G., Hagner, T., Jaencke, L., Tempelmann, C., Hinrichs, H. & Heinze. H.J. (2002). Delayed striate cortical activation during spatial attention. *Neuron, 35*, 575-587.

Posner, M. I. & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & Bouwhis (Eds.), *Attention & Performance X* (pp. 531-556). Hillsdale, N.J.: Erlbaum Associates.

Posner, M. I., Nissen, M. J., & Ogden, W. C. (1978). Attended and unattended processing models: The role of set for spatial locations. In H. L. Pick & F. J. Saltzman (Eds.), *Modes of perceiving and processing information* (pp. 137-157). Hillsdale, N. J.: Erlbaum.

Posner, M. I. & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience 13*, 25-42.

Potter, M. C. (1976). Short-term conceptual memory for pictures. *Journal of Experimental Psychology: Human Learning and Memory, 2*, 509-522.

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *Journal of Neuroscience, 19*, 1736-1753.

Reynolds, J.H. & Desimone, R. (2001). Neural mechanisms of attentional selection. In J. Braun, C. Koch & J.L. Davis (Eds.), *Visual Attention and Cortical Circuits* (pp. 121-136). Cambridge Mass: MIT Press

Roelfsema, P.R., Lamme, V.A.F., & Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature, 395*, 376–381.

Schroeder, C.E., Mehta, A.D. & Foxe, J.J. (2001). Determinants and mechanisms of attentional modulation of neural processing. *Frontiers in Bioscience, 6*, 672-684.

Shapiro, K. L., Arnell, K. M., & Raymond, J. E. (1997). The attentional blink: A view on attention and a glimpse on consciousness. *Trends in Cognitive Science, 1*, 291-296.

Spence, C. & Driver, J. (1997). Audiovisual links in exogenous covert spatial orienting. *Perception & Psychophysics, 59*, 1-22.

Spence, C., Nicholls, M. R., Gillespie, N., & Driver, J. (1998). Crossmodal links in exogenous covert spatial orienting between touch, audition, and vision.

Perception & Psychophysics, 60, 544-557.

Shulman, G.L., d'Avossa, G., Tansy, A.P., & Corbetta, M. (2002). Two attentional processes in the parietal lobe. *Cerebral Cortex, 12*, 1124–1131.

Tootell, R.B., Hadjikhani, N., Hall, E.K., Marrett, S., Vanduffel, W., Vaughan, J.T. & Dale, A.M. (1998). The retinotopy of visual spatial attention. *Neuron, 21*, 1409-22.

Treisman, A. (1988). Features and objects: The Fourteenth Bartlett Memorial Lecture. *Quarterly Journal of Experimental Psychology, 40*, 201-237.

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12*, 97-136.

Vidyasagar, T.R. (1999). A neuronal model of attentional spotlight: parietal guiding the temporal. *Developmental Brain Research, 30*, 66–76.

Vogel, E. K., & Luck, S. J. (2000). The visual N1 component as an index of a discrimination process. *Psychophysiology, 37*, 190-123.

Vogel, E. K., & Luck, S. J. (2002). Delayed working memory consolidation during the attentional blink. *Psychonomic Bulletin & Review, 9*, 739-743.

Vogel, E. K., Luck, S. J., & Shapiro, K. L. (1998). Electrophysiological evidence for a postperceptual locus of suppression during the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance, 24*, 1656-1674.

Watson, R. T., Valenstein, E., Day, A. & Heilman, K. M. (1994). Posterior neocortical systems subserving awareness and neglect. *Archives of Neurology 51*, 1014-1021.

Wojciulik, E., & Kanwisher, N. (1999). The generality of parietal involvement in visual attention. *Neuron, 23,* 747-764.

Woldorff, M. G. (1993). Distortion of ERP averages due to overlap from temporally adjacent ERPs: Analysis and correction. *Psychophysiology, 30*, 98-119.

Woldorff, M.G., Hazlett, C., Fichtenholtz, H.M., Weissman, D., Dale, A., Song, A.W. (Accepted, pending revision). Functional parcellation of attentional control regions of the human brain. *Journal of Cognitive Neuroscience.*

Woldorff, M., Fox, P. T., Matzke, M., Lancaster, J. L., Veeraswamy, S., Zamarripa, F., Seabolt, M., Glass, T., Gao, J. H., Martin, C. C., Jerabek, P. (1997). Retinotopic organization of early visual spatial attention effects as revealed by PET and ERPs. *Human Brain Mapping 5*, 280-286.

Wolfe, J. M. (1994). Guided search 2.0: A revised model of visual search. *Psychonomic Bulletin & Review, 1*, 202-238.

Wolfe, J. M., O'Neill, P., & Bennett, S. C. (1998). Why are there eccentricity effects in visual search? Visual and attentional hypotheses. *Perception & Psychophysics, 60*, 140-156.

Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature, 400*, 867-869.

Woodman, G. F., & Luck, S. J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology: Human Perception and Performance, 29*, 121-138.

Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature, 396*, 72-75.

Figure Legends

Figure 1. (A) Averaged ERPs recorded from four scalp sites in response to stimuli in the upper left visual field in a spatial attention experiment by DiRusso et al. (2003). Note that positive is plotted downward in all figures here. Stimuli were small circular checkerboards flashed in random order to the upper left and right visual fields while subjects attended to one field at a time. Superimposed ERP waveforms compare conditions when the upper left stimuli were attended (solid lines) versus when stimuli in the opposite field were attended (dashed lines). Note that the P1 (80-130 ms) and N1 (140-200 ms) components are enhanced in amplitude by spatial attention. Head with voltage map shows the contralateral occipital scalp distribution of the late phase of the P1 (100-130 ms) that is enhanced by attention. (B) Dipole model of the neural sources of the enhanced contralateral and ipsilateral P1 components indicates neural generators in ventral occipital cortex. (C) Co-registration of dipolar sources of the enhanced P1 with fMRI activations (shaded spots) in the ventral fusiform gyrus obtained from the same subjects performing the same experiment in a different session.

Figure 2. Spatial correspondence between calculated positions of dipoles accounting for different components of the visual ERP (based on grand average waveforms) and fMRI activations in response to the same stimuli in a single subject. fMRI activations in response to circular checkerboard stimuli flashed to the lower right visual field are projected onto a flattened cortical representation of the left hemisphere. Dashed white lines represent the boundaries between the different visual areas determined by visual field sign mapping. Coronal and saggital sections display those activations (before flattening) that correspond in position to the dipoles representing the different components. From DiRusso et al. (2001).

Figure 3. Example of typical stimuli (A) and ERP waveforms (B) in an N2pc experiment. In the task shown here, stimulus arrays consist of 16 upright and inverted T shapes, 15 drawn in black and 1 drawn in white. Subjects are instructed to attend to the white item and press one of two buttons for each array to indicate whether this item is an upright or inverted T. The ERP waveforms are averaged separately for trials on which the target is ipsilateral versus contralateral to a given electrode site. That is, the ipsilateral waveform consists of left visual field targets for left hemisphere electrodes averaged with right visual field targets for right hemisphere electrodes, and the contralateral waveform consists of right visual field targets for left hemisphere electrodes averaged with right visual field targets for left hemisphere electrodes. The contralateral waveform is typically more negative (less positive) from approximately 200-300 ms, and the difference in amplitude between the contralateral and ipsilateral waveforms is used to measure the N2pc component.

Figure 4. (A) Stimuli from the study of Woodman and Luck (1999). Subjects searched for a target (a square with a gap on the left side), which was present on 50% of trials. When present, the target was one of the two red items in the array (represented in figure by white items outlined in black). One of the red items was near fixation and the other was far from fixation. Even though the target was equally likely to be near or far, subjects

tend to search the near item first. (B) ERP waveforms from target-absent trials. When the near and far red items were in opposite hemifields, the N2pc first appeared as a negativity contralateral to the near item (ca. 200-300 ms) and then appeared as a negativity contralateral to the far item (ca. 300-400 ms). This pattern is consistent with a serial shifting of attention from nontarget to nontarget.

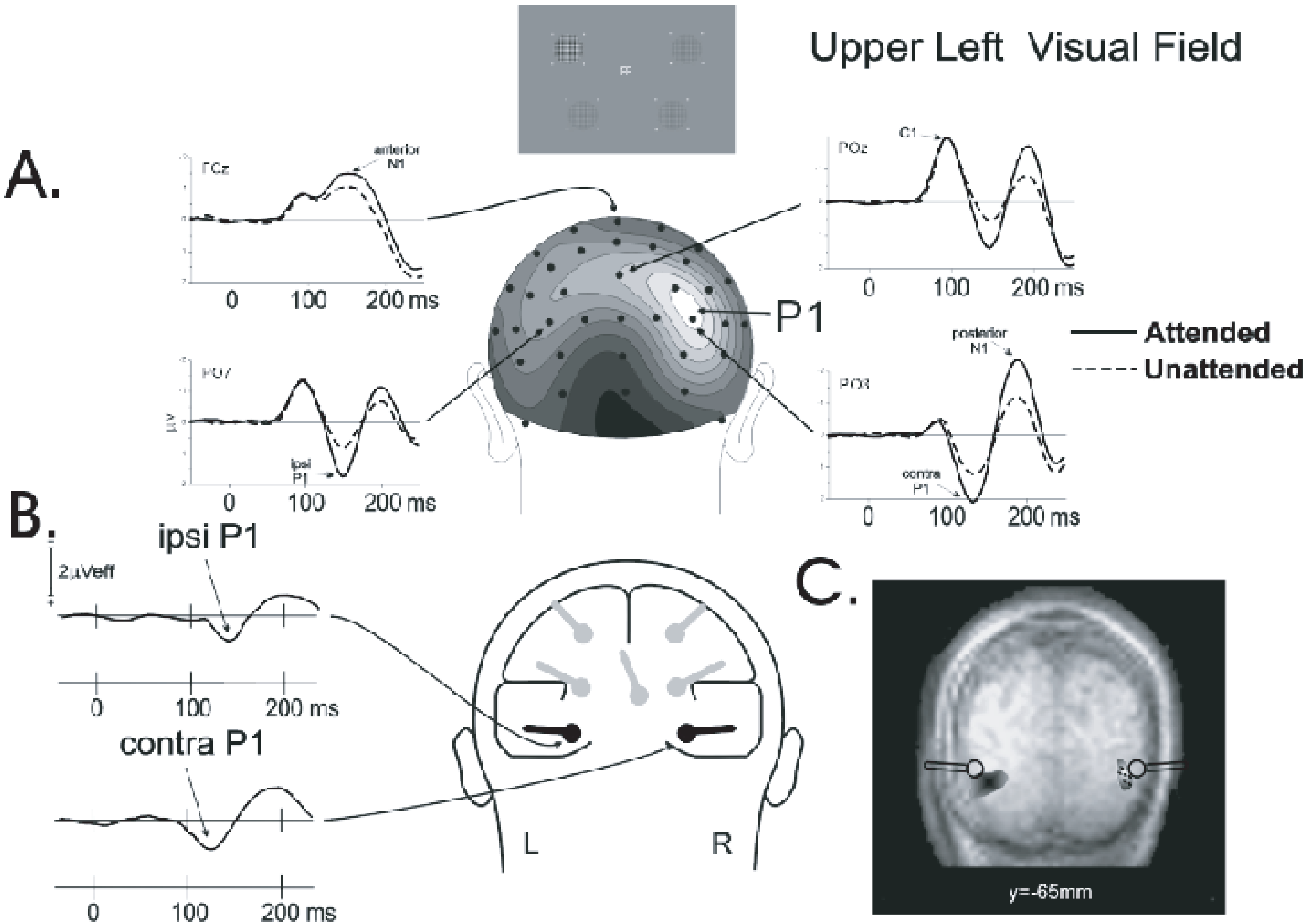
Figure 5. Averaged ERPs and scalp voltage topographies from a study of reflexive attention by Hopfinger & Mangun (1998). (A) ERPs to target stimuli at the short cue-to-target ISIs (34-234 ms), collapsed over contralateral scalp sites (data from the left hemisphere for right visual field targets combined with data from the right hemisphere for left visual field targets). ERP data are from lateral occipital electrodes OL and OR which are located midway between T5 and O1, and T6 and O2, respectively, of the International 10-20 system of electrode placement (Jasper, 1958). Cued-location targets (solid lines) elicited a significantly enhanced P1 component compared to uncued-location targets (dashed lines). At middle and right are shown scalp topographic voltage maps, collapsed over contralateral and ipsilateral scalp sites. The left scalp hemisphere of each map represents the ipsilateral hemisphere (data from the left hemisphere for left visual field targets combined with data from the right hemisphere for right visual field targets), while the right scalp hemisphere of each map represents the contralateral hemisphere. The small black dots on each topographic map indicate the location of the electrodes. Voltage maps are shown from a back view of the head, for the time period corresponding to the P1 component (110-120 msec). At these short ISIs, the cued-location targets (left map) produced a significantly enhanced P1 component relative to uncued-location targets (right map). (B) ERPs to target bar stimuli at the long cue-to-target ISIs (566-766 ms), collapsed over contralateral scalp sites. Cued-location targets (solid lines) elicited a significantly smaller P1 component compared to uncued-location targets (dashed lines). Scalp topographic voltage maps of the time period corresponding to the P1 component (110-120 msec) are shown at middle and right. At the long ISIs, the cued location targets (left map) produced a significantly reduced P1 component relative to uncued-location targets (right map). As with the short ISI trials, the distribution of activity during this time period was highly similar, with the main difference being the strength of the P1.

Figure 6. Typical attentional blink paradigm and behavioral results. In this version, alphanumeric characters are presented at fixation at a rate of 10/s, and a trial consists of a sequence of 30 stimuli. Of these, 28 are letters and two are numbers. The two numbers are the targets (T1 and T2) and must be reported at the end of the trial. The lag between T1 and T2 varies between 1 and 8 (e.g., at lag 1, T2 immediately follows T1; at lag 3, T2 is the third item after T1). In most experiments, accuracy is fairly high at lag 1, drops to a minimum at lag 3, and then recovers to asymptote by lag 5-8. Accuracy is thought to be relatively high at lag 1 because of temporal imprecision in the process of transferring perceptual representations into working memory. That is, when T1 is detected, both T1 and T2 are transferred into working memory, leading to fairly accurate performance when T2 is the item that immediately follows T1.

Figure 7. Results from Hopfinger, Buonocore, and Mangun (2000) showing selective attention effects in visual processing regions overlaid on an averaged proton density MRI scan (slice at y=-64). (A) Top panels show attention effects in response to the attention-

directing cue stimuli. Left panels show regions showing greater cue-related activity for attend left than attend right conditions; right panels shows regions exhibiting greater activity for attend right cues then attend left cues. Cue-induced activity was greater contralateral to the direction of attention in ventral lingual/fusiform regions and in a more dorsal region of the cuneus. B. Bottom panels show regions with differential activity for target processing as a function of where attention was focused. Target processing was significantly enhanced contralateral to the direction of attention, and the effects were in regions that closely overlapped with where the attention effects were seen in response to the cue stimuli (compare with upper panels). Adapted with permission from Hopfinger, Buonocore, & Mangun, Nature Neuroscience, 2000, copyright Nature America, Inc.

Figure 1



Upper Left Visual Field
A.
FCz
anterior N1
0
100
200 ms
POz
C1
P1
posterior N1
Attended
Unattended
PO7
μV
ipsi P1
PO8
contra P1
B.
ipsi P1
2μVeff
contra P1
L
R
C.
y=-65mm

Figure 2

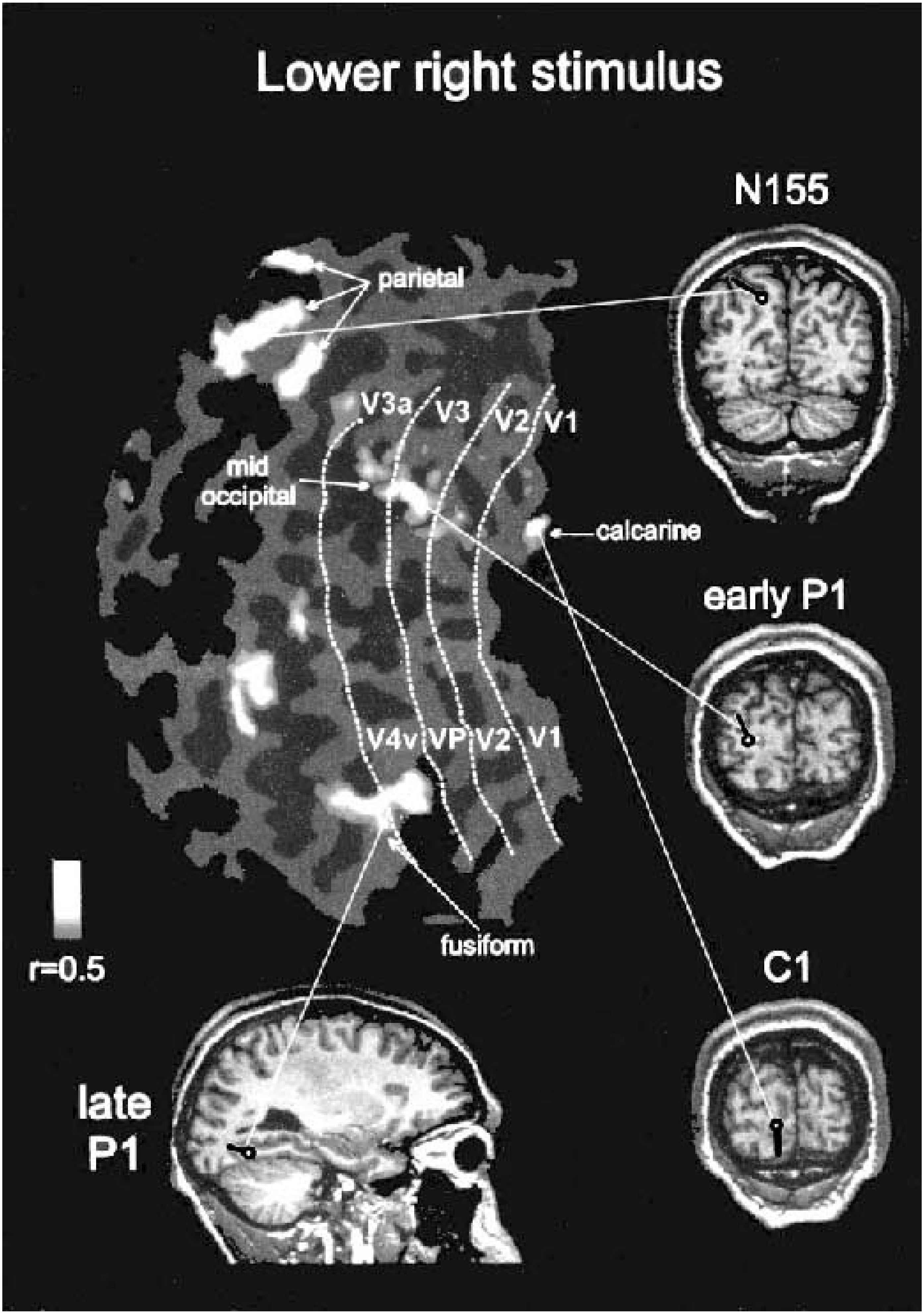

Lower right stimulus
N155
parietal
V3a
V3
V2
V1
mid occipital
calcarine
early P1
V4v
VP
V2
V1
r=0.5
fusiform
C1
late P1

Figure 3

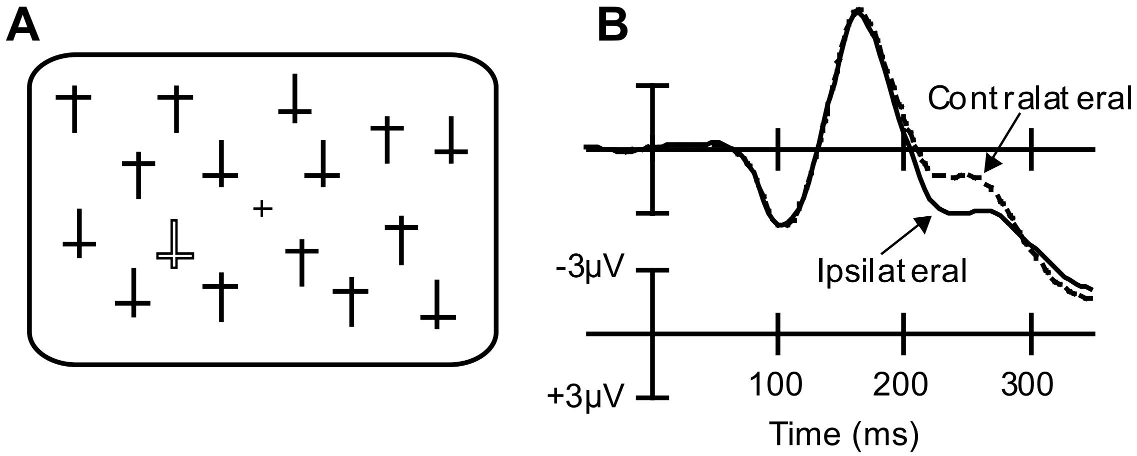


Figure 4

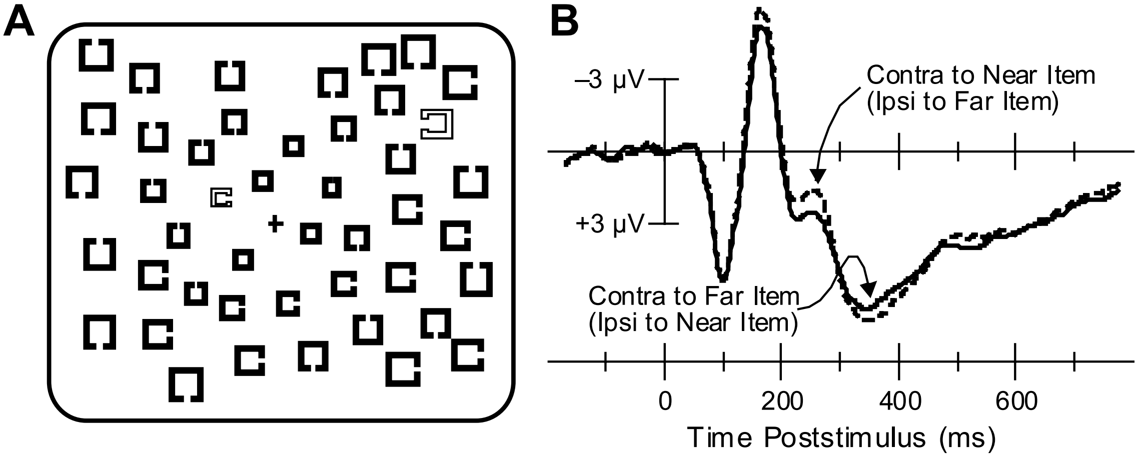

A
B
–3 µV
+3 µV
Contra to Near Item
(Ipsi to Far Item)
Contra to Far Item
(Ipsi to Near Item)
0
200
400
600
Time Poststimulus (ms)

Figure 5

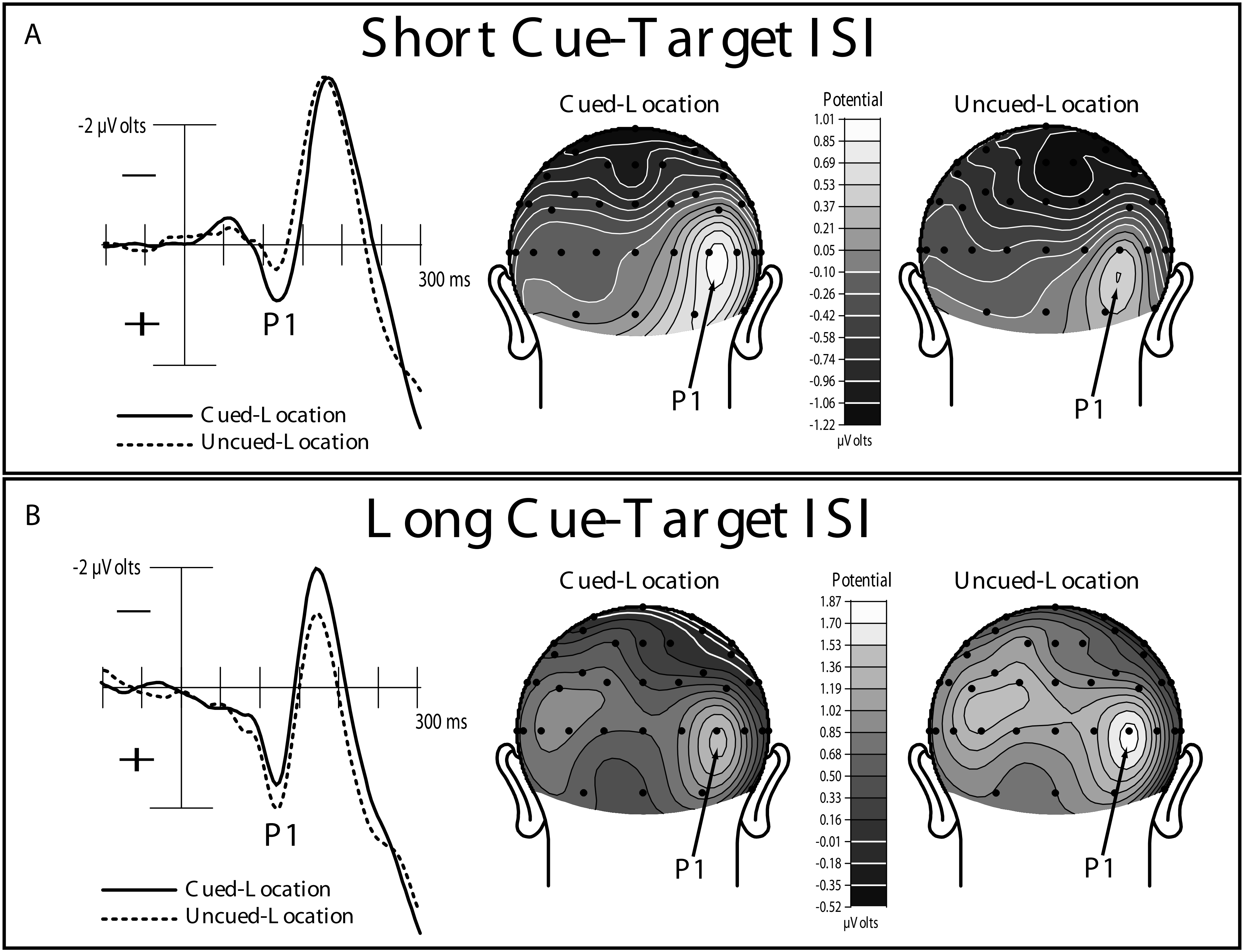

A
Short Cue-Target ISI
-2 µVolts
—
+
P1
300 ms
Cued-Location
Uncued-Location
Cued-Location
Potential
1.01
0.85
0.69
0.53
0.37
0.21
0.05
-0.10
-0.26
-0.42
-0.58
-0.74
-0.96
-1.06
-1.22
µVolts
Uncued-Location
P1
P1
B
Long Cue-Target ISI
-2 µVolts
—
+
P1
300 ms
Cued-Location
Uncued-Location
Cued-Location
Potential
1.87
1.70
1.53
1.36
1.19
1.02
0.85
0.68
0.50
0.33
0.16
-0.01
-0.18
-0.35
-0.52
µVolts
Uncued-Location
P1
P1

Figure 6

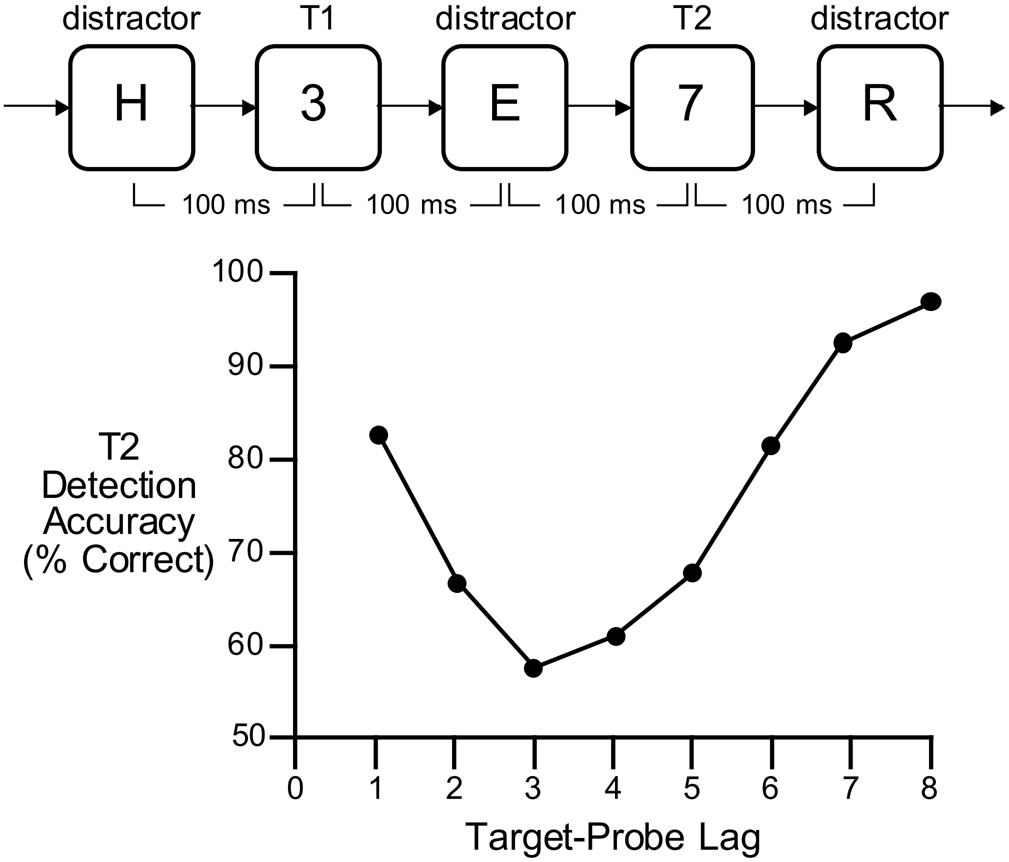
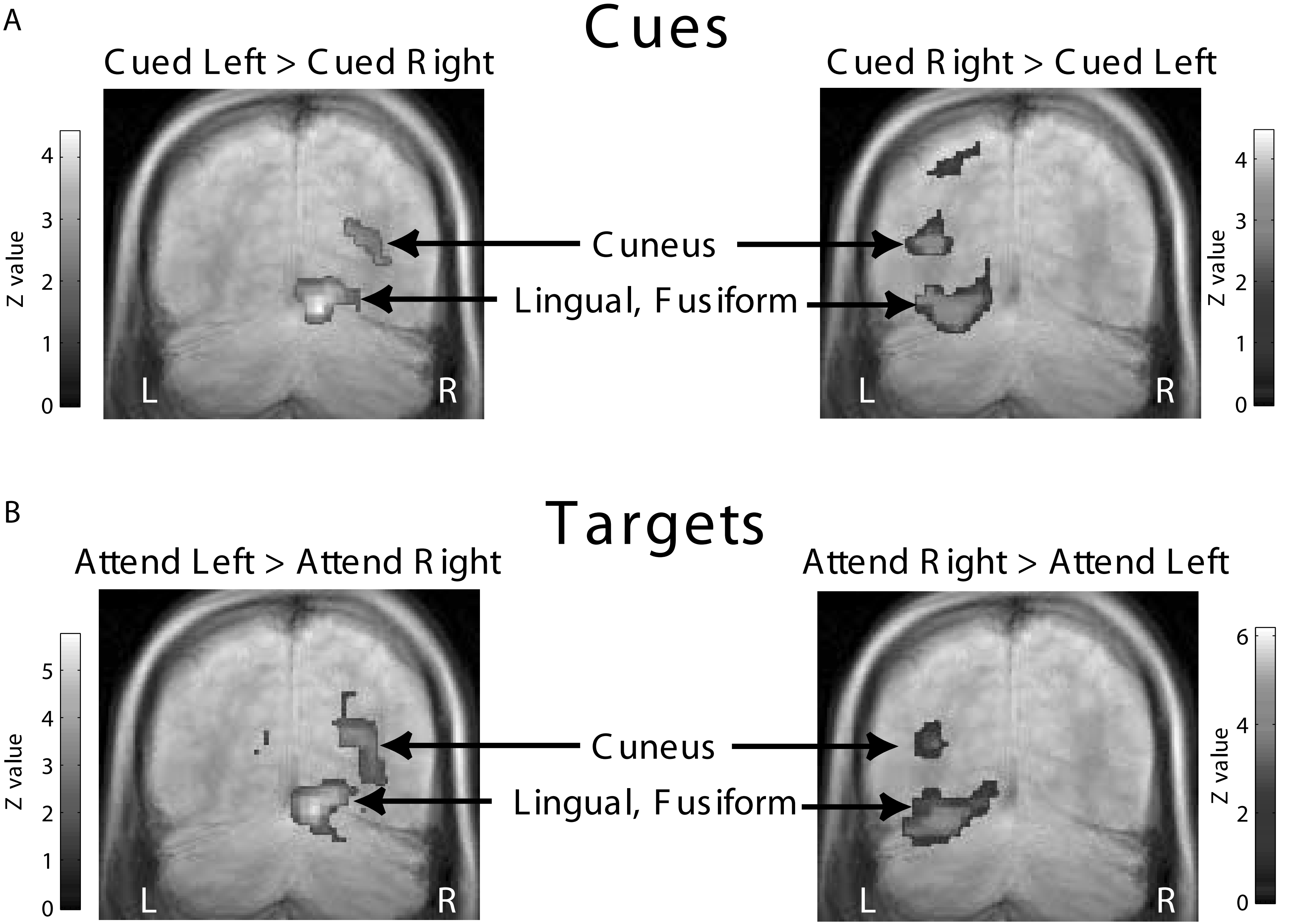

distractor
T1
distractor
T2
distractor
H
3
E
7
R
100 ms
100 ms
100 ms
100 ms
T2 Detection Accuracy (% Correct)
100
90
80
70
60
50
0
1
2
3
4
5
6
7
8
Target-Probe Lag

Figure 7


A
Cues
Cued Left > Cued Right
Cued Right > Cued Left
Z value
0
1
2
3
4
L
R
Cuneus
Lingual, Fusiform
B
Targets
Attend Left > Attend Right
Attend Right > Attend Left
Z value
0
1
2
3
4
5
6
L
R
Cuneus
Lingual, Fusiform