FOR DISTINGUISHED EARLY CAREER CONTRIBUTION TO PSYCHOPHYSIOLOGY: AWARD ADDRESS, 1993

Neural mechanisms of visual selective attention

GEORGE R. MANGUN

Department of Psychology and Center for Neuroscience, University of California, Davis

Abstract

Visual selective attention improves our perception and performance by modifying sensory inputs at an early stage of processing. Spatial attention produces the most consistent early modulations of visual processing, which can be observed when attention is voluntarily allocated to locations. These effects of spatial attention are similar when attention is cued in a trial-by-trial, or sustained, fashion and are manifest as changes in the amplitudes, but not the latencies, of evoked neural activity recorded from the intact human scalp. This modulation of sensory processing first occurs within the extrastriate visual cortex and not within the striate or earlier subcortical processing stages. These relatively early spatial filters alter the inputs to higher stages of visual analysis that are responsible for feature extraction and ultimately object perception and recognition, and thus provide physiological evidence for early precategorical selection during visual attention. Moreover, the physiological evidence extends early selection theories by providing neurophysiologically precise information about the stages of visual processing affected by attention.

Descriptors: Event-related potentials, Selective attention, Vision, Human

In everyday situations we are faced with a myriad of sensory inputs that compete for access to mental resources and, ultimately, for the control of behavior. The nervous system utilizes selection mechanisms to control the flow of these inputs, the result being profound effects on the way that attended and ignored events are subjectively perceived and later recalled. The principles by which this "selective attention" may operate have been considered by psychologists for more than 100 years (e.g., James, 1890/1950; Von Helmholtz, 1924) and remain of intense interest today (for critical theoretical reviews, see Allport, 1993; Van der Heijden, 1992).

The mechanisms of selective attention in humans have most often been investigated by measuring the influence of attentional

Address reprint requests to: Dr. George R. Mangun, Center for Neuroscience, University of California, Davis, Davis, CA 95616, USA. E-mail: grmangun@ucdavis.edu.

processes on performance. For example, Posner, Nissen, and Ogden (1978) showed changes in reaction time (RT) to visual stimuli as a function of attention. Human subjects were faster to respond to stimuli at expected (attended) versus unexpected (unattended) spatial locations. In these studies, focused attention was induced by prior cuing of the most probable locations at which an upcoming target stimulus would occur. Performance benefits such as these have been observed for various types of stimuli and task situations. For example, attention-related performance benefits have been reported for letter and luminance targets presented in either an empty (Posner et al., 1978; Posner, Snyder, & Davidson, 1980; Van der Heijden, Wolters, Groep, & Hangenaar, 1987) or cluttered (Eriksen & Yeh, 1985; Hoffman & Nelson, 1981: Müller & Findlay, 1987) visual field. Although attention to visual events often includes foveation of the relevant stimulus, these spatial attention effects have been obtained in the absence of eye movements and thus are not the result of changes in the retinal position of the stimulus. Under such circumstances, attention is said to have been directed "covertly" to locations in the visual field.

Behavioral Studies of Spatial Cuing

In principle, behavioral improvements with spatial attention may result from changes at various stages of information processing and task performance (e.g., Broadbent, 1958, 1970; Deutsch

This work was supported by grants from NIMH, NINDS, the Office of Naval Research, the Human Frontier Science Program Organization, and the McDonnell and Pew Foundations.

I thank Jonathan Hansen, Hans-Jochen Heinze, Thomas Münte, Sönke Johannes, and Steven Luck for their important contributions to the work reviewed here, and Steve Hackley, Marty Woldorff, Michael Gazzaniga, Marta Kutas, Vince Clark, Mado Proverbio, Todd Handy, Clif Kussmaul, Amy Adamson, Amishi Jha, Joe Hopfinger, and Tamara Swaab for helpful comments and support. The work described here would not have been possible without the advice, support, collaboration, and friendship of Steven Hillyard.

& Deutsch, 1963; Norman, 1968; Treisman, 1969). Faster RTs in cuing tasks might result from improved sensory and perceptual analysis, more rapid stimulus identification and semantic encoding, or changes in decision and response generation processes. It has been proposed that the speeded RTs to attended stimuli result from the facilitating effects of focal attention on perceptual processing of the cued versus uncued targets, thereby leading either to better perceptual representations for attended stimuli or to a faster uptake of information from the attended locus (e.g., Posner, 1980). With this "perceptual facilitation" mechanism, improved representations of sensory events could facilitate responses to those events by decreasing the time necessary to discriminate their features and/or by reducing the time it would take for the amount of information about an event to accumulate to the point that it could be registered by the brain and trigger a response.

Several researchers have noted that, although the perceptual facilitation mechanism is plausible, the speeded RTs to cued targets might not result from changes in sensory/perceptual processing but rather from differences in the subject's willingness to respond (i.e., decision/response criterion) to targets occurring at cued versus uncued locations (e.g., Müller & Findlay, 1987; Shaw, 1984; Sperling, 1984; Sperling and Dosher, 1986). Thus, if subjects were to set higher criterion for information quality or quantity from unattended as opposed to attended events, the result would be slowed RTs for the former.

Event-Related Potentials in Studies of Spatial Cuing

If precuing of the location of a target leads to changes in sensory/perceptual processing, it should be possible to observe such effects by utilizing physiological measures of visual information processing of cued and uncued stimuli. Such an approach was followed in several experiments (e.g., Mangun, Hansen, & Hillyard, 1987; Mangun & Hillyard, 1991). The design used in these studies was similar to that of Posner et al. (1978, 1980), with each trial beginning with an arrow cue (200-ms duration) presented at fixation. The arrow pointed randomly to either the left or right visual field, and was followed by a left or right lateralized target stimulus after a variable interval (600-1,000 ms in different experiments). The arrow cue predicted (valid trial) the visual hemifield in which the target was most likely to occur (p = .75), but on some trials (p = .25) the target occurred in the opposite visual field location (invalid trial). Thus, because the cue manipulation induced the subjects to expect the target at one location, this presumably led them to voluntarily attend to that locus. This type of cuing is known as endogenous or symbolic cuing because a decoding of cue information must occur first, which can then be followed by a voluntary attentional allocation.

If the RT effects of spatial cuing are due to changes in perceptual processing, then the early (i.e., 50–250 ms) sensory eventrelated potentials (ERPs) would be affected by cue validity. Alternatively, if RT effects are the result of changes in decision and/or response stages, then one would expect only changes in longer latency ERP components related to decision or response processes. Comparisons of ERPs to validly and invalidly cued target stimuli are shown in Figure 1. Reliable changes in the amplitudes of the occipital P1 (80–130 ms) and N1 (170–210 ms) components of the ERPs were obtained as a function of cue validity. Both of these ERP peaks were larger in amplitude when Although the ERP evidence is very clear in demonstrating changes in early visual processing with spatial cuing, these data alone cannot exclude the possibility that the effects of spatial cuing on RT (e.g., Posner, 1980) might result from changes in decision and response criteria alone (e.g., Müller and Findlay, 1987; see also Eimer, 1993a, 1993b, 1994a, 1994b). Nonetheless, the ERP evidence provides important information about the mechanisms underlying expectancy-based cuing effects and shows that such methods do induce attention-based early visual processing changes that are consistent with the idea of a rela-

RIGHT FIELD STIMULI



Figure 1. Grand-average ERPs from right and left field target stimuli when validly and invalidly precued. Subjects made a two-choice height discrimination for the targets. Recordings are from parietal (PAR) and lateral-occipital (OCC) scalp sites of the left hemisphere (left column) and right hemisphere (right column) (Mangun & Hillyard, 1991).

tive perceptual facilitation of cued inputs. The ERP data is also in line with recent experiments utilizing signal detection methods that have also provided support for the idea that expectancybased cuing of target locations leads to changes in sensory/ perceptual processing. Signal detection theory permits perceptual sensitivity (d') to be characterized separately from the effects of decision and response bias (beta). Cuing studies have found improvements in detection sensitivity in the absence of changes in decision criterion in spatial cuing tasks (e.g., Downing, 1988; Hawkins et al., 1990; Luck et al., 1994). Such results support the idea that perceptual processing is relatively improved with focal attention in trial-by-trial, expectancy-based cuing paradigms.

The task used in the experiment presented in Figure 1 was to discriminate the height of the stimulus bars and to make a speeded two-choice RT response: that is, press one button for tall bars, the other button for short bars. Interestingly, in a second experiment where the task did not involve discrimination but simply speeded responses to the onset of the stimulus bars (i.e., simple RTs), the results differed from those described above. In the simple RT experiment, the occipital P1 component showed similar amplitude modulations to those found in the discriminative RT cuing study, but the later N1 peak showed no such modulations (Figure 2). Such a pattern suggests a dissociation between the visual attentional processes reflected by each of these ERP components. One possible model is that, although the predictive cues lead to a focusing of attention on the cued location (indexed by P1), when the task involves only a simple RT response, detailed perceptual processing of the target features is not required (e.g., the N1 stage of analysis). This suggests a fundamental dissociation of the visual and attentional processes indexed by the P1 and N1 components of the flashevoked ERP. This possibility is discussed in the last section of this paper.1

The P1 and N1 cuing effects shown in Figure 1 are essentially identical to ERP attention effects on these components that have been reported in tasks where attention was selectively maintained on a single location over a block of many trials (e.g., Eason, 1981; Eason, Harter, & White, 1969; Hillyard & Münte, 1984; Mangun & Hillyard, 1987, 1988, 1990a; Neville & Lawson, 1987; Rugg, Milner, Lines, & Phalp, 1987; Van Voorhis & Hillyard, 1977). These ERP amplitude modulations with attention in both the sustained and trial-by-trial designs can be interpreted as evidence that relatively early stages of visual processing are affected by whether or not a stimulus is attended or ignored (e.g., Eason, 1981; Heinze, Luck, Mangun, & Hillyard, 1990; Hillyard & Mangun, 1987; Näätänen, 1987; Wijers et al., 1987).

Peripheral Sensory Cuing of Target Locations

The ERP experiments described in the previous section utilized attention-directing cues that were symbolic, requiring first a decoding of cue information (i.e., left or right) and then the vol-

untary allocation of attention to a spatial location. This method can be contrasted with cuing wherein the cue information is delivered in the form of a sensory event at the to-be-attended location, such as a peripheral flash (e.g., Jonides, 1981; Posner & Cohen, 1984). In a fashion analogous to the central arrow cues, the peripheral cues can be valid (cue occurs at location of subsequent target stimulus) or invalid (cue occurs at location other than location of subsequent target). Some evidence indicates that peripheral cues capture attention to locations in the visual field through mechanisms partly or wholly different than do symbolic cues such as the centrally presented arrows described earlier. Specifically, peripheral cues have been shown to capture attention in a more automatic fashion than do symbolic cues. The automatic nature of peripheral cues is manifest most clearly as significant cue validity effects (faster RTs to validly versus invalidly cued target stimuli) regardless of whether the peripheral cue predicted the position of the subsequent target stimulus. In addition, it has been shown that it is difficult for observers to ignore peripheral cues and that peripheral cues are

RIGHT FIELD STIMULI



Figure 2. Same as Figure 1 except the subjects' task was to make a speeded RT response to the target (Mangun & Hillyard, 1991).

¹It is worth emphasizing once again that eye movements did not contribute to any of the attention effects in the ERPs because eye movements were rigorously monitored, and trials or sessions were discarded if they occurred. Because these experiments involved trial-by-trial cuing of the to-be-expected/to-be-attended spatial location, it was possible to obtain high-resolution measures of eye position (approximately 0.33° of the visual angle) from electrooculographic recording (EOG) using signal averaging (for a detailed discussion see Experiment 4 of Mangun & Hillyard, 1991).

Neural mechanisms of visual selective attention

relatively insensitive to the influence of distracting stimuli or competing tasks (e.g., Yantis & Jonides, 1990).

The time course of cue validity effects is also different for peripheral versus symbolic cues. For example, peripheral cues produce a facilitation in RTs for validly cued targets at cuetarget stimulus onset synchronics (SOAs) as short as 50-100 ms (e.g., Posner & Cohen, 1984). Interestingly, with the passage of time post-cue, the facilitation in RT at the peripherally cued location can be replaced by cuing effects that are generated by the meaning of the cue, as in the case of cues that indicate that the target is actually more likely to be at another visual field location (e.g., Müller & Rabbitt, 1989; Yantis & Jonides, 1990). At the peripherally cued location, a second effect that appears with time post-cue is known as "inhibition of return," wherein RTs are actually slowed for the cued location relative to neutral conditions. These interesting temporal characteristics of peripheral cues are not induced by symbolic cuing and raise the question of whether these two types of attentional orienting are reflections of different underlying mechanisms.

To investigate the relationship between peripheral and symbolic cues, Briand and Klein (1987) investigated the effects of each type of cuing in a visual search paradigm. They found that the size of the cue validity effects were greater for targets defined by conjunctions-of-features versus simple-feature targets when peripheral cuing was used. But this difference between conjunction and feature targets was not obtained in conditions using symbolic cuing of target locations. Such results provide evidence that peripheral and symbolic cuing involve partly or completely distinct attentional mechanisms.

In comparing symbolic and peripheral cuing, it is important to consider some possible sources of confound that may introduce apparent differences in attentional processing. For example, during peripheral cuing there is the possibility that some sensory interactions may occur between the cue itself and the target. This is the case because they both stimulate similar or identical sensory receptors and, hence, similar neurons in the ascending visual pathways. Thus, the cue may induce either excitatory or refractory states of visual neurons that would then influence the processing of the subsequent target stimuli.

In attempts to reduce the possibility of cue-target sensory interactions, some researchers have manipulated the manner in which the peripheral cues were presented. By showing that similar cuing effects could be induced by peripheral cues that either dimmed or brightened, Posner, Rafal, and Cohen (1982) argued that the facilitation and the subsequent inhibition in response speed seen with peripheral cues could not be merely the result of sensory interactions. Such an argument does not hold, however, because both increases and decreases in luminance/contrast result in changes in visually responsive neurons, beginning in the retina and continuing through higher stages of visual processing. It is difficult to separate the contributions of pure sensory effects from those of attention under the conditions of peripheral cuing, but it is clear that the early facilitation seen under these conditions is a pattern opposite from that to be expected from simple refractory interactions of cue and target.

The findings of differences between symbolic and peripheral attentional cuing have been interpreted as evidence that dissociable brain systems are involved in each of these aspects of attentional orienting. ERPs were used to provide further information about the underlying mechanism contributing to symbolic versus peripheral cuing. If different brain systems are involved in these two types of visual-spatial attention, then one would predict differences in the electrophysiological indices of cue-target validity for symbolic and peripheral cuing.

ERPs and behavioral responses were obtained under two conditions of cuing: symbolic and peripheral. For the central cue condition, each trial began with an arrow presented (34 ms) to fixation, which pointed to the left or right visual field (p = .50). The arrow cue was valid on 75% of trials and invalid on the remaining 25% of trials. The stimuli were either tall ($2.1 \times 0.7^{\circ}$) or short ($1.9 \times 0.7^{\circ}$), vertical white bars that were briefly flashed (50 ms) in the left or right visual field (6.4° eccentricity). The cue-to-target SOAs varied between 600 and 800 ms in a rectangular distribution, and the intertrial interval was 1.8 s. The left and right field stimulus locations were continuously marked: Four small "dots" were placed at the corners of an imaginary vertical rectangle within which the stimuli flashed.

In the peripheral cue condition, each trial started with a sensory cue that occurred at one of the two possible lateral field target locations. The cue consisted of the disappearance (50 ms) and reappearance of the four dots that continuously marked the possible target locations. These peripheral cues were either valid (occurred where the subsequent target would, p = .75) or invalid (occurred in the opposite visual field, p = .25). The subjects were required to keep their eyes fixated on a central spot, and the task was to press a left-hand button for short target bars and a right-hand button for tall target bars.

The subjects were significantly faster to the validly versus invalidly cued targets in both the symbolic and peripheral cuing conditions (both p < .001), and these effects were not significantly different for the two types of cuing (symbolic: 520 vs. 562 ms, peripheral: 537 vs. 573 ms). However, the pattern of ERP effects was different for symbolic and peripheral cuing. In the symbolic cuing condition, the effects of cue validity were amplitude differences in the P1 and N1 components recorded over posterior scalp regions; that is, these components were of greater amplitude for the validly cued targets (Figure 3). The P3 component (300-400 ms) was also found to be significantly larger for invalidly cued stimuli, but a longer lasting positive shift (400-700 ms) was similar in amplitude for valid and invalid targets. This pattern of results was the same as that obtained for symbolic cuing described in Figures 1 and 2.

In contrast to the findings in the symbolic cue condition, in the peripheral cue condition there was no modulation of the early occipital P1 component as a function of cue validity. The effects of cue validity were all confined to the later N1, N2, and P3 components. As with the symbolic cue condition, the N1 and N2 components were observed to be significantly larger to validly cued stimuli than invalidly cued stimuli at most scalp sites (Figure 4).

Overall, the effects of symbolic and peripheral cuing (at long SOAs) on visual processing showed many similarities, but also some notable differences. The similarity between symbolic and peripheral cuing effects on RTs and the later ERP components suggests that at least partly overlapping mechanisms must be involved in these types of visual-spatial cuing. This conclusion is in line with the RT findings of Warner, Juola, and Koshino (1990) who also suggested many similarities between symbolic and peripheral cuing. Given that the peripheral cues used here were predictive of target location (75% of time), and the SOA between cue and target were relatively long, these similarities might well be expected because, as used here, both types of cuing probably involved the voluntary allocation of attention to cued locations. Given this, however, it is surprising to find that there



Figure 3. Grand-average ERPs to targets that were validly and invalidly precued by centrally located symbolic cues. ERPs to right visual field targets are shown in the left two columns, and to left visual field targets in the right two columns. Subjects were required to discriminate the height of the target bars (Hillyard, Luck, & Mangun, 1994).



Figure 4. Same as Figure 3 except the cue was a peripheral cue. Note the absence of a P1 attention effect in comparison to Figure 3 (Hillyard, Luck, & Mangun, 1994).

Neural mechanisms of visual selective attention

was an absence of any P1 attention effect in the peripheral cue condition. This dissociation between symbolic and peripheral cuing in the short-latency P1 attention effect suggests that significant differences may exist in the ability of the attention system to invoke and/or maintain early attentional filtering in the presence of peripheral sensory cues. Such a finding may, in part. form the basis for reported findings of differences in symbolic and peripheral cuing effects (e.g., Briand & Klein, 1987); however, such a proposal is beyond the scope of this study. Numerous differences in task parameters exist between the present study and those comparing different types of cuing using behavioral methods. Indeed, one plausible explanation for the lack of early attentional modulation with the peripheral cues is that some form of sensory-sensory interaction between the cue and target led to an absence of the P1 attention effect. Such a possibility exists on purely theoretical grounds and has been hypothesized based on other studies using peripheral cues (Eimer, 1994b).

An alternative interpretation, however, is that the absence of the P1 attention effect for peripheral cues at longer cue-target SOAs may be related to the "inhibition of return" phenomenon. Inhibition of return refers to the slowing of RTs to valid targets following peripheral cues for SOAs greater than about 150 ms (Posner & Cohen, 1984; Rafal, Calabresi, Brennan, & Sciolto, 1989). In the present study, the RTs were significantly faster for validly cued targets at this long SOA; thus, the RT pattern does not show inhibition of return. Indeed, the inhibition-of-return pattern might not be expected given the predictive nature of the peripheral cues that were used. Over time, two competing influences would tend to have opposing effects: The inhibition of return effects would tend to lengthen the RTs to the validly cued targets, whereas the voluntary allocation of attention would tend to shorter RTs to validly cued targets. Thus, perhaps in our study with peripheral cues, the automatic effects of peripheral cues in inducing inhibition of return were manifest as reductions or the complete absence of the P1 attention effects in the ERPs. In contrast, the effects of the voluntary allocation of attention to the cued location (due to the predictiveness of the cue) lead to attention-related amplitude enhancements in the later N1, N2, and P3 components of the ERPs, as well as speeded RTs for the cued-location targets. This possibility remains plausible even given the simpler sensory-sensory interaction explanation because in the present study the peripheral cues did not physically overlap the visual field location of the target stimulus; instead they were immediately adjacent (i.e., the dots), and thus the possibilities for pure sensory-sensory interactions such as neuronal refractoriness were greatly minimized (cf. Eimer, 1994b).

Anatomical Localization of Early ERP Attention Effects

The preceding studies involved the use of ERPs to investigate the mechanisms of spatial attention by applying the ERP method to address current questions about attentional processes in common cognitive designs (i.e., spatial cuing studies). These results, together with a body of ERP studies on spatial and nonspatial attention (for reviews, see Harter & Aine, 1984; Näätänen, 1992), indicate that visual attention can begin to affect visual afferent processing within 70–90 ms after stimulus onset. Such information informs us as to the time course and mechanisms of early attentional selection. The localization of these early attention effects with respect to the anatomy of the visual pathways will now be discussed.

It has been hypothesized that the early ERP attention effects, such as the P1 amplitude modulation, may reflect processing in the visual cortex, subcortical structures, or even in the retina itself (e.g., Eason, 1981; Eason, Oakley, & Flowers, 1983; Harter & Aine, 1984; Hillvard & Mangun, 1987; Van Voorhis & Hillvard, 1977). However, little direct evidence exists that links these attention-sensitive ERPs to specific brain structures. The short latency of the P1 attention effect for spatial attention is consistent with the idea that P1 reflects a stage of visual processing that precedes complete perceptual analysis. The evidence is that the P1 component behaves like an "exogenous" ERP component in that it is sensitive to the physical attributes of the evoking stimulus as well as the direction of attention in space (e.g., Regan, 1989). In addition, P1 latency is consistent with processing in visual cortex as evidenced by recordings in animals (e.g., Robinson & Rugg, 1988). Unfortunately, the latency of the P1 merely places an upper limit on the time of occurrence of the attention effects reflected in P1 amplitude. This is because modulations of P1 with spatial attention may reflect attention effects at an earlier stage of processing that are passed along the ascending visual pathways to the P1 generator. Given the uncertainties in the anatomical locus of generation of the P1 wave, and the nature of its attentional modulations, it is important to establish two critical pieces of information: (1) where in the visual pathways the P1 component is generated and (2) whether earlier stages (inputs to P1) of visual processing can be affected by spatial attention.

To address these questions, the scalp distribution of the early P1 effect was investigated to provide clues as to the possible brain generators of this important ERP component. Figure 5A shows isovoltage contour maps at the peak latency of the P1 that were elicited by attended and ignored stimuli in a sustainedattention design (Hillyard & Mangun, 1987). These maps show a positive voltage maximum that overlays the medial occipital scalp and is contralateral to the visual hemifield of the stimuli. Left visual field stimuli produce a right occipital maximum, and right field stimuli produce a left occipital maximum. These effects were maximal at electrode sites O1 and O2 (International 10-20 System), which are known to be positioned directly over the striate cortex (Homan, Herman, & Purdy, 1987). Based on such maps, it is tempting to assume that the P1 is generated in striate cortex. Indeed, this seems a plausible conclusion given its scalp localization and evidence that there are evoked components in this time range that appear to be generated in striate cortex. However, these arguments are not satisfactory for two principal reasons. First, one cannot assume that the generator of a scalp-recorded ERP component is situated in the immediately underlying neuronal tissue, and second, many of the evoked components modeled to striate cortex have unclear relationships to the attention-sensitive P1 under discussion here. Specifically, the well-known P100 component to pattern-reversing stimulation used clinically is not the same ERP component as the flash onset-offset evoked P1 investigated in attention studies (for review, see Regan, 1989).

One additional shortcoming of the data in Figure 5A is that the topographic maps it displays are based on recordings from only 11 recording sites on the scalp and only 2 sites over the occipital scalp. Such a sparse electrode array does not have the resolution to provide either good clues as to the generators of scalp-recorded activity or to properly characterize the pattern

Attend right



Attend midline

Figure 5. A: Grand-average scalp topographic voltage maps taken at the peak of the occipital P1 component for left (top) and right (bottom) field stimuli when attending left (left), midline (middle), and right (right) field locations. The P1 maximum is located over medial occipital scalp regions (dark heavy lines) (Hillyard & Mangun, 1987). B: Data from a replication study wherein more occipital electrode sites were recorded. Note the more lateral scalp maxima of the P1 positivity in comparison with A (Mangun & Hillyard, 1988).

A

Attend left

Neural mechanisms of visual selective attention

of voltage fluctuations on the scalp. Figure 5B makes this last point very clearly. When the number of recording sites over the occipital scalp was increased (to a total of 14 on the scalp), the topographic maps in a replication study were very different (Mangun & Hillyard, 1988). The scalp maximum of the P1 effect was found to be more lateral than could be discerned from the data of Figure 5A. The sensory-evoked P1 when attended and ignored showed scalp maxima over lateral, rather than medial, occipital scalp sites. Thus, these data raised questions about whether the striate cortex was the generator of the attentionsensitive P1 peak.

Based on the scalp topographies and peak latency of the P1 peak, we (Mangun & Hillyard, 1990b) proposed that the attentionsensitive P1 was generated in the lateral occipital, extrastriate visual cortex rather than the more medial striate cortex, which provides input to both the dorsal and ventral cortical visual processing streams (Ungerleider & Mishkin, 1982). Such a proposal has significant consequences for both psychological and physiological theories about visual–spatial attention. On the one hand, this proposal suggests that attention affects visual processing in cortical areas involved in visual perceptual analysis (evidence for early selection); on the other hand, it suggests that these effects may not occur in primary (striate) sensory cortex or the subcortical visual pathways (evidence against subcortical gating of sensory inputs with selective attention).

To address this question, we recorded ERPs elicited by attended and ignored stimuli from a dense electrode array over the posterior scalp (>28 channels posteriorly; Mangun, Hillyard, & Luck, 1993). This allowed a fine-grained mapping of scalp voltage distributions to be obtained for the P1 attention effect. In addition to a more detailed mapping of scalp voltage fields, we also manipulated the placement of the evoking stimuli in the visual field. This was done to take advantage of the unique anatomical organization of the striate cortex that results in characteristic ERP patterns for stimuli presented to the four visual field quadrants. Because the striate cortex is folded within the depths of the calcarine fissure on the medial aspect of the contralateral occipital lobe, upper and lower visual hemifields are mapped to separate, oppositely oriented, cortical sheets across the calcarine fissure (Figure 6). As a result, ERP components generated in striate cortex show polarity reversals on the scalp for upper versus lower field stimuli (Butler et al., 1987; Jeffreys & Axford, 1972). Thus, polarity reversals of an early, occipital ERP component for upper versus lower field stimuli would be a sign of generation in striate cortex in the calcarine area.

Even though these studies of visual evoked potentials in nonattentional tasks had proposed evoked components that were generated in striate and extrastriate cortex, it was not sufficient to merely compare these data with data from those ERP spatial attention studies reviewed earler. This is for the simple reason that there were significant differences in the stimulus and task parameters between our studies and prior visual evoked potential experiments. These differences were sufficient to preclude a simple comparison across studies to address the question of where the attention-sensitive P1 was generated. The solution adopted was to combine the methodology that permitted Jeffreys and Axford (1972) to model evoked responses to striate versus extrastriate cortex with the methods required to study spatial selective attention (e.g., Eason, 1981). Thus, the goal was to identify the attention-sensitive P1 component and to investigate whether or not it showed a pattern of polarity inversions on the scalp that would be consistent with a neural



Figure 6. Mapping of visual field onto diagram of calcarine visual area. Stimuli presented at locations 2 and 3 in the visual field would excite cortical neurons with geometrically opposed orientations within the depths of the calcarine fissure according to the cruciform model.

generator within the depths of the calcarine sulcus of the striate cortex.

In this experiment, an ERP component was indeed identified that polarity inverted for upper versus lower field stimuli, but it was found to have a shorter latency than the P1 wave that peaks after a latency of 100 ms. This component, here termed the NP80 wave (onset at 50-60 ms, peak at 80-90 ms), was maximal in amplitude over midline parietal-occipital scalp sites and dropped off in amplitude as one moved in the direction of the lateral occipital scalp sites where the P1 wave was found to be largest (Figure 7). These characteristics of the NP80 were consistent with a striate cortex generator as first proposed by Jeffreys and Axford (1972, their CI component). Importantly, attention did not affect this striate ERP component. In contrast, the P1 component (onset 80-90 ms, peak 125 ms) did not show any evidence of polarity inversions for upper versus lower field stimuli (Figure 7), but it was attention sensitive as described elsewhere (e.g., Eason, 1981; Harter, Aine, & Schroeder, 1982; Hillyard & Münte, 1984; Mangun & Hillyard, 1988, 1990a; Neville & Lawson, 1987; Rugg et al., 1987; Van Voorhis & Hillyard, 1977) (Figure 8).

Topographic scalp current density (SCD) maps showed that the locus of maximum P1 amplitude for the left field stimuli was over the lateral occipital scalp of the right (contralateral) hemisphere, and the maximum for the right field stimuli was over the lateral occipital scalp of the left hemisphere (Figure 9). Interestingly, in both cases a smaller, mirror-image current focus could be observed over the ipsilateral scalp, peaking 10–15 ms after the contralateral P1 maximum. As an aside, studies (Mangun, Luck, Gazzaniga, & Hillyard, 1991; Tramo et al., in press) of these brain potentials in neurological patients have clearly



Figure 7. Grand-average ERPs to upper versus lower quadrant stimuli when unattended. Electrode locations at left lateral occipital (OL; left), right lateral occipital (OR; right), and a parietal-occipital midline (POz; middle) sites. Note the apparent polarity inversion in the time period of 50–100-ms latency at the POz site. In contrast, at lateral-occipital sites, neither P1 nor N1 components alter their polarity with upper versus lower field stimuli (Mangun, Hillyard, & Luck, 1993).

demonstrated that this secondary ipsilateral hemisphere P1 peak is eliminated following callosotomy (Figure 10), thus indicating that the ipsilateral P1 represents activation of the ipsilateral hemisphere through the corpus callosum (Mangun & Hillyard, 1988; Rugg, Milner, & Lines, 1985; Saron & Davidson, 1989).



Figure 8. Grand-average ERPs from right lateral occipital sites (OR) in response to left field stimuli (left column), and left lateral occipital sites (OL) in response to right field stimuli (right). Significant attention effects can be observed on both the P1 and N1 components (Mangun, Hillyard, & Luck, 1993).

This reinforces the idea that the attention-sensitive P1 component is not generated in the striate cortex because in the two hemispheres it is not interconnected through the corpus callosum.

The P1 attention effects were related to the underlying cortical anatomy by mapping the SCD maxima onto magnetic resonance imaging (MRI) scans for some of the subjects. Electrode sites were marked on the subjects' heads by attaching small oil capsules that could be visualized in the images, thereby permitting the scalp-recorded ERPs to be brought into the same reference frame as the MRI scans. The MRI scan in Figure 11 shows the P1 current flow out of the skull to be located over the ventrolateral extrastriate cortex, which corresponds to areas 18 and 19 of the occipital lobe. Subsequent ERP studies using inverse dipole modeling techniques have modeled the NP80 and P1 responses to striate and lateral extrastriate cortical regions. respectively (Clark, 1993; Gomez Gonzalez, Clark, Fan, Luck, & Hillyard, in press) and have also failed to find effects of attention on the NP80 from striate cortex while showing significant spatial attention effects on the later P1 component from extrastriate cortical regions (Clark, 1993; Gomez Gonzalez et al., in press). A recent replication of Mangun, Hillyard, and Luck (1993) using magnetoencephalography (MEG) has also yielded similar lateral extrastriate localizations for the P1 attention effect, as well as an earlier striate activity that was not attention sensitive (Mangun, Sams, Ilmoniemi, & Simpson, 1994).

Together, the results of these localization studies do not support an attentional gating mechanism at the level of the lateral geniculate nucleus or striate cortex. Rather, it appears that the earliest processing stage where spatial selective attention modulates visual processing is in the extrastriate cortex. This conclusion is consistent with most studies in monkeys that have found no evidence for attentional modulation of single-unit



Figure 9. Grand-average scalp current density maps for all four quadrant stimuli when attended (left column) and unattended (middle column). At right, the unattended map has been subtracted from the attended map to yield the scalp distribution of the attention effects. Note the growing current focus over the hemisphere ipsilateral to the stimulus (Mangun, Hillyard, & Luck, 1993).

activity in primary visual cortex (e.g., Moran & Desimone, 1985; Wurtz, Goldberg, & Robinson, 1980; however, see Motter, 1993) and recent studies using combined PET and ERP approaches in humans (e.g., Mangun et al., 1993; Heinze et al., 1994). The role of subcortical systems appears limited from the perspective of input filtering and selective sensory processing. Much recent evidence has accumulated to suggest that subcortical visual processing in the retino-geniculo-striate system is not



Figure 10. Grand-average scalp voltage topographic maps to right field stimuli for two callosotomy (split-brain) patients (top) and eight healthy controls (bottom). Whereas the controls show a normal interhemispheric transfer of the P1 component over time, this effect is eliminated in the split-brain patients. A similar mirror-symmetric pattern was obtained for left field stimuli (not shown) (Mangun, Luck, Gazzaniga, & Hillyard, 1991).

modulated by visual selective attention. However, other subcortical structures may play key roles in the systems of brain structures organized to process selectively external stimulus inputs. For example, the pulvinar of the thalamus appears to occupy a crucial position in a complex network of brain structures, which includes frontal and parietal cortex, whose coordinated actions control the selection of spatially mapped inputs into the object-perception system of the temporal lobe (e.g., Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; Corbetta, Miezin, Shulman, & Peterson, 1993; Desimone, Wessinger, Thomas, & Schneider, 1990; LaBerge, 1990; Petersen, Robinson, & Morris, 1987; Rafal & Posner, 1987).

Cortical Processing Streams and ERP Components

The preceding section discussed the occipital P1 component and the earlier NP80 but did not include a discussion of the posterior scalp N1 component. The N1 is amplitude modulated by spatial attention, as noted earlier. The N1 attention effect during visual attention is a robust finding for lateralized stimuli presented in isolation and was in fact the first electrical sign of visual attention to be identified (Eason et al., 1969); subsequent studies revealed that the shorter-latency P1 component was also affected by spatial attention (Eason, 1981; Van Voorhis & Hillyard, 1977).

The relationship between the posterior N1 component and the occipital P1 has been hypothesized to be serial and hierarchical such that the stage reflected by the N1 receives inputs from the P1 processing stage (e.g., Eason, 1981). However, based on analysis of SCD mapping, it has also been suggested (Mangun, Hillyard, & Luck, 1993) that the P1 and N1 components reflect processing in separate cortical processing streams (e.g., Unger-

leider & Mishkin, 1982) corresponding to the ventral (occipitaltemporal) and dorsal (occipital-parietal) projection pathways. This latter proposal has been difficult to substantiate because unlike the P1, which has a narrow scalp distribution, the N1 has a very broad scalp distribution over occipital, temporal, and parietal scalp areas, as well as more anterior scalp regions. Such a pattern is consistent with either brain activity in multiple cortical regions, or a more unitary neural generator located at greater depth in the brain, thereby producing a broad scalp signature. As a result, inverse dipole modeling of the visual N1 component has proven difficult. One hint that the posterior N1 component is actually the superposition at the scalp of the activity of two or more neural generators is that the peak latency of the posterior N1 is different for occipital-temporal versus parietal scalp regions; it is slightly shorter in peak latency over parietal scalp (~15 ms). This small apparent shift in peak latency might reflect either multiple N1 generators or differential overlap of the N1 with other activity at more posterior scalp regions, for example, where the P1 component is maximal.

Until recently, it has been difficult to determine the extent to which the posterior visual N1 component reflected a singular neural process as opposed to activity in multiple, separate brain regions. Progress on this question has been made in a recent visual attention study where topographic evidence for separate parietal N1 and occipital-temporal N1 components was obtained (Johannes, Hughes, & Mangun, 1992; Johannes, Muente, Heinze, & Mangun, 1994). The subjects (N = 12) viewed a display that contained left and right visual hemifield stimuli that were presented at two luminance levels (bright stimuli: 15.5 footlamberts [53.1089 cd/m²] and dim stimuli: 0.4 footlamberts [1.3705 cd/ m²]). The stimuli were located about 5.0° lateral to fixation and consisted of vertical bars that flashed for 67 ms in a rapid (~3/s) random sequence. A small percentage (~15%) were slightly



Figure 11. Horizontal section of an MRI scan for one normal subject from the study described in Figures 6-9. Indicated on the MRI (left side = right hemisphere) are markers where the maximal scalp current density was located for the stimuli presented to the four visual field quadrants (ll, lower left; ul, upper left; lr, lower right; ur, upper right). These current sources lie over lateral extrastriate cortical regions (Mangun, Hillyard, & Luck, 1993).

shorter target stimuli requiring a response if on the attended side; attention was sustained to either the right or left stimuli for a block of many trials. The goals of the study included investigation of the interactions of luminance and spatial attention and considerations about the nature of attention modulations observed on ERP components, but these will not be reviewed here. Rather, the effects of stimulus luminance on the latencies of the P1 and N1 components will be considered independently of the effects of attention.

Changes in stimulus luminance influenced the ERPs by affecting both their latency and amplitude. Although increased stimulus luminance generally led to increased amplitude or shorter peak latencies, not all ERP components were similarly affected. Amplitude increased with luminance for the occipital P1 component, and also for the parietal N1 component (the latter was not statistically reliable), but it did not affect their peak latencies. In contrast, increased luminance resulted in shorter peak latencies for the occipital-temporal N1 but not for the N1 component recorded from parietal scalp regions. Thus, luminance affected the latency of the occipital-temporal N1 but not the earlier P1 component. This finding indicates that the luminance may have separate effects on the posterior N1 component as a function of where it is recorded. The implication being that separate parietal and occipital-temporal N1 waves are being evoked, one being luminance sensitive and the other not being luminance sensitive. This distinction can be viewed by mapping the scalp topographies of the ERPs at different time periods after the stimulus for the low-luminance stimuli, to which there is a maximal separation in time between the occipital-temporal N1 and parietal N1.

Figure 12 shows topographic voltage maps for three time windows for left visual field (top) and right visual field stimuli (bottom). As previously described, the P1 component is maximal at contralateral occipital-temporal scalp regions (Mangun, Hillyard,



Figure 12. Grand-average topographic scalp voltage maps to unattended low-luminance left (LVF) and right (RVF) stimuli. Note the contralateral P1 maxima (dark) and the two different "N1" topographies (light). At 150–190 ms the N1 negative maxima is located over medial parietal areas, whereas by 190–220 ms the N1 has a much more lateral occipital-temporal distribution (Johannes, Hughes, & Mangun, 1992).

& Luck, 1993). The N1 maps are, however, very different over the course of the following 100 ms. Immediately following P1, there is a parietal N1 focus that is slightly contralateral to the field of stimulation. However, by 200 ms latency a distinctly different pattern emerges. In this later time period, the N1 is maximal over contralateral posterior occipital-temporal regions. This striking pattern suggests that two distinct posterior N1 components can be distinguished, one representing information in parietal brain regions, the other in more lateral occipitaltemporal regions. Although the specificity of the brain localization of these two distinct N1 peaks is limited due to the inherent difficulty in inferring brain localization from scalp distributions alone, these data argue for the presence of two distinct visual processes that are active in the latency range from 150 to 225 ms poststimulus. Future research must clarify the precise localization of these processes.

How does this result affect the above-described model proposed by Mangun, Hillyard, and Luck (1993) as to how the P1 and N1 components in the human may map onto the two main cortical visual projection systems identified in monkeys (e.g., Desimone & Ungerleider, 1989; Ungerleider & Mishkin, 1982)? In this formulation, the P1 component was proposed to be generated in the ventral stream projecting to the inferior temporal lobe involved in object discrimination. The N1 was hypothesized to represent activity in the dorsal stream, projecting from the striate cortex to the posterior parietal lobe and encoding spatial aspects of visual information. In contrast to this simple model, the present data reveal an occipital-temporal N1 component whose peak latency was affected by stimulus luminance that could be dissociated from a parietal N1 peak whose latency was not affected. Thus, a revised interpretation in light of the present data would suggest that an occipital-temporal projection pathway might be reflected in the human ERPs by the occipital P1 and occipital-temporal N1 components, whereas the occipitalparietal projection may give rise to the parietal N1 component. Given this proposal, one important area for future study is to examine the differential effects of attention on these two, apparently distinct, ERP signs of cortical visual processing.

General Conclusions

The evidence reviewed here suggests that visual-spatial selective attention involves powerful neural mechanisms that are capable of significantly modulating the perceptual processing of incoming sensory signals. This must result from the influence of descending neural projections onto the neurons within the modality-specific sensory systems, which alter their excitability and thus responsivity to sensory stimulation. However, these effects are limited to processing that takes place at the cortical level, first modulating inputs at 80-100 ms poststimulus in extrastriate cortical areas. At present, this early stage of selective processing appears to be limited to selection for spatial locations, which has both a central role in visual perception and is robustly represented in the retinotopic coding of the external world at many stages within the visual system. Whether these earliest forms of selective visual attention based on spatial location ultimately turn out to represent a first and preeminent stage of attentional processing must remain for future studies to ascertain. Nonetheless, at present the body of evidence argues for such a hierarchical system of selection, with selective attention to other elementary nonspatial stimulus features following the initial segmentation of the visual world by spatially defined processes (e.g., Van der Heijden, 1992). The consequence of these spatial selection operations is to alter the signal-to-noise ratio for inputs across the visual field, thereby providing a relative facilitation in the transmission of attended-location events to higher stages of perceptual analysis.

REFERENCES

- Allport, A. (1993). Attention and control: Have we been asking the wrong questions? A critical review of 25 years. In D. Meyer & S. Kornblum (Eds.), Attention and performance (Vol. 14). Cambridge: MIT Press.
- Briand, K. A., & Klein, R. M. (1987). Is Posner's "beam" the same as Treisman's "glue"?: On the relationship between visual orienting and feature integration theory. *Journal of Experimental Psychology: Human Perception and Performance*, 13, 228-241.
- Broadbent, D. E. (1958). *Perception and communication*. New York: Pergamon.
- Broadbent, D. E. (1970). Stimulus set and response set: Two kinds of selective attention. In D. I. Mostofsky (Ed.), *Attention: Contemporary theory and analysis* (pp.51-60). New York: Appleton-Century-Crofts.
- Butler, S. R., Georgiou, G. A., Glass, A., Hancox, R. J., Hopper, J. M., & Smith, K. R. H. (1987). Cortical generators of the CI component of the pattern-onset visual evoked potential. *Electroencephalography and Clinical Neurophysiology*, 68, 256–267.
- Clark, V. C. (1993). Localization and identification of functional regions within the human visual system. Unpublished doctoral dissertation, University of California, San Diego.
- Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1991). Selective and divided attention during visual discriminations of shape, color and speed: Functional anatomy by positron emission tomography. *Journal of Neuroscience*, 11, 2383– 2402.
- Corbetta, M., Miezin, F., Shulman, G., & Petersen, S. (1993). A PET study of visuospatial attention. *Journal of Neuroscience*, 13, 1202– 1226.
- Desimone, R., & Ungerleider, L. G. (1989). Neural mechanisms of visual processing in monkeys. In F. Boller & J. Grafman (Eds.), *Handbook* of neuropsychology (Vol. 2, pp. 267–299). New York: Elsevier.
- Desimone, R., Wessinger, M., Thomas, L., & Schneider, W. (1990). Attentional control of visual perception: Cortical and subcortical mechanisms. In Cold Spring Harbor Symposium (pp. 963-971). New York: Cold Spring Harbor Press.
- Deutsch, J. A., & Deutsch, D. (1963). Attention: Some theoretical considerations. Psychological Review, 70, 80-90.
- Downing, C. J. (1988). Expectancy and visual-spatial attention: Effects on perceptual quality. *Journal of Experimental Psychology: Human Perception and Performance*, 14, 188–202.
- Eason, R. G. (1981). Visual evoked potential correlates of early neural filtering during selective attention. *Bulletin of the Psychonomic Soci*ety, 18, 203–206.
- Eason, R., Harter, M., & White, C. (1969). Effects of attention and arousal on visually evoked cortical potentials and reaction time in man. *Physiology and Behavior*, 4, 283–289.
- Eason, R. G., Oakley, M., & Flowers, L. (1983). Central neural influences on the human retina during selective attention. *Physiological Psychology*, 11, 18-28.
- Eimer, M. (1993a). Effects of attention and stimulus probability on ERPs in a go/no-go task. *Biological Psychology*, 35, 123-138.
- Eimer, M. (1993b). Spatial cuing, sensory gating and selective response preparation: An ERP study on visuo-spatial orienting. *Electroencephalography and Clinical Neurophysiology*, 88, 408-420.
- Eimer, M. (1994a). "Sensory gating" as a mechanism for visual-spatial orienting: Electrophysiological evidence from trial-by-trial cuing experiments. *Perception and Psychophysics* (in press).
- Eimer, M. (1994b). An ERP study on visual spatial priming with peripheral onsets. *Psychophysiology*, 31, 154-163.
- Eriksen, C. W., & Yeh, Y. Y. (1985). Allocation of attention in the visual field. Journal of Experimental Psychology: Human Perception and Performance, 11, 583–597.
- Gomez Gonzalez, C. M., Clark, V. P., Fan, S., Luck, S. J., & Hillyard, S. A. (in press). Sources of attention-sensitive visual event-related potentials. *Brain Topography*.

- Harter, M. R., & Aine, C. J. (1984). Brain mechanisms of visual selective attention. In R. Parasuraman & D. R. Davies (Eds.), Varieties of attention (pp. 293-321). New York: Academic Press.
- Harter, M. R., Aine, C. J., & Schroeder, C. (1982). Hemispheric differences in the neural processing of stimulus location and type: Effects of selective attention on visual evoked potentials. *Neurop*syhologia, 20, 421–438.
- 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., Luck, S. J., Mangun, G. R., & Hillyard, S. A. (1990). Visual event-related potentials index focused attention within bilateral stimulus arrays: I. Evidence for early selection. *Electroencephalography and Clinical Neurophysiology*, 75, 511-527.
- Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Scholz, M., Münte, T. F., Gös, A., Scherg, M., Johannes, S., Hundeshagen, H., Gazzaniga, M. S., & Hillyard, S. A. (1994). Combined spatial and temporal imaging of brain activity during visual selective attention in humans. Manuscript submitted for publication.
- Hillyard, S. A., Luck, S. J., & Mangun, G. R. (1994). The cuing of attention to visual field locations: Analysis with ERP recordings. In H. J. Heinze, T. F. Münte, & G. R. Mangun (Eds)., Cognitive electrophysiology: Event-related brain potentials in basic and clinical research. Birkhauser: Boston.
- Hillyard, S. A., & Mangun, G. R. (1987). Sensory gating as a physiological mechanism for visual selective attention. In R. Johnson, R. Parasuraman, & J. W. Rohrbaugh (Eds.), *Current trends in eventrelated potential research* (pp. 61-67). Amsterdam: Elsevier.
- Hillyard, S. A., & Münte, T. F. (1984). Selective attention to color and locational cues: An analysis with event-related brain potentials. *Perception and Psychophysics*, 36, 185–198.
- Hoffman, J. E., & Nelson, B. (1981). Spatial selectivity in visual search. Perception and Psychophysics, 30, 283–290.
- Homan, R. W., Herman, J., & Purdy, P. (1987). Cerebral location of international 10-20 system electrode placement. *Electroencephalog*raphy and Clinical Neurophysiology, 66, 376-382.
- James, W. (1950). *The principles of psychology*. New York: Dover. (Original work published 1890)
- Jeffreys, D. A., & Axford, J. G. (1972). Source locations of patternspecific components of human visual evoked potentials. I: Components of striate cortical origin. *Experimental Brain Research*, 16, 1–21.
- Johannes, S., Hughes, H. C., & Mangun, G. R. (1992). Attention to locations in space: The neurophysiology of early selection. Society for Neuroscience Abstracts, 18, 334.
- Johannes, S., Muente, T. F., Heinze, H. J., & Mangun, G. R. (1994). Luminance and spatial attention effects on early visual processing. Manuscript submitted for publication.
- Jonides, J. (1981). Voluntary versus automatic control over the mind's eye's movement. In J. B. Long & A. D. Baddeley (Eds.), Attention and performance (Vol. 9, pp. 187-203). Hillsdale, NJ: Erlbaum.
- LaBerge, D. (1990). Thalamic and cortical mechanisms of attention suggested by recent positron emission tomographic experiments. *Jour*nal of Cognitive Neuroscience, 2, 358–372.
- 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.
- Mangun, G. R., Hansen, J. C., & Hillyard, S. A. (1987). The spatial orienting of attention: Sensory facilitation or response bias? In R. Johnson, Jr., J. W. Rohrbaugh, & R. Parasuraman (Eds.), *Current* trends in event-related potential research (pp. 118–124). Amsterdam: Elsevier.
- Mangun, G. R., & Hillyard, S. A. (1987). The spatial allocation of visual

attention as indexed by event-related brain potentials. Human Factors, 29, 195-211.

- Mangun, G. R., & Hillyard, S. A. (1988). Spatial gradients of visual attention: Behavioral and electrophysiological evidence. *Electroen*cephalography and Clinical Neurophysiology, 70, 417-428.
- Mangun, G. R., & Hillyard, S. A. (1990a). Allocation of visual attention to spatial location: Event-related brain potentials and detection performance. *Perception and Psychophysics*, 47, 532-550.
- Mangun, G. R., & Hillyard, S. A. (1990b). Electrophysiological studies of visual selective attention in humans. In A. B. Scheibel & A. F. Wechsler (Eds.), *Neurobiology of higher cognitive function* (pp. 271-295). New York: Guilford.
- Mangun, G. R., & Hillyard, S. A. (1991). Modulation of sensory-evoked brain potentials provide evidence for changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychol*ogy: Human Perception and Performance, 17, 1057-1074.
- Mangun, G. R., Luck, S. J., Gazzaniga, M. S., & Hillyard, S. A. (1991). Electrophysiological measures of interhemispheric transfer of visual information: Studies in split-brain patients. Society for Neuroscience Abstracts, 17, 866.
- Mangun, G. R., Hillyard, S. A., & Luck, S. J. (1993). Electrocortical substrates of visual selective attention. In D. Meyer & S. Kornblum (Eds.), Attention and performance (Vol. 14, pp. 219-243). Cambridge: MIT Press.
- Mangun, G. R., Heinze, H. J., Burchert, W., Hinrichs, H., Münte, T. F., Scholz, M., Gös, A., Hundeshagen, H., Gazzaniga, M. S., & Hillyard, S. A. (1993) Combined PET and ERP studies of spatial selective attention in humans. Society for Neuroscience Abstracts, 19, 1285.
- Mangun, G. R., Sams, M., Ilmoniemi, R. J., & Simpson, G. V. (1994). Combined MEG and ERP measures of visual spatial selective attention in humans. Society for Neuroscience Abstracts, 20, 1000.
- Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. Science, 229, 782-784.
- Motter, B. C. (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.
- Müller, H. J., & Findlay, J. M. (1987). Sensitivity and criterion effects in the spatial cuing of visual attention. *Perception and Psychophys*ics, 42, 383-399.
- Müller, H. J., & Rabbit, P. M. A. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception and Performance*, 15, 315-330.
- Näätänen, R. (1987). Event-related brain potentials in research of cognitive processes – A classification of components. In E. van der Meer & J. Hoffmann (Eds.), *Knowledge aided information processing* (pp. 241-273). Amsterdam: Elsevier.
- Näätänen, R. (1992). Attention and brain function. Hillsdale, NJ: Erlbaum.
- Neville, H. J., & Lawson, D. (1987). Attention to central and peripheral visual space in a movement detection task. I. Normal hearing adults. *Brain Research*, 405, 253-267.
- Norman, D. A. (1968). Toward a theory of memory and attention. Psychological Review, 75, 522-536.
- Petersen, S. E., Robinson, D. L., & Morris, J. (1987). Contributions of the pulvinar to visual spatial attention. *Neuropsychologia*, 25, 97-105.
- Posner, M. I. (1980). Orienting of attention. Quarterly Journal of Experimental Psychology, 32, 3–25.
- Posner, M. I., & Cohen, Y. (1984). Components of attention. In H. Bouma & D. Bowhuis (Eds.), *Attention and performance* (Vol. 10, pp. 531-556). Hillsdale, NJ: Erlbaum.
- Posner, M. I., Nissen, M. J., & Ogden, W. C. (1978). Attended and unattended processing modes: The role of set for spatial location. In H. L. Pick & I. J. Saltzman (Eds.), *Modes of perceiving and processing information* (pp. 137-157). Hillsdale, NJ: Erlbaum.
- Posner, M. I., Rafal, R., & Cohen, Y. (1982). Neural systems control of spatial orienting. *Philosophical Transactions of the Royal Soci*ety of London B 298, 187-198.
- Posner, M. I., Snyder, C. R. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, 109, 160-174.

- Rafal, R. D., & Posner, M. I. (1987). Deficits in human visual spatial attention following thalamic lesions. *Proceedings of the National Academy of Sciences USA*, 84, 7349-7353.
- Rafal, R. D., Calabresi, P., Brennan, C. W., & Sciolto, T. K. (1989). Saccade preparation inhibits reorienting to recently attended locations. Journal of Experimental Psychology: Human Perception Performance, 15, 673-683.

Regan, D. (1989). Human brain electrophysiology. New York: Elsevier.

- Robinson, D. L., & Rugg, M. D. (1988). Latencies of visually responsive neurons in various regions of the Rhesus monkey brain and their relation to human visual responses. *Biological Psychology*, 26, 111-116.
- Rugg, M. D., Milner, A. D., & Lines, C. R. (1985). Visual evoked potentials to lateralized stimuli in two cases of callosal agenesis. *Journal* of Neurology, Neurosurgery and Psychiatry, 48, 367-373.
- Rugg, M. D., Milner, A. D., Lines, C. R., & Phalp, R. (1987). Modulation of visual event-related potentials by spatial and non-spatial visual selective attention. *Neuropsychologia*, 25, 85-96.
- Saron, C. D., & Davidson, R. J. (1989). Visual evoked potential measures of interhemispheric transfer time in humans. *Behavioral Neu*roscience, 103, 1115-1138.
- Shaw, M. L. (1984). Division of attention among spatial locations: A fundamental difference between detection of letters and detection of luminance increments. In H. Bouma & D. G. Bowhuis (Eds.), *Attention and performance, Vol 10: Control of language processes* (pp. 109-121). Hillsdale, NJ: Erlbaum.
- Sperling, G. (1984). A unified theory of attention and signal detection. In R. Parasuraman & D. R. Davies (Eds.), Varieties of attention (pp. 103-181). London: Academic.
- Sperling, G., & Dosher, B. A. (1986). Strategy and optimization in human information processing. In K. Boff, L. Kaufman, & J. Thomas (Eds.), *Handbook of perception and performance* (Vol. 1, pp. 2.1-2.65). New York: Wiley.
- Tramo, M., Baynes, K., Fendrich, R., Mangun, G. R., Phelps, E., Reuter-Lorenz, P., & Gazzaniga, M. (in press). Hemispheric specialization and interhemispheric integration: Insights from experiments in callosotomy patients. In A. Reeves & D. Roberts (Eds.), *Epilepsy* and the corpus callosum. New York: Plenum.
- Treisman, A. (1969). Strategies and models of selective attention. *Psychological Review*, 76, 282–299.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), Analysis of visual behavior (pp. 549-586). Cambridge: MIT Press.
- Van der Heijden, A. H. C. (1992). Selective attention in vision. New York: Routledge.
- Van der Heijden, A. H. C., Wolters, G., Groep, J. C., & Hagenaar, R. (1987). Single-letter recognition accuracy benefits from advance cuing of location. *Perception and Psychophysics*, 42, 503-509.
- Van Voorhis, S., & Hillyard, S. A. (1977). Visual evoked potentials and selective attention to points in space. *Perception and Psychophys*ics, 22, 54-62.
- Von Helmholtz, H. (1924). *Treatise on physiological optics*. New York: Optical Society of America.
- Warner, C. B., Juola, J. F., & Koshino, H. (1990). Voluntary allocation versus automatic capture of visual attention. *Perception and Psychophysics*, 48, 243–251.
- Wijers, A. A., Okita, T., Mulder, G., Mulder, L. J. M., Lorist, M. M., Poiesz, R., & Scheffers, M. K. (1987). Visual search and spatial attention: ERPs in focused and divided attention conditions. *Biological Psychology*, 25, 33-60.
- Wurtz, R. H., Goldberg, M. E., & Robinson, D. L. (1980). Behavioral modulation of visual responses in the monkey. In J. M. Sprague & A. N. Epstein (Eds.), *Progress in psychobiology and physiological psychology*, (Vol. 9, pp. 43-83). New York: Academic.
- Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. Journal of Experimental Psychology: Human Perception and Performance, 16, 121-134.

(RECEIVED May 20, 1994; ACCEPTED August 29, 1994)

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.