10.1 INTRODUCTION

Research on visual attention over the past few decades has attempted to specify the levels of processing at which different kinds of sensory information are selected for further analysis (e.g., Hoffman 1986; Johnston and Dark 1986). This “levels-of-selection” issue can be formulated in both psychological and physiological terms. Within a psychological framework, one can ask whether paying attention affects the quality of sensory information that is extracted from attended versus unattended inputs (early selection), or whether the influence is upon subsequent stages of decision, categorization, or response selection (late selection). In support of early selection mechanisms, human psychophysical studies have identified attentional influences on processes of feature registration (Prinzmetal, Presti, and Posner 1986), visual encoding (Reinitz 1990), and threshold-level luminance detection (Hawkins et al. 1990).

In an analogous fashion, neurophysiological studies in animals have begun to define the specific anatomical levels of the visual pathways at which attention modulates the responsiveness of neurons that encode form, color, and spatial information (e.g., Wurtz, Goldberg, and Robinson 1980; Yin and Medjbeur 1988; Desimone and Ungerleider 1989).

In humans, physiological and psychological aspects of selection may be studied concurrently by noninvasively recording event-related brain potentials (ERPs) to attended and unattended stimuli (e.g., Hillyard and Picton 1987). ERPs are voltage fluctuations in the ongoing EEG that can be extracted by signal-averaging techniques; these field potentials reflect synchronous neuronal activity associated with sensory, motor, or cognitive events. The successive positive and negative voltage deflections (components) in an ERP waveform have latencies that reveal the time course of activation of the contributing neuronal populations, and scalp distributions that are determined by the anatomical position and geometry of those active neurons. Because of these properties, ERP recordings can yield information about the timing, sequential order, and anatomical location of attentional selection processes.

The ERPs elicited by briefly flashed visual stimuli include a series of positive (P) and negative (N) components over the posterior scalp that begins as early as 35–40 msec poststimulus and continues for hundreds of milliseconds there-
after (e.g., Hackley, Woldorff, and Hillyard 1990). Typically, however, the stimuli used in psychological experiments are of relatively low intensity, such that only the larger, more prominent of these ERP components can be readily observed. These include the P1 (peaking between 90 and 140 msec), N1 (160–190 msec), P2 (200–250 msec), and N2 (260–300 msec) components (fig. 10.1). All of these latter ERP components are sensitive to spatial attention and are typically enlarged in amplitude when attention is directed to the location of the evoking stimulus (Eason, Harter, and White 1969; Harter, Aine, and Schroeder 1982; Hillyard and Munte 1984; Mangun and Hillyard 1987; Neville and Lawson 1987; Van Voorhis and Hillyard 1977). The amplitude enhancements of the earliest of these components (P1 and N1) over visual cortical areas have been interpreted as manifesting an attentional mechanism that operates as a sensory “gain control” in the visual pathways (Mangun and Hillyard 1988); such early modulation of the sensory signals arising from

![Diagram showing ERP components](image)

**Figure 10.1** Schematic representation of the visual ERP components in a typical spatial attention experiment. In this example, left and right stimuli are shown being presented one at a time to the left and right visual fields. While continuously maintaining fixation on a central point (+), the subjects are instructed to attend to one stimulus position while ignoring the other; the goal is to detect target stimuli embedded within the sequence of target and nontarget stimuli at the attended location. The effects of attention are most validly assessed by comparing the ERPs elicited by the stimuli at a given position when that position was attended as compared to when attention was directed to the opposite visual field location: ERPs to left-field stimuli are indicated at bottom. The ERP waveform consists of a sequence of positive and negative deflections (components) labeled P1, N1, P2, and N2 (positive is plotted downward). These components are sensitive to the direction of attention and are typically larger in amplitude when the evoking stimulus is attended. Since these ERP components are relatively small in comparison to the ongoing EEG, signal averaging of the responses to many stimulus presentations is required to obtain a reliable waveform.
attended locations may underlie improvements in perceptual accuracy and response speed for those stimuli.

Interestingly, the concurrent amplitude enhancements of the early P1 and N1 components are uniquely associated with visual-spatial attention. Very different patterns of attention-related ERP components emerge when selection is based upon other stimulus attributes such as color, orientation, or feature conjunctions. In these cases, the most prominent component elicited by attended stimuli is typically a broad “selection negativity” that begins at 140–200 msec and may extend for several hundred milliseconds thereafter (Harter, Aine, and Schroeder 1982; Harter and Aine 1984; Wijers et al. 1987). Based on differences in the latency of this negativity, Harter, Aine, and Schroeder (1982) proposed that the selection of different attributes occurs in the following order: location, contour, color, spatial frequency, orientation, and feature conjunctions. Moreover, under certain circumstances, the selection of stimuli on the basis of color appears to be hierarchically dependent upon the prior selection for location (Hillyard and Munte 1984). Together, these results reinforce the hypotheses that location has a unique status as a cue for visual selection (e.g., Treisman 1988) and that spatial attention can modulate the registration of simple feature information (e.g., Prinzmetal, Presti, and Posner 1986).

10.2 NEURAL SUBSTRATES OF SPATIAL ATTENTION

Our understanding of the neural mechanisms involved in the attention-related changes in human ERPs can be advanced by considering the information about visual processes that is available from animal experiments. Studies of the anatomy and neurophysiology of the central visual pathways in monkeys have identified separate dorsal and ventral processing systems or “streams” that originate in primary visual (striate) cortex and mediate different aspects of visual perception (e.g., Desimone and Ungerleider 1989). The dorsal stream projects through prestriate area V2 to the posterior parietal lobe and is important for encoding the spatial aspects of visual inputs and for guiding visuomotor performance. In contrast, the ventral stream relays through prestriate areas V2, V3, and V4 of the occipital lobe and conveys information about stimulus form, color, and pattern to the inferior temporal lobe. Single-cell recordings from these visual cortical areas have shown that spatial selective attention exerts a strong influence on visually evoked neuronal activity in both the dorsal (posterior parietal lobe) and ventral (area V4 and inferior temporal lobe) streams, but not in prestriate area V2 or the striate cortex itself (Wurtz, Goldberg, and Robinson 1980; Desimone and Ungerleider 1989).

The anatomical and functional segregation of the visual pathways with respect to selective attention has been studied in humans with both neurobiological and electrophysiological mapping techniques (Corbetta et al. 1990; Harter and Aine 1984; Mangun and Hillyard 1990b). As noted earlier, ERP recordings have revealed separate components over posterior cortical areas that are enhanced in response to stimuli presented at attended locations. The
earliest attention-sensitive ERP component (the P1 wave beginning at 70–90 msec) has an amplitude maximum over the lateral occipital scalp, approximately overlying the ventrolateral prestriate cortex (Mangun and Hillyard 1987, 1988, 1990a). In contrast, the subsequent negative deflection (the N1 wave at 140–190 msec) is of maximal amplitude over parietal scalp sites for stimuli at attended locations (Harter, Aine, and Schroeder 1982; Mangun and Hillyard 1987, 1990a; Neville and Lawson 1987). Harter and Aine (1984) proposed that this negativity reflects the initial selection of stimulus location in the posterior parietal cortex.

The objective of the first experiment presented in this chapter was to localize the brain generators of the attention-sensitive P1 and N1 components of the human ERP with greater accuracy than previous studies had achieved. We wanted to determine whether the attentional modulation of the P1 and N1 components could indeed be assigned to separate cortical areas, perhaps in different functional streams of visual processing. The first step was to investigate whether the P1 component is actually generated in the lateral prestriate cortex itself, as suggested by Mangun and Hillyard (1990b), or in the more mesial striate cortex that provides input to both the dorsal and ventral streams.

To address this question, we recorded ERPs from a closely spaced array of electrode sites over the posterior scalp while subjects performed a visual-spatial attention task. The electrode array allowed a detailed mapping of voltage and current density distributions to be obtained for the P1 and N1 attention effects. Separate stimuli were presented in each of the four quadrants of the visual field in order to activate discrete zones of the primary visual (striate) cortex.

The striate cortex has a unique anatomical organization that results in characteristic ERP patterns for stimuli presented to the four visual field quadrants. Specifically, the striate cortex is folded within the depths of the calcarine fissure on the mesial aspect of the contralateral visual cortex. As a result, portions of the upper and lower visual half-fields are mapped upon separate, opposing sheets of cortical tissue facing each other across the calcarine fissure (fig. 10.2). Because of the opposed orientation of these cortical slabs, ERP components generated in striate cortex can be identified by observing polarity reversals on the scalp for upper- versus lower-field stimuli (Jeffreys and Axford 1972; Butler et al. 1987). The present study exploited this unique situation in order to distinguish between striate and prestriate generators of attention-sensitive ERP activity.

Methods

Eight university students participated in the experiment as paid volunteers. Subjects reclined in comfortable chairs facing video monitors. They were required to maintain fixation of their eyes upon a central cross while white rectangular bars were flashed in random order to the four visual field quadrants (fig. 10.3, top). The subjects' task was to attend exclusively to the bars in one
Figure 10.2. Diagrammatic representation of the visual field (top) and its projection onto the striate cortex (bottom). The figure at bottom is a posterior view of a coronal section taken through the occipital pole. The left and right hemispheres are shown with the calcarine fissure as indicated. The striate cortex is represented in outline surrounding the left and right calcarine fissures. The numbers correspond to those on the visual field map (top) and indicate the regions of striate cortex that receive inputs from a given contralateral zone of visual space. Stimuli in the upper- and lower-right visual field quadrants (near positions 2 and 3) would produce activation of cortical neurons that were oppositely oriented with respect to one another within the depths of the calcarine fissure in the left hemisphere (arrows). Adapted after Butler et al. (1987).

selected quadrant (ignoring the other three) and to press a button upon detecting each of the occasional, shorter “target” bars presented there. Each quadrant was selectively attended in different runs of 50 sec duration each; a total of twelve runs was presented under each of the four attention conditions.

The bars were flashed to the four quadrants in random order at intervals varying randomly from 250–550 msec for 67 msec duration each. The bars were either 3.75 (standard) or 3.25 (target) degrees in height. In each quadrant, the centers of the bars were positioned 5.8 degrees lateral to the fixation point and 3.5 degrees above or below the horizontal meridian. Thus, the horizontal separation between the stimuli was greater than the vertical separation (fig. 10.3, top). The probabilities of the standard and target stimuli in each quadrant were 0.83 and 0.17, respectively. The stimulus sequences included single bars flashed to only one of the four quadrants at a time (two-thirds of the stimuli),
Figure 10.3 ERP changes in a spatial-attention task. Stimuli were presented in random order to the four quadrants of the visual field while subjects focused attention on one of the quadrants at a time for runs of 50 sec each. ERPs were recorded from 30 scalp sites (dots on the schematic head) and computer-averaged separately for each stimulus and attention condition. ERP waveforms are grand averages over all eight subjects in response to upper-left flashes under the four conditions of attention. The scalp distribution of the P1 component for attended upper-left flashes (measured at 108 msec) is shown on the rear view of the head with darker areas representing greater positive voltages. Interpolation between recording sites was done by the spherical spline method of Perrin et al. (1989).

and bilateral bars flashed to left and right quadrants simultaneously, either both above or both below the horizontal meridian. Only ERPs to the single-position, nontarget stimuli will be considered here; the averages computed from these trials yielded waveforms with the highest signal-to-noise ratios and were also free from motor-related potentials, since no overt responses were made to these stimuli. For each subject, ERPs were averaged over approximately 240 nontarget stimuli per quadrant for each attention condition.

ERPs were recorded from thirty scalp sites using tin electrodes mounted in an elastic cap. Eye movements and blinks were monitored by recordings of the vertical and horizontal EOG; eye fixation was additionally verified by horizontal and vertical infrared corneal reflectance. The half-amplitude recording
Table 10.1  Amplitudes of P1 and N1 Components for Standard Stimuli in Each of the Four Quadrants as a Function of Attention Condition. Mean Amplitudes (Base-to-peak Measures in Microvolts) over Eight Subjects

<table>
<thead>
<tr>
<th>Stimulus Location</th>
<th>Attended Location</th>
<th>Upper Left</th>
<th>Upper Right</th>
<th>Lower Left</th>
<th>Lower Right</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>0.68</td>
<td>1.38</td>
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<tr>
<td></td>
<td>Upper Right</td>
<td>0.40</td>
<td>1.29</td>
<td>1.04</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
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<td>0.70</td>
<td>0.49</td>
<td>1.82</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td>Lower Right</td>
<td>0.35</td>
<td>0.75</td>
<td>1.02</td>
<td>0.98</td>
</tr>
</tbody>
</table>

N1 Amplitude

<table>
<thead>
<tr>
<th>Stimulus Location</th>
<th>Attended Location</th>
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<th>Upper Right</th>
<th>Lower Left</th>
<th>Lower Right</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>−0.80</td>
<td>−1.69</td>
<td>−1.31</td>
</tr>
<tr>
<td></td>
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<td>−2.10</td>
</tr>
<tr>
<td></td>
<td>Lower Left</td>
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<td>−2.88</td>
<td>−1.90</td>
</tr>
<tr>
<td></td>
<td>Lower Right</td>
<td>−0.82</td>
<td>−0.91</td>
<td>−1.95</td>
<td>−2.71</td>
</tr>
</tbody>
</table>

bandpass for all sites was 0.01–100 hz. ERPs were computer-averaged for each stimulus type over epochs beginning 200 msec before stimulus onset and lasting for 1200 msec thereafter.

Results and Discussion

Grand average ERPs elicited by the bars flashed to the upper-left position are shown in figure 10.3 (bottom). As in previous studies, the amplitudes of the contralateral P1, N1, and N2 components increased when the subjects’ attention was directed to the location of the evoking stimuli (Eason 1981; Harter, Aine, and Schroeder 1982; Hillyard and Munte 1984; Mangun and Hillyard 1987, 1988, 1990a; Neville and Lawson 1987; Rugg et al. 1987; Van Voorhis and Hillyard 1977). The lines and shaded areas on the schematic head show iso-voltage contours for the P1 component. The locus of maximum P1 amplitude for the left-field stimuli was over the lateral occipital scalp of the right (contralateral) hemisphere. A smaller, mirror-image focus arose over the left (ipsilateral) scalp some 15–20 msec after the contralateral P1 maximum and most likely represents activation of the ipsilateral hemisphere via the corpus callosum (Mangun and Hillyard 1988; Rugg, Milner, and Lines 1985; Saron and Davidson 1989).

Table 10.1 presents the P1 and N1 amplitudes for all four stimulus positions and attention conditions. The tabled values were measured at the scalp site.
where each component was largest (lateral occipital for P1; occipitoparietal for N1). For the P1 component, the mean amplitude in response to the bars when in the attended quadrant was larger (1.36 uV) than the amplitude of the responses they elicited when attention was directed to any other quadrant; this difference was significant when attention was directed away from the evoking stimulus and to the other quadrant in the same visual half-field (0.87 uV, \( p < .05 \)), the opposite visual field at the same elevation (0.59 uV, \( p < .005 \)), and the diagonally opposite position (0.55 uV, \( p < .005 \)). For the N1 wave, the attended amplitude \( (-2.11 \text{ uV}) \) was similarly larger (more negative) than unattended amplitudes for the same-field \( (-1.45 \text{ uV}, \ p < .001 \), opposite-field \( (-1.50 \text{ uV}, \ p < .005 \), and diagonal \( (-1.04 \text{ uV}, \ p < .001 \) quadrants.

To localize the cortical generator(s) of the P1 component more precisely, voltage maps like those in figure 10.3 were transformed into current source density (CSD) maps. The CSD is calculated as the second spatial derivative of the voltage across the scalp. It provides a reference-free estimate of the instantaneous electrical currents flowing from the brain perpendicular to the scalp at each location at the specified time point (Nunez 1981). In comparison with voltage topographies, the CSD distributions emphasize superficial current sources, thus allowing more accurate localization of cortical ERP generators (Pernier, Perrin, and Bertrand 1988). Both the voltage and CSD maps shown here were calculated using the spherical spline interpolation algorithm developed by Perrin et al. (1989).

![Attended, Unattended, Difference](image)

**Figure 10.4** Scalp topography of grand average current source densities calculated for the P1 component (at 108 msec) in response to upper-left (UL) and upper-right (UR) stimuli. Separate CSD maps are shown for the P1 component elicited by those flashes when attended and when unattended (averaged over the 3 other attention conditions). At far right is the CSD distribution of the attention-related P1 difference formed by subtracting the ERPs in the unattended condition from those in the attended. The darkest zones represent current sources (currents flowing out of the head), whereas the lightest zones represent current sinks. Each map is individually scaled to indicate 10 levels of CSD between the minimum and maximum values observed for that map.
The CSD maps for the P1 component reveal a narrowly focused current source over the contralateral occipital scalp (fig. 10.4), with a maximum situated about 6 cm lateral to the midsagittal plane. The location of this source in response to a given stimulus remained the same whether it was attended or unattended. Accordingly, the location on the scalp of the current source in the attention-difference map (attended—minus unattended CSD maps) was similar to that of the sensory-evoked P1 component (i.e., the unattended P1 current source). This equivalence supports the “sensory gain” hypothesis (Mangun and Hillyard 1988, 1990b) that spatial attention acts to regulate the amplitude of sensory evoked activity in the visual pathways without engaging additional neural generators (in the latency range of the P1 wave).

Figure 10.5 shows that maximal current density for the P1 attention effect remained unchanged in polarity and was highly similar in location for upper-versus lower-quadrant stimuli; this was also true for the P1 distributions for the attended and unattended stimuli. Such an invariance suggests that the P1 effect is not generated in striate cortex, because according to the model illustrated in figure 10.2, a striate generator for P1 would lead to a marked shift in CSD distribution and/or polarity due to the opposed orientation of active cortical neurons for the upper versus lower visual field stimuli. Instead, these relatively invariant and sharply localized CSD distributions suggest a generator in lateral prestriate cortex.

Figure 10.5 Current source density maps for the P1 difference wave (attended minus unattended) for stimuli in each of the four quadrants. The location of the CSD maximum is most affected by the left or right visual field position of the stimulus, in accordance with the contralateral projection of the visual pathways. In contrast, upper versus lower field stimulus position had little, if any, effect on the locus of maximal CSD for the P1 component.
Figure 10.6  MRI scans of subject K.S.M. Image of midsagittal plane (left) shows depressions over posterior scalp where oil capsules were attached to identify midline electrode sites. Line through sagittal section indicates plane of horizontal section (right) that passes through lateral occipital electrode sites where the current sources of the P1 attention effect were maximal. Arrows indicate locations of maximum CSD for the P1 attention effect elicited by flashes in lower-left (ll), upper-left (ul), lower-right (lr), and upper-right (ur) quadrants. Note that the horizontal brain section is right-left reversed, as is conventional for MRI scans.

The relation of the CSD distributions at the scalp to the underlying cortical anatomy was studied further by obtaining magnetic resonance images (MR scans) of the experimental subjects' brains. During the MR procedure, several electrode sites were marked on the subjects' heads by attaching small oil capsules that could be visualized in the obtained images. This procedure allowed the surface CSD maps to be brought into register with specific cortical gyri and sulci visible in the MR images.

Figure 10.6 (right panel) shows an MR section from one subject in a near-horizontal plane passing through the locus of maximum current density for the P1 attention effect. The maximum CSD locus for upper-left (ul) and lower-left (ll) stimuli are similar to one another, as are those for upper-right (ur) and lower-right (lr) stimuli. The indicated areas are situated over the ventrolateral prestriate cortex, which contains areas 18 and 19 of the occipital lobe.

The relative locations of the CSD maxima for the P1 and N1 attention effects (averaged over all subjects) are shown in a lateral view of the left hemisphere in figure 10.7. The P1 current source was situated ventrolaterally relative to the N1 maximum (a current sink), which lay near the border of the occipital and posterior parietal lobes. This difference in distribution is in line with the idea that the P1 attention effect reflects modulation of information flow along the ventral prestriate stream of visual processing (Mangun and Hillyard 1990b), whereas the N1 enhancement may be a sign of stimulus selection processes in the more dorsal pathways directed towards the parietal lobe (Harter and Aine 1984). Consistent with this proposal, the onset latency of the P1 effect corresponds well with the average latency of evoked unit
Scalp Current Density

Figure 10.7 Superimposition of grand average CSD contours for P1 (P110) and N1 (N180) attention effects to upper-right stimuli upon a "classic" cytoarchitectonic map of the left hemisphere. The maximum CSD sink for the N1 effect is situated dorsally in relation to the CSD source of the P1 effect. This correspondence between the surface CSD and the underlying cortical areas must be considered approximate at present, since group-averaged ERP data were used and the relationship of electrode sites to Brodmann’s areas was based on the averaged radiographic data of Homan, Herman, and Purdy (1987).

discharge in monkey prestriate area V4, reported to be in the 70–80 msec range (Robinson and Rugg 1988; Fischer and Boch 1985; Moran and Desimone 1985), whereas the average latencies of posterior parietal units are some 10–15 msec longer. Given our current lack of knowledge about the functional neuroanatomy of the prestriate cortex in humans, however, the hypothesis that the P1 and N1 effects are indices of attentional processes in separate processing streams must be regarded as tentative.

Although the results presented in figures 10.3 to 10.6 are strongly supportive of the view that the attention-related enhancement of the P1 wave is generated in prestriate rather than striate cortex, the question remains as to whether the underlying stimulus selection process takes place within the prestriate cortex itself or at an earlier level of the visual pathways. Given the retinotopic organization of the visual afferent structures, attentional selection of inputs based on stimulus location could, in principle, be accomplished in primary visual cortex or even at subcortical levels and "passed along" to prestriate levels to become manifest as an amplitude modulation of the P1 component. Such a subcortical selection mechanism was proposed by Yingling and Skinner (1976) on the basis of their finding (in cats) that thalamo-cortical
transmission of sensory information could be controlled via inhibitory inputs from the thalamic reticular nucleus onto the thalamic relay neurons (see also Eason 1981; Crick 1984).

To gain further information about the anatomical level(s) at which spatial attention affects visual processing, the ERP waveforms of the present study were further examined for components showing polarity inversions for upper versus lower visual field stimuli that would be indicative of a striate cortex generator. As shown in figure 10.8, such a component was identified and was found to have a shorter latency than the P1 wave (onset at 50–60 msec, peak at 80–90 msec). This component, termed the NP80 wave, reversed its polarity from negative for upper-field stimuli to positive for lower-field stimuli. Further, its maximal amplitude was over parieto-occipital scalp sites near the midline, dropping off in amplitude toward the lateral occipital scalp sites where the P1 wave was largest. These characteristics of the NP80 are all consistent with a striate cortex generator; this wave probably corresponds to the Cl wave that was hypothesized by Jeffreys and Axford (1972) to originate in striate cortex.

Under the conditions of the present experiment, no attention-related amplitude enhancements could be observed for the NP80 component ($p > .10$ at parieto-occipital sites). Moreover, whereas the polarity of NP80 was inverted for upper- versus lower-field unattended stimuli ($p < .05$), the only effects of attention in this latency range (nonsignificant) could be ascribed to the leading edge of the positive-going enhancement of the P1 wave that began about 20 msec after the onset of the NP80 and was distributed more laterally on the scalp; in no case did the attention effect itself show a polarity inversion indicative of a striate cortex generator. Accordingly, these results are not supportive of an attentional gating mechanism at the level of the lateral
geniculate nucleus, since a subcortical modulation of visual input should affect striate cortex ERPs as well as subsequent prestriate activity. Rather, it appears that the earliest level where spatial attention modulates visual processing is in the prestriate cortex. This conclusion is consistent with studies in monkeys that found no evidence for attentional modulation of single-unit activity in primary visual cortex (Wurtz, Goldberg, and Robinson 1980; Moran and Desimone 1985). A recent study by Oakley and Eason (1990), however, did report significant changes in the time range prior to P1 in a spatial-attention paradigm, which suggests that the question of striate cortex involvement may need further study.

Although the present study obtained no evidence that spatial attention affects transmission through the lateral geniculate relay, this does not rule out an important role for the thalamus in the brain's attentional systems. Several lines of evidence have implicated the pulvinar nucleus in particular as playing a key role in stimulus selection processes in both monkeys (Desimone et al., in press; Peterson, Robinson, and Morris 1987) and humans (LaBerge 1990; Rafal and Posner 1987). According to recent proposals (Desimone et al., in press), projections from the pulvinar to prestriate cortex would have the capability of modifying visual processing at higher cortical levels without necessarily affecting transmission through the lateral geniculate relay. Such a mechanism would fit well with the present ERP results.

10.3 SPATIAL CUEING PARADIGMS

In order to test the generality of the ERP findings reported above, it was important to make comparable recordings from subjects performing in the spatial-attention paradigms most widely studied in the behavioral literature, which involve trial-by-trial cueing or priming procedures. In such designs, an initial cue or prime stimulus indicates the most likely location at which a subsequent test stimulus will occur (e.g., Posner 1980; Eriksen and Yeh 1985). Test stimuli presented to the precued (attended) location are generally detected and discriminated with greater speed and/or accuracy than are those at unattended locations. These behavioral effects have been attributed to improved sensory/perceptual processing by some authors (Posner 1980; Downing 1988) and to postperceptual factors such as decision bias by others (Shaw 1984; Sperling 1984).

Recordings of ERPs provide information relevant to this controversy. If the early, modality-specific ERP components could be shown to vary with spatial cueing, this would suggest an attention effect at the sensory/perceptual level. Although an early study of this type failed to observe significant effects on the P1 component during spatial cueing (Hillyard, Munte, and Neville 1985), that result may have been due to the somewhat long interval (1.8 sec) between the cues and targets that was used. More recent studies that employed cue-target intervals of 600–800 msec have indeed shown robust enhancement of the P1 component to targets at precued locations (Mangun, Hansen, and Hillyard 1987; Mangun and Hillyard 1991).
<table>
<thead>
<tr>
<th>Cue/Target Combination</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Valid Left</td>
<td>&lt; 0.375</td>
</tr>
<tr>
<td>Invalid Left</td>
<td>&gt; 0.125</td>
</tr>
<tr>
<td>Valid Right</td>
<td>&gt; 0.375</td>
</tr>
<tr>
<td>Invalid Right</td>
<td>&lt; 0.125</td>
</tr>
</tbody>
</table>

![Graph of ERP waveforms](image)

**Figure 10.9** Grand average ERPs for six subjects in a spatial cueing task in which subjects made simple reaction-time responses to both valid ($p = 0.75$) and invalid ($p = 0.25$) targets. ERPs were averaged separately for valid and invalid targets in left (LVF) and right (RVF) visual fields; the ERPs shown were recorded from the contralateral occipital scalp. Lateral eye movements were monitored by a high-gain EOG to ensure that subjects did not move their eyes toward the cued location. Data from Mangun and Hillyard (1991).

The effect of spatial cueing on P1 amplitude is illustrated in figure 10.9 for a simple reaction-time task (Mangun and Hillyard 1991). Each trial consisted of a cue and subsequent target stimuli. The cue (an arrow) appeared at fixation and indicated the most likely ($p = 0.75$) location of a subsequent target bar that was flashed to either the right or left visual field. The subjects had to make a speeded right-hand button press to all targets regardless of whether they occurred on the cued (valid) or uncued (invalid) side. Validly cued targets elicited significantly larger P1 components and shorter reaction times (230 vs. 254 msec). The later positive deflection that occurred 200–500 msec after the onset of the target stimulus is most likely a composite of a P3 (P300) component associated with the subjects' detection of the task-relevant target and the return to baseline of a prior negativity (CNV).

A similar enhancement of P1 amplitude for valid flashes has also been observed in a choice reaction-time task (fig. 10.10). The design of this experiment was equivalent to that illustrated in figure 10.9, except that subjects made a choice response based on the height of the target bar, pressing with the right hand for tall bars (2.1 degrees) and the left hand for short bars (1.9 degrees).
Figure 10.10 Grand average ERPs for fourteen subjects in a spatial cueing task where subjects made choice reaction-time responses to the target bars. Bars at both valid \((p < 0.75)\) and invalid \((p = 0.025)\) locations could be either “tall” or “short” (equiprobably), and subjects responded differentially according to bar height. ERPs were averaged over both tall and short bars and displayed as in figure 10.9. Topographic voltage maps (top view) are for the P1 validity effect measured as the P1 amplitude (112 msec) in the valid minus invalid difference wave. Maximum P1 enhancement for valid cues is over contralateral occipital scalp. Data from Mangun and Hillyard (1991).
In this choice task, unlike the simple reaction-time task, valid flashes elicited enlarged N1 as well as P1 components in association with faster reaction times (Mangun and Hillyard 1991). The voltage topography maps for the P1 attention effect show that the enhanced positivity was maximal over the same lateral occipital scalp sites as in the sustained attention tasks described in the previous section.

Harter and colleagues have observed similarly enhanced P1/N1 components for targets occurring at cued locations in a related design (Harter et al. 1989; Harter and Anlio-Vento 1991). In their task, a central arrow cue was followed 600 msec later by a target presented equiprobably to the left or right visual field; the subjects had to respond (finger-lift) to targets in the cued field but not to targets in the uncued field. The P1 and N1 amplitudes (measured peak-to-peak) were again most enlarged over the occipital scalp contralateral to the field of the attended target.

Importantly, Harter and his colleagues also identified slow lateralized ERPs within the cue-target interval. At around 200 msec postcue, a negative component appeared over the contralateral centroparietal scalp, which was interpreted as a sign of executive processes involved in directing attention in space. A later positive component (400 msec) was seen over the contralateral occipital scalp and was hypothesized to reflect the differential excitability of the visual projection pathways receiving input from relevant versus irrelevant visual fields.

The consistent finding in all these cueing studies of an enlarged P1 component over visual cortex for valid targets indicates that precueing of target location can facilitate sensory processing and does not act solely by biasing decision processes. This accords with recent observations that symbolic precues (e.g., arrows) can improve the detectability of near-threshold luminance targets at cued peripheral locations, an effect that cannot be accounted for by changes in decision bias (Downing 1988; Hawkins et al. 1990).

10.4 ATTENTION TO MULTI-ELEMENT STIMULUS ARRAYS

All of the ERP studies considered in the preceding sections used experimental designs in which single, isolated stimuli were presented to either attended or unattended locations in the visual fields. Although such designs do allow for the ready comparison of ERPs to attended versus unattended stimuli, they may not provide optimal conditions for spatial selection. There is considerable evidence, for example, that solitary stimuli presented in an “empty” visual field tend to draw attention to their locations automatically, regardless of whether or not they are supposed to be attended (Jonides 1981; Muller and Rabbitt 1989). In contrast, the selective processing of attended locations is generally facilitated when multiple stimuli are presented to different regions of the visual field simultaneously, and a subset of those stimuli is cued to receive attention (e.g., Jonides 1981; Eriksen and Yeh 1985). Experiments using multielement arrays have also revealed strong effects of spatial precueing on neural activity
in monkey prestriate cortex (Moran and Desimone 1985), which adds incentive to search for corresponding effects in human scalp recordings.

In several recent ERP studies, we have investigated the differential processing of attended and unattended subregions within multielement displays (Luck and Hillyard 1989; Heinze et al. 1990; Heinze, Mangun, and Hillyard 1990; Luck et al. 1990). These experiments exploit the predominantly contralateral organization of the projections of the left and right visual fields onto the cerebral hemispheres. Because of this organization, the early visual ERPs (P1 and N1) are generally largest over the hemisphere contralateral to the visual field of a lateralized stimulus. Thus, the two hemispheres would be activated approximately equally by a bilateral stimulus with equal physical energy in the left and right visual fields. However, if attention is directed selectively to one side of a bilateral display, and if attention acts by increasing the gain of the sensory pathways that carry information from the attended half-field, a relative enlargement should occur in the early ERPs over the hemisphere contralateral to the direction of attention.

In one experiment that followed this approach (Heinze et al. 1990), two pairs of letters were presented simultaneously on each trial, one pair on each side of the fixation point (see fig. 10.11, top). These bilateral arrays were presented at a varying rate (280–520 msec) and contained random letter combinations from the set E, L, T, F. Subjects were instructed to attend to the left or right side during a 30-sec stimulus sequence and to press a button whenever the two letters on the attended side were identical (targets); identical letter pairs could also occur on the unattended side but did not require a response.

Figure 10.11 (bottom) shows the ERPs recorded over the visual areas of the left and right hemispheres when subjects attend to either the left or right half of such displays. The amplitude of the P1 component over a given hemisphere was significantly larger (p < .001) when the contralateral visual hemifield was being attended. This effect is further illustrated by the CSD maps of the P1 component shown in figure 10.11 (middle). The bilateral stimuli produced a current source in both hemispheres, overlying the prestriate visual cortex, but the source was stronger over the hemisphere contralateral to the direction of attention. In contrast to the P1 component, however, there was no tendency for the N1 component to be enlarged over the contralateral hemisphere. Rather, during the N1 latency range the waveforms obtained over the scalp site contralateral to the attended field remain more positive.

As a further index of lateralized attention to these displays, ERPs were recorded to irrelevant, unilateral rectangular “probe” flashes randomly interspersed within the sequences of bilateral letter stimuli. These white probes were flashed to either the right or left letter-pair locations but did not disrupt the assigned task of detecting letter matches. Again, the P1 component was considerably enlarged over the contralateral occipital scalp (p < .005) for probes presented to the attended versus unattended half-fields (fig. 10.12, top). This finding strongly supports the hypothesis that P1 modulation reflects an
early selection for location that is applied equally to task-irrelevant probes and task-relevant letters. Once again, however, there was a conspicuous absence of any enhancement of N1 amplitudes to attended-field probes. As in figure 10.11, the waveform for attended-side probes remained more positive throughout the P1 and N1 latency ranges.

The strong spatial selection produced in this task was also evident in the ERPs to the letter-match stimuli (fig. 10.12, bottom). Letter matches (targets) in the attended field elicited an enlarged contralateral N2 wave at 250–350 msec followed by a P3 or P300 component at 400–600 msec. However, these late endogenous components were greatly reduced when letter matches occurred in the unattended field. The diminished N2 amplitude is of particular interest, since the visual N2 component has been interpreted as a sign of stimulus classification processes that may proceed automatically outside the focus of attention (Ritter, Vaughan, and Simson 1983; Wijers et al. 1987). Yet in the present study, there was little sign of any automatic classification of stimuli (targets vs. nontargets) at the unattended location. We consider this as evidence for the efficiency of the early spatial selection in preventing the
transmission of information from the unattended half of the display to higher levels of pattern analysis and target classification indexed by the N2 and P3 components.

A further study was undertaken to examine the perceptual correlates of this focusing of attention upon one-half of a bilateral array (Heinze, Mangun, and Hillyard 1990). In this study, bilateral arrays of four “nonsense” symbols (two in each half-field) were flashed in rapid succession. The subjects had to focus attention on the symbol pairs on one side and make a match/mismatch judgment about occasional unilateral “target” symbols that would occur on one side or the other at random. As before, the unilateral target elicited a much larger P1 component when they occurred on the attended side. In conjunction with this P1 enhancement was a marked improvement in sensitivity (d') for matching targets to the preceding symbols; no significant attention effects were observed in decision criterion (Beta). These results support the view that the contralateral P1 enhancement observed for bilateral arrays and unilateral
probes is associated with improved perceptual information from the attended locations.

10.5 GENERAL DISCUSSION

The ERP data described here strongly support the hypothesis that early selection in modality-specific cortex is a basic property of human visual-spatial attention. In three different types of paradigms, involving either sustained or precued focusing of attention upon a designated location, it was found that attended stimuli elicit an enlarged P1 component over the contralateral occipital scalp. The short latency of this P1 effect (onset at 70–90 msec) and its localization over ventrolateral prestriate cortex are consistent with an attentional process that modulates the flow of information arising from attended versus unattended locations (Eason 1981; Mangun and Hillyard 1990b). The stability of the earlier NP80 component attributed to the striate cortex suggests that spatial attention does not affect transmission through the lateral geniculate nucleus or the primary visual cortex but acts instead at higher, prestriate levels.

The finding that the contralateral P1 component was similarly enlarged for both relevant (patterned) and irrelevant (bar probe) stimuli flashed to the attended side of a bilateral display provides further evidence for an early selection process based solely on location (Heinze et al. 1990). The consequences of this early selection process were evident in both the reduced perceptual accuracy for detecting targets at unattended locations and in the diminished amplitudes of later, decision-related ERP components observed for unattended targets (Heinze, Mangun, and Hillyard 1990; Mangun and Hillyard 1990a, 1990b). These ERP findings converge with recent behavioral evidence indicating that spatial attention can affect the quality of sensory/perceptual information in the visual pathways (Downing 1988; Hawkins et al. 1990; Reinitz 1990).

The dissociation of the P1 and N1 attention effects observed in different task conditions raise the possibility that these ERPs index the operation of different attentional systems. Whereas the P1 effect was present in all of the spatial-attention paradigms considered here, the N1 effect was found to be greatly reduced or absent under conditions where (1) the target at a precued location did not need to be discriminated, (2) the stimulus sequence consisted mainly of bilateral arrays, and (3) a unilateral attended stimulus was immediately preceded by another stimulus at the same location (Luck et al. 1990). One possible interpretation would be that the N1 component is enlarged under conditions in which a stimulus calls for a switching or additional allocation of attention to its location, thereby allowing a further analysis of its features and properties. This interpretation of the N1 effect fits with evidence from single-unit recordings (Wurtz, Goldberg, and Robinson 1980) and studies of human patients (Posner et al. 1984, 1987), which point to a key role for the dorsal (posterior parietal) pathways in redirecting attention in space. Thus, while the
P1 attention effect is interpreted to be a reflection of preset changes in the gain of certain prestriate neurons during spatial attention, the N1 attention effect may signify the operation of a partially or completely independent parallel system that acts to allocate further attentional resources to the processing of the task-relevant stimulus.

Topographical CSD analyses indicated that the N1 attention effect arose from generators situated more dorsally than those of the P1 effect. This anatomical segregation suggests the intriguing possibility that the P1 effect may reflect attention-related modulation of activity along the ventral stream of visual processing that projects to the inferior temporal lobe and carries out object recognition functions. In contrast, the N1 effect may reflect the spatially selective functions of the dorsal stream that projects to the inferior parietal lobe. Such a correspondence is consistent with findings that spatial attention modulates neuronal responsiveness in monkeys along both the ventral (area V4, temporal lobe) and dorsal (posterior parietal lobe) pathways at latencies analogous to the human P1 and N1 components (Desimone and Ungerleider 1989; Robinson and Rugg 1988; Wurtz, Goldberg, and Robinson 1980).

While the above considerations conform well with the proposed assignment of the P1 and N1 attention effects to different attentional subsystems, additional work is also required to link them specifically with the ventral and dorsal processing streams identified from studies in monkeys. In particular, studies that combine the several imaging technologies now available for human research (ERPs, MEG, PET, and MRI) with neurophysiological and anatomical tracing studies in animals are required to expand and refine these proposals.

NOTES

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1. There is no uniform nomenclature used in the ERP literature. However, many authors label their ERP components using "P" or "N" to indicate positive or negative polarity components, respectively, and either a latency value or digit to indicate the time or order of appearance of the component within the waveform. Thus, "P1" designates a component that is the first major positive deflection in the visual ERP under the present conditions. The reader is cautioned not to assume that the P1 component defined here is necessarily the same as the P100 component elicited by pattern-reversal stimuli, or the C1 component described in early visual ERP studies (e.g., Jeffreys and Axford 1972; see text). The relationships among the various ERP components described in the literature can only be established by careful comparisons of their behavior over a range of stimulus and task parameters.

2. The data presented in figure 10.11 are actually from a related study (Heinze, Mangun, and Hillyard 1990) that utilized a similar design to that of Heinze et al. (1990). The effects described were identical in the two studies. These data were used in figure 10.11 because more scalp sites were recorded, and thus, it was more valid to plot the data as topographic CSD maps.
REFERENCES


Mangun, Hillyard, and Luck


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Electrocortical Substrates of Visual Selective Attention


