Attention-Related Modulation of Sensory-Evoked Brain Activity in a Visual Search Task

Steven J. Luck, Silu Fan, and Steven A. Hillyard

University of California, San Diego

Abstract

■ When subjects are explicitly cued to focus attention on a particular location in visual space, targets presented at that location have been shown to elicit enhanced sensory-evoked activity in recordings of event-related brain potentials (ERPs). The present study sought to determine if this type of sensory facilitation also occurs during visual search tasks in which a feature conjunction target must be identified, presumably by means of focal attention, within an array of distractor items. In this experiment, subjects were required to discriminate the shape of a distinctively colored target item within an array containing 15 distractor items, and ERPs were elicited by task-irrelevant probe stimuli that were presented at the location of

the target item or at the location of a distractor item on the opposite side of the array. When the delay between search-array onset and probe onset was 250 msec, the sensory-evoked responses in the latency range 75–200 msec were larger for probes presented at the location of the target than for probes presented at the location of the irrelevant distractor. These results indicate that sensory processing is modulated in a spatially restricted manner during visual search, and that focusing attention on a feature conjunction target engages neural systems that are shared with other forms of visual–spatial attention.

INTRODUCTION

In many natural situations, the human visual system must identify objects that are embedded in large and complex arrays of potentially distracting visual information. To reduce the influence of this distracting information, selective attention may be used to restrict visual processing to discrete regions of space in a manner analogous to a spotlight (LaBerge, 1983) or zoom lens (Eriksen & Yeh, 1985). Two experimental techniques have been used extensively to study visual-spatial attention over the past 20 years, namely spatial cuing and visual search. In spatial cuing studies, the location to be attended is typically indicated by a symbolic cue such as an arrow or by a peripheral cue presented at the to-be-attended location, and the cue is followed by a target that is usually presented at the precued location. The precuing of attention to a target's location has been shown to increase both the speed and the accuracy of target detection and discrimination; these effects have been interpreted as manifestations of early sensory facilitation by some authors (Bashinski & Bacharach, 1980; Downing, 1988; Hawkins, Hillyard, Luck, Mouloua, Downing, & Woodward, 1990), while others have argued that postsensory, decision processes can account for these results (Muller & Findlay, 1987; Shaw, 1984; Sperling, 1984).

In visual search tasks, an array of stimuli is presented and subjects must report the presence or absence of a specified target item within the array, irrespective of its location. Instead of comparing performance for attended and unattended stimuli, as in cuing tasks, visual search experiments typically compare performance across different search arrays that vary in the number and type of objects they contain. A large number of these experiments have shown that search performance is fast and parallel when the target differs from the distractor objects in terms of a simple feature, whereas targets defined by conjunctions of features appear to be identified by the serial application of focal attention to the items in the array (e.g., Bergen & Julesz, 1983; Treisman & Gelade, 1980; Treisman & Souther, 1985).

While these search and cuing experiments have provided much of the data for current theories of attention, only a few studies have addressed the issue of whether the attentional processes engaged in these two types of paradigms are equivalent. Briand and Klein (1987) posed this question directly, asking whether "Posner's Beam" (the cued orienting of attention) was equivalent to "Treisman's Glue" (the focusing of attention onto feature conjunctions during visual search). These authors and others (Prinzmetal, Presti, & Posner, 1986; Treisman, 1985) obtained evidence for such an equivalence by showing that

targets defined by conjunctions of features are affected by spatial cuing more than are simple feature targets, a result that accords with visual search experiments showing that focal attention is particularly important when targets are defined by conjunctions (e.g., Treisman & Gelade, 1980). However, the special role of attention in the perception of conjunctions has been questioned for both cuing paradigms (Tsal, 1989) and visual search paradigms (Duncan & Humphreys, 1989; Wolfe, Cave, & Franzel, 1989), so the relationship between cuing and visual search paradigms requires further examination.

Another method for assessing the similarity between the attentional processes used in spatial cuing and visual search paradigms was employed by Sagi and Julesz (1986), who used a dual task paradigm (see also Hoffman & Nelson, 1981). In this study, subjects were required to discriminate the orientation of a line segment and subsequently to report the presence or absence of a small dot presented at a variable distance from the line. The discrimination task presumably caused attention to be allocated to the line, and Sagi and Julesz found that detection accuracy for the dot increased as the distance between the line and the dot decreased. Thus, focusing attention onto an object to identify it appears to increase detection accuracy, just as spatial cuing does. However, due to the nature of Sagi and Julesz's design, false alarms could not be attributed to particular positions, and the changes in detection accuracy may have been due to changes in decision bias rather than sensory sensitivity (cf. Hawkins et al., 1990).

In the present study, we used electrophysiological recordings of brain activity to evaluate the proposed equivalence of the attentional processes employed during spatial cuing and visual search tasks. In particular, we investigated whether the focusing of attention during visual search produces changes in event-related brain potentials (ERPs) that are comparable to the attentionrelated changes in ERPs that have been observed in previous cuing studies. ERPs can be recorded noninvasively from the scalp in human subjects and typically reflect the summated postsynaptic potentials of large groups of cortical neurons that are activated in synchrony during information processing. The positive and negative voltage deflections (also called "waves" or "components") in the ERP waveform have latencies that reveal the time course of neural activation and scalp distributions that reflect the neuroanatomical location of the active cortical regions. Accordingly, by comparing the patterns of ERP activity during spatial cuing and visual search paradigms, it is possible to determine the degree to which these tasks share common neural mechanisms.

In previous ERP experiments, visual–spatial attention has been studied in spatial cuing paradigms (e.g., Harter, Miller, Price, LaLonde, & Keyes, 1989; Mangun, Hansen, & Hillyard, 1987; Mangun & Hillyard, 1991) and in sustained attention tasks, in which subjects monitor one location for an entire trial block, looking for occasional

targets at that location and ignoring stimuli presented at other locations (e.g., Eason, Harter, & White, 1969; Harter, Aine, & Schroeder, 1982; Mangun & Hillyard, 1988, 1990; Neville & Lawson, 1987; Rugg, Milner, Lines, & Phalp, 1987; Van Voorhis & Hillyard, 1977). In both of these paradigms, the early sensory ERP components are enlarged when attention is directed to the location of the evoking stimulus (for reviews, see Harter & Aine, 1984; Hillyard, Mangun, Luck, & Heinze, 1990; Mangun & Hillyard, 1990; Mangun, Hillyard, & Luck, 1993). There are three early components that are typically modulated by spatial attention: P1, which is largest occipitally and typically peaks around 100 msec; anterior N1, which is largest frontally and typically peaks around 150 msec; and posterior N1, which is largest parietally or occipitally and typically peaks around 190 msec.

In these attention tasks, enhancement of the sensory-evoked ERP components has been observed not only in the ERPs elicited by attended, task-relevant stimuli, but also in the ERPs elicited by irrelevant "probe" stimuli presented occasionally at the attended location (Heinze, Luck, Mangun, & Hillyard, 1990; Mangun & Hillyard, 1990). This enhancement of early sensory-evoked activity for both relevant and irrelevant stimuli at the attended location supports the proposal that spatial attention produces a facilitation of the visual pathways that affects all stimuli appearing within the focus of attention, consistent with early selection models of attentional processing (e.g., Broadbent, 1958; Treisman, 1969).

To compare these mechanisms of spatial selective attention with the attentional processes that operate during visual search, the present study combined the probe technique of Heinze et al. (1990) with a visual search task. The target in this task was defined by its distinctive color, allowing subjects to localize it in a relatively constant time period and thereby facilitating the recording of time-locked ERPs (see Fig. 1). In order to ensure that focal attention would be applied to the target, subjects were also required to discriminate the target's shape, conjoining color, and form information. Nissen (1985) used a similar paradigm and found evidence that focal attention is indeed necessary for discriminating the shape of an object selected from a search array on the basis of its color. Shortly after the onset of each stimulus array, an ERP-eliciting probe stimulus was presented either at the location of the target item or at the location of a distractor item on the opposite side of the array. If the focusing of attention during visual search engages the same attentional systems that are employed during spatial cuing and sustained attention tasks, then a probe stimulus presented at the location of the target item should evoke enhanced P1 and N1 components relative to a probe stimulus occurring at a distractor location, as in the cuing and sustained attention studies reviewed above.

To assess the time course of attentional processing in this experiment, the stimulus onset asynchrony (SOA) between the search array and the probe could be either

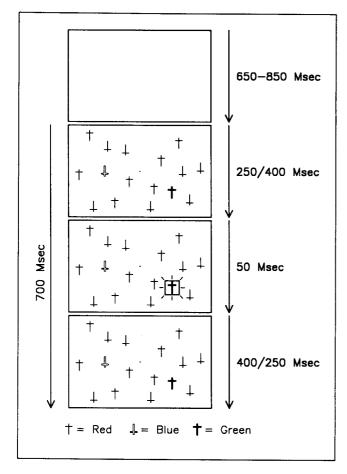


Figure 1. Example of the sequence of events that occurred on a single trial. This sequence repeated continuously in 2-min blocks with randomized within-block changes in the positions of the various stimulus elements and interstimulus intervals. The probe stimulus, a white outlined square, could occur around either the blue item (represented by the hollow T) or the green item (represented by the thick T), but never around a red item. The duration of the search array was always 700 msec, so the amount of time between probe offset and array offset varied inversely with the amount of time between array onset and probe onset.

250 or 400 msec. These values were chosen because we assumed that most attentional processes would begin within 250 msec of search array onset in this task, and that some of these processes might terminate by 400 msec poststimulus. Another important attribute of the present experiment was that the stimuli were designed so that a particular item was used as a target in some trial blocks and as a distractor in other blocks, thus allowing the comparison of ERPs elicited by identical physical stimulus configurations.

RESULTS

Behavioral Results

Subjects correctly discriminated the identity of the relevantly colored item on 97% of trials, and accuracy was unaffected by the presence or absence of the probe or

by its position. Reaction times, listed in Table 1, were 10 msec faster when the relevantly colored item was in the left visual field rather than the right visual field, but this effect did not quite reach significance [F(1,9) = 4.35, p < 0.07]. Reaction times were slightly slower when the probe stimulus occurred at the location of the relevantly colored item, but this effect was quite small and did not approach statistical significance (p > 0.20).

Electrophysiological Results

Figure 2 displays ERP waveforms that were time locked to the search arrays for trials on which no probe was presented; trials are divided according to whether the relevantly colored item was ipsilateral or contralateral to the position of the electrode site. At posterior scalp sites, the contralateral ERP was more negative than the ipsilateral ERP in the 200–300 msec and 400+ msec latency ranges. The lateral asymmetry between 200 and 300 msec was highly significant [F(1,9)] = 24.57, p < 0.001 and

Table 1. Mean Reaction Time (in msec) for Left and Right Targets, Sorted According to Probe SOA and Target Position

| | Left Target | Right Target | |
|------------------------|-------------|--------------|--|
| No probe | 619 | 637 | |
| Left probe, short SOA | 627 | 628 | |
| Right probe, short SOA | 633 | 644 | |
| Left probe, long SOA | 625 | 630 | |
| Right probe, long SOA | 623 | 638 | |

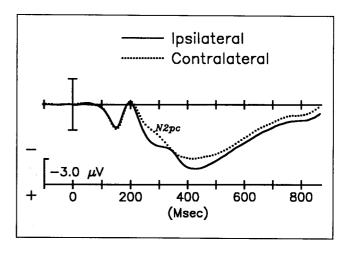


Figure 2. ERP waveforms elicited by the search arrays on trials without a probe stimulus, averaged over the 10 subjects. These waveforms were recorded from posterior temporal electrode sites ipsilateral (solid line) or contralateral (dotted line) to the position of the task-relevant object. Note that negative is plotted upward. All ERP waveforms presented here were digitally low-pass filtered before plotting by convolving the waveforms with a gaussian finite impulse response function with a standard deviation of 10 msec and a 50% amplitude cutoff of 20 Hz.

appears to correspond to the N2pc component described by Luck and Hillyard (1990).

Figures 3 and 4 compare ERP waveforms for probes presented at the locations of the relevantly and irrelevantly colored objects. When the delay between the search array and the probe was 250 msec, the P1, anterior N1, and posterior N1 components were larger for probes that were presented at the location of the item that was being identified than for probes occurring at the location of an irrelevant item. This enhancement was present primarily at contralateral sites for the P1 component and primarily at ipsilateral sites for the posterior N1 component, and was slightly larger ipsilaterally for the anterior N1 component. The P1 enhancement was present from about 75 to 125 msec poststimulus, and was largest at the occipital and posterior temporal electrode sites. The anterior and posterior N1 enhancements had overlapping scalp distributions, but differed in their onset latencies (ca. 95 msec at anterior sites and 135 msec at posterior sites).

Similar effects were observed for the anterior and posterior N1 components at the 400 msec SOA, but no P1 enhancement was observed with this delay interval.

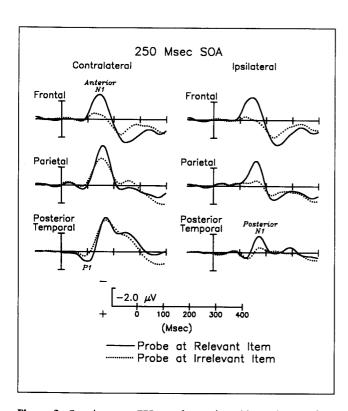


Figure 3. Grand average ERP waveforms elicited by probe stimuli that were presented 250 msec after the onset of the search array. These waveforms were recorded from frontal, parietal, or posterior temporal electrode sites contralateral (left) or ipsilateral (right) to the position of the probe. Separate waveforms are plotted for trials on which the probe occurred at the location of the relevant item (solid line) or at the location of the irrelevant item (dotted line). These waveforms reflect the overlap-subtraction procedure described above.

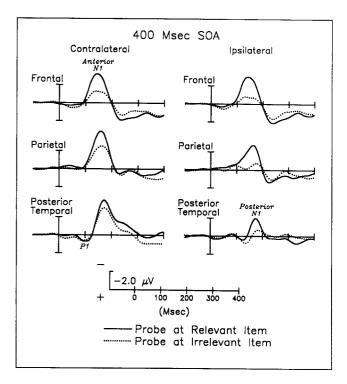


Figure 4. Same as Figure 3 for probes presented 400 msec after the onset of the search array.

These ERP enhancements for probes presented at the location of the relevantly colored object resulted in significant relevance and relevance \times contralaterality ANOVA effects for all three components, as listed in Table 2. Since the P1 enhancement was present only at the shorter SOA, significant SOA \times relevance and SOA \times relevance \times contralaterality interactions were also observed for this component. Although the posterior N1 attention effect was larger ipsilaterally, it is important to note that the posterior N1 itself was substantially larger at contralateral sites, producing a highly significant main effect of contralaterality [F(1,9) = 42.99, p < 0.001].

DISCUSSION

In this study, the P1, anterior N1, and posterior N1 components evoked by an irrelevant probe stimulus were larger when the probe surrounded a target item undergoing form discrimination rather than an irrelevant distractor item. These effects occurred at short latencies: the P1 effect began approximately 75 msec after probe onset, near the time at which probe-evoked activity would be expected to begin in prestriate visual cortex (Robinson & Rugg, 1988). These changes in sensory-evoked activity provide strong evidence that sensory transmission is modulated when attention is focused onto a target item within a search array to identify it. Since the probe stimulus was not task relevant, these results also indicate that this facilitation affects the processing of all information presented at the location of

Table 2. Summary of ANOVA Effects Involving the Relevance Factor

| | P1 | | Anterior N1 | | Posterior N1 | |
|--|--------|-------|----------------|-------|-----------------|------|
| | F(1,9) | p | F(1,9) | p | F(1,9) | p |
| Relevance (R) | 13.62 | 0.005 | 42.97 | 0.001 | 6.79 | 0.05 |
| $R \times contralaterality$ | 7.84 | 0.05 | 21.68 | 0.002 | 10.24 | 0.02 |
| $R \times SOA$ | 8.20 | 0.02 | 0.64 | n.s. | 1.27 | n.s. |
| $R \times \text{contra} \times \text{SOA}$ | 5.41 | 0.05 | 0.01 | n.s. | 0.05 | n.s. |

the item being identified, and is not limited to the specific features of the target. In addition, the probe stimulus surrounded the objects but did not physically overlap them, suggesting that the attentional facilitation extends beyond the boundaries of the object being identified.

Similar electrophysiological effects have been observed in experiments that directed attention to a location via explicit cues or instructions (e.g., Mangun et al., 1993; Heinze et al., 1990), which suggests that common attentional mechanisms are employed in both spatial cuing and visual search paradigms. This conclusion accords with previous behavioral studies showing that cuing facilitates the object recognition processes involved in visual search (Briand & Klein, 1987; Prinzmetal et al., 1986; Treisman, 1985) and that focal attention during visual search can affect the speed and accuracy of detection for the types of targets typically used in cuing tasks (Klein, 1988; Sagi & Julesz, 1986). The present results also extend the findings from the previous behavioral studies, demonstrating that the same neural systems are utilized across the different paradigms and showing that attention affects sensory processing at an early stage during visual search.

Although the P1 and anterior N1 effects in the present experiment mirror the results of spatial cuing and sustained attention experiments, there are also some differences from previous results. For example, most previous experiments have found large, contralateral enhancements of the posterior N1 component for attendedlocation stimuli (e.g., Harter et al., 1989; Mangun & Hillyard, 1990; Neville & Lawson, 1987), which contrasts with the small, ipsilaterally maximal N1 effect observed at posterior scalp sites in the present experiment. These variations may reflect intrinsic differences between the attentional systems employed in the different tasks, but it should be noted that atypical N1 effects such as these have also been observed in spatial cuing and sustained attention experiments. For example, Mangun and Hillyard (1991) have shown that the posterior N1 attention effect is eliminated in the spatial cuing paradigm when a simple RT task is used instead of a choice RT task. In addition, Heinze et al. (1990) and Luck, Heinze, Mangun, and Hillyard (1990) have shown that the posterior N1 attention effect is reduced or eliminated in sustained attention tasks when the stimulus sequences contain a high proportion of bilateral stimuli. Further research is needed to determine the significance of these differences in ERP attention effects.

The P1 component was enhanced at the 250 msec SOA but not at the 400 msec SOA, whereas the anterior and posterior N1 components were enhanced at both delay intervals. One likely explanation for the lack of a P1 effect at the longer SOA is that the stage of attentional processing indexed by the P1 may have been completed before the onset of the long-SOA probe. The N1 enhancements were present at both SOAs, however, suggesting that the attentional mechanisms indexed by these components have a longer time course, and perhaps play a different functional role than the attentional mechanism indexed by the P1 enhancement. This difference between the P1 and N1 attention effects is consistent with previous studies that have demonstrated clear dissociations between these indices of attentional processing (Heinze et al., 1990; Luck et al., 1990; Mangun & Hillyard, 1991). Many theories of visual perception consider spatial selective attention to be a single process, but the diversity of attentional processes revealed by these electrophysiological results indicates that multiple attentional processes must be postulated.

Moran and Desimone (1985) have shown that singleunit responses elicited by task-irrelevant stimuli in macaque area V4 are suppressed when a concurrently presented stimulus is being identified, resulting in a relative enhancement of activity for the object being identified. The same sort of attentional mechanism may be reflected by the relative suppression of stimulus-evoked activity for probes occurring at the locations of irrelevant objects in the present study. Indeed, Mangun et al. (1993) have shown that the focus of current flow for the P1 attention effect is located over lateral prestriate cortex, approximately overlying the border between Brodmann's areas 18 and 19, where the human homologue of macaque area V4 may well be located.² This approximate region of cortex has also been implicated as a locus of attentional processing in a study using positron emission tomography (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990).

In summary, the results of this study indicate that fo-

cusing attention on a visual search target produces a relative enhancement of sensory transmission at the location of the target and a relative suppression of transmission at the locations of distractor objects. These effects are evident in the earliest probe-elicited ERP component, the P1, which begins at about 75 msec poststimulus and appears to be generated in prestriate visual cortex, indicating that attentional selection begins at an early stage of cortical visual processing. The similarity between the P1 and anterior N1 effects observed here during visual search and those observed in previous spatial cuing and sustained attention experiments suggests that these very different task situations engage a common or overlapping set of attentional processes.

METHODS

Subjects

The subjects in this experiment were 10 right-handed, neurologically normal college student volunteers between 18 and 27 years old who were paid for their participation. All subjects had normal or corrected-to-normal visual acuity and reported normal color vision.

Stimuli

The stimuli were presented on a computer-controlled video monitor placed 70 cm from the subject. Each trial consisted of a search array followed by a probe flash, as diagrammed in Figure 1. The search arrays consisted of a set of 16 T-shaped items, each of which subtended $0.4 \times 0.8^{\circ}$ of visual angle and could be upright or inverted with equal probability. Fourteen of these items were red and were randomly distributed across an 11 \times 11° area that was centered around a fixation point. Of the remaining two items, one was blue and one was green. These color-deviant items were placed on opposite sides of the display within $3 \times 5^{\circ}$ areas that were centered 4° to left and right of the fixation point; the left/ right position of a given color-deviant item varied at random across stimulus arrays. Each search array was presented for a duration of 700 msec, and successive arrays were separated by a variable-duration blank interval of 650–850 msec during which only the fixation point was visible.

The probe stimulus was a $1.6 \times 1.6^{\circ}$ white outline box that surrounded, but did not cover, either the blue T or the green T. The stimulus onset asynchrony (SOA) between the search array and the probe stimulus was 250 or 400 msec, and the duration of the probe was 50 msec. On 20% of trials the search arrays were presented without a subsequent probe stimulus to allow the ERP elicited by the search array to be recorded without the overlapping ERP waveform elicited by the probe, as discussed below. The presence or absence of the probe, the color

of the object around which it was placed, and the SOA all varied unpredictably within each trial block.

Procedure

At the beginning of each trial block, subjects were told that either the blue T or the green T was relevant for that block. For each search array, subjects were required to press one button if the T of the relevant color was upright and another button if it was inverted. The thumb and index finger of the right hand were used for these responses, respectively. No discrimination was required for any of the other items in the search array, and the probe stimulus was also irrelevant for the task. Subjects were instructed to maintain fixation throughout each trial block and were told that eye movements were being monitored.

Each trial block consisted of 80 search arrays, and each subject experienced 40 trial blocks in a single session. The green T and the blue T were each relevant for half of the blocks, and the order of the blocks was randomized across subjects. Subjects received one practice block for each of these two conditions before the ERP recordings began.

Recording and Analysis

The EEG was recorded from non-polarizable electrodes mounted in an elastic cap, located at standard left and right hemisphere positions over frontal, central, parietal, occipital, and posterior temporal areas (International 10/ 20 System sites F3, F4, C3, C4, P3, P4, O1, O2, T5, T6) using the algebraically computed average of the left and right mastoids as a reference. The horizontal electrooculogram (EOG) was recorded from electrodes placed 1 cm lateral to the left and right external canthi to measure eye movements, and the vertical EOG was recorded from an electrode beneath the left eye to detect blinks; trials containing these artifacts or incorrect behavioral responses were excluded from the averaged ERP waveforms.3 The EEG and EOG signals were amplified by a Grass Model 12 polygraph with a bandpass of 0.01–100 Hz, digitized at 250 Hz by a minicomputer, and averaged offline.

Because the ERP waveforms elicited by the search arrays overlapped the ERP waveforms elicited by the subsequent probe stimuli (see Woldorff, 1993), a subtraction procedure was used to extract the probe-elicited ERP waveforms. Volume-conducted voltage fields summate linearly, and so subtracting the waveforms from trials with a search array and no probe from the array-plus-probe waveforms will yield the activity elicited by the probe stimulus. Averaged waveforms were therefore computed, time locked to the search arrays, and the waveforms from trials without probe stimuli were subtracted from the waveforms from trials containing probes. The waveforms could then be shifted in time so

that time zero corresponded either to the onset of the probe stimulus or the onset of the search array.⁴

Three different ERP components were measured in the probe-elicited ERP waveforms: P1, anterior N1, and posterior N1. The amplitude of each of these components was quantified as the mean voltage within a specified latency range, relative to the mean prestimulus voltage. The P1 was measured from 90 to 120 msec at the occipital and posterior temporal sites, the anterior N1 from 100 to 175 msec at the frontal, central, and parietal sites, and the posterior N1 from 125 to 200 msec at the occipital and posterior temporal sites. Separate repeated measures ANOVAs were then computed for each component, using five factors: relevance (probe at the location of the relevant or irrelevant item), SOA (250 or 400 msec), electrode location (in the anterior-posterior dimension), hemisphere (left or right), and contralaterality (ipsilateral or contralateral probe relative to the hemisphere of the electrode).

Acknowledgments

This study was supported by ONR Contract N00014–89-J-1806, by grants from NIMH (MH-25594) and NINCDS (NS 17778), and by a graduate fellowship to S.J.L. from the McDonnell-Pew Center for Cognitive Neuroscience at UCSD. We are grateful to Jon Hansen and Paul Krewski for technical support, to Ron Mangun and Marty Woldorff for discussions of this research, and to Hal Pashler for helpful comments on the manuscript.

Notes

- 1. There is no way of determining whether the attention effects observed in this study represent an enhancement of processing at the attended location or a suppression of processing at the unattended location. The terms "enhancement" and "suppression" will therefore be used to indicate relative differences between the attended and unattended locations, and not absolute changes from some known baseline of processing.
- 2. The generators of the anterior and posterior N1 components are not yet known, but it is important to note that the designation of these components as "anterior" and "posterior" on the basis of scalp distribution does not necessarily reflect the location of their generators. For example, the frontally maximal, bilateral scalp distribution of the anterior N1 could in principle be produced by a generator on the ventral surface of the contralateral occipital lobe.
- 3. Approximately 10% of trials were rejected for these reasons, and there were typically 550–600 trials remaining for each combination of left and right relevant T and left probe, right probe, and no probe for every subject.
- 4. This procedure assumes that the electrophysiological response to the search array was unaffected by the presence of the subsequent probe stimulus, and any changes in the array-elicited ERP caused by the probe stimulus will appear in the probe-elicited ERP waveforms. However, since such changes in search array processing would have been caused by the appearance of the probe stimulus, it is equally reasonable to consider them responses to the probe stimulus (see Woldorff, 1989, 1993, for a discussion of this issue).

Reprint requests should be sent to Steven J. Luck, Department

of Neurosciences 0608, University of California, San Diego, La Jolla, CA 92093-0608.

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