Visual event-related potentials index focused attention within bilateral stimulus arrays. II. Functional dissociation of P1 and N1 components

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(Accepted for publication: 8 September 1989)

Summary
Event-related potentials (ERPs) were recorded from 12 subjects as they attended to the left or right hemifield of a visual display while fixing a central point. Stimuli were presented to the left or right visual fields on separate trials (unilateral stimuli) or to both fields simultaneously (bilateral stimuli). In different conditions, the stimulus sequences contained only bilateral stimuli, only unilateral stimuli, or a mixture of unilateral and bilateral stimuli.

Bilateral stimuli elicited an enhanced positivity lasting from about 75 to 250 msec that was largest at posterior electrode sites contralateral to the attended hemifield. The early phase of this attention-related positivity appeared to be an enhancement of the exogenous P1 component. In contrast, both the posterior P1 and N1 components were enhanced in response to attended unilateral stimuli. Moreover, the N1 attention effect was reduced when the preceding stimulus contained elements in the attended field. It was concluded that modulations of the N1 and P1 components in these experiments represent different aspects of visual spatial attention: N1 may represent the orienting of attention to a task-relevant stimulus, whereas P1 may represent a facilitation of early sensory processing for items presented to a location where attention is already focused.

Key words: Selective attention; Bilateral stimuli; Event-related potentials

In the preceding study (Heinze et al. 1990), event-related potentials (ERPs) were recorded from subjects as they focused attention upon a spatially discrete region of a multi-element visual display. The bilateral stimuli each consisted of 2 letters in the left visual field and 2 letters in the right, and subjects were required to attend to the letters in 1 hemifield, ignoring the other. ERPs were recorded to sequences of these task-relevant bilateral stimuli as well as to occasional unilateral ‘probe’ stimuli that were randomly interspersed in either the attended or unattended hemifield. Since the early attention-related changes in the ERPs are typically larger at scalp sites contralateral to the attended visual field (Mangun and Hillyard 1987, 1988), attend-left and attend-right conditions were expected to produce opposite patterns of hemispheric asymmetries in the early ERP components.

It was found that both the bilateral letter arrays and the unilateral probes elicited an enhanced early positivity in the ERPs that was larger over the contralateral scalp and coincided temporally with the P1 wave (onset at 90–100 msec). In the case of the probes, the attention-related positivity extended into the latency range of the N1 (150–200 msec) and P2 (200–250 msec) components as well. This contrasts with the enhancement of both P1 and N1 components that has typically been observed for attended field stimuli in experiments that presented unilateral stimuli to attended and unattended locations in random order (Eason et al. 1969; Eason 1981; Harter et al. 1982; Hillyard and Münte 1984; Mangun and Hillyard 1987; Neville and Lawson 1987; Rugg et al. 1987).

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The present study investigates alternative explanations for the different patterns of ERP attention effects observed in sequences of unilateral versus bilateral stimuli. Both the stimuli and the task used by Heinze et al. (1990) were somewhat different from those used in previous studies, and one goal of the present study was to replicate their exclusively positive early attention effect using bilateral stimuli that were shown by Mangun (1987; see also Mangun and Hillyard 1990) to produce both P1 and N1 enhancements when presented unilaterally. Heinze et al. proposed that the early contralateral positivity they observed consisted of the same enhanced P1 wave typically found for attended unilateral stimuli, followed by a more extended positivity, and lacking an N1 enhancement. They suggested that the N1 may represent the orienting or engaging of an attentional system, and that this orienting may be reduced in sequences of bilateral stimuli due to the simultaneous occurrence of elements in both the attended and unattended fields. In particular, the frequent repetition of attended field elements may allow attention to remain engaged at the attended location throughout the stimulus sequences, thus obviating the need for re-orienting. In contrast to the N1, the P1 wave was proposed to represent a facilitation of sensory input for stimuli occurring in the attended location, a process that operates similarly for both bilateral and unilateral stimuli.

These proposals were investigated in a spatial attention task that compared stimulus sequences composed of only bilateral stimuli, only unilateral stimuli, or mixed sequences of both. If bilateral stimuli minimize the re-orienting of attention and therefore the N1 attention effect, then there should be a larger N1 effect for unilateral stimuli in sequences composed entirely of unilateral stimuli than for unilateral stimuli in sequences that include bilateral stimuli. Similarly, the N1 attention effect should be larger for bilateral stimuli in mixed sequences than for bilateral stimuli in sequences composed entirely of bilateral stimuli. As a further test of this idea, a sequential analysis of the ERPs to unilateral stimuli was conducted. If the N1 enhancement is associated with the re-orienting of attention, this attention effect should be largest when an attended-field stimulus is preceded by an unattended-field stimulus; in contrast, when an attended-field stimulus is preceded by an attended-field or bilateral stimulus, attentional re-orienting would be reduced or even eliminated and the N1 attention effect should be minimized.

Previous studies have proposed that the increased positivity evident for attended stimuli in the P1 latency range represents an amplitude modulation of the exogenous P1 wave (Hillyard and Mangun 1987; Mangun and Hillyard 1988). This proposal may be questioned by the results of the study of Heinze et al., in which the attention effect was manifested as a broad positivity lasting much longer than the P1 wave. This positivity may consist of a unitary endogenous wave, or it may represent a modulation of the exogenous P1 wave overlapped with a later positivity. These possibilities were tested by comparing the scalp distributions of the attention effect and the unattended P1 wave and assessing the existence of different generator sources. In addition, a principal components analysis was conducted to determine if the attention-related positivity elicited by bilateral stimuli behaves as a unitary component or if it can be broken down into functionally distinct subcomponents.

Methods

Subjects

Twelve undergraduate and graduate students (7 male) were paid to participate in this experiment. The subjects were between 18 and 26 years old, were right-handed, and had normal or corrected-to-normal vision. Two original subjects were unable to maintain fixation and were replaced.

Stimuli

The stimuli in this experiment consisted of unilateral or bilateral arrays containing the letters F and L, with 4 letters per side (cf., Mangun 1987). The letters were arranged in a circle or hemi-circle with a radius of 3° around a central fixation point (see Fig. 1). Each letter was 0.7° high and 0.5° wide. The assignment of Fs and Ls to each of the
positions varied randomly from one stimulus to the next. For 20% of the stimuli, one of the positions contained a T rather than F or L; these were the targets. The stimuli were presented at a distance of 85 cm on a black and white computer monitor. The inter-stimulus interval varied randomly between 310 and 450 msec and the stimuli were presented in runs of 240 trials, each lasting 90 sec.

Procedure

At the beginning of each run, subjects were instructed to attend to either the left or right visual hemifield for that run and to press a button whenever the target letter, T, was detected in the array on the attended side. Subjects were told not to respond to stimuli containing the target letter on the unattended side (the term ‘target letter’ refers to the letter T occurring on either the attended or unattended side, although this letter was not responded to when it occurred on the unattended side). Accuracy was stressed rather than speed. Half of the subjects pressed with the left hand and half with the right hand. A T occurred on the attended side for 10% of the total stimuli (i.e., 20% of the attended-side stimuli). At the beginning of the experiment, subjects were told that they must always look directly at the fixation point and that the experimenter was monitoring eye position via electrodes placed around the eyes. Throughout the experiment, subjects were reminded to maintain fixation. Whenever eye movements were detected in the EOG recordings, the subject was gently reprimanded and that run was thrown out and replaced later in the session.

There were 3 main conditions, and each was run under attend-left and attend-right instructions. The conditions differed in the types of stimulus sequences presented: they were either all bilateral, all unilateral (50% left and 50% right), or mixed bilateral and unilateral (33% bilateral, 33% left unilateral, and 33% right unilateral). In order to present roughly 500 instances of each non-target stimulus type for each condition, there were 6 runs with all-bilateral stimuli, 12 runs with all-unilateral stimuli, and 16 runs with mixed bilateral and unilateral stimuli. The order of runs was randomized across subjects. Subjects were given short rest periods after each run to avoid eye fatigue.

Recording

The EEG was recorded from F3, F4, C3, C4, P3, P4, O1, O2, T5, T6, and A2 sites (international 10–20 system), all referenced to A1. The ERPs were algebraically re-referenced to the average of A1 and A2 off-line. The recordings were made through tin electrodes mounted in an electrode cap (Electro-Cap International). The horizontal EOG was recorded between the left and right outer canthi to monitor lateral eye movements, and the vertical EOG was recorded from beneath the left eye (referenced to A1) to monitor blink activity. The EEG and EOG recordings were amplified with an 8 sec time constant and a 60 Hz low pass filter (frontal and central sites) or with a 9.2 sec time constant and a 100 Hz low pass filter (all other sites). The EEG and EOG were digitized at 256 Hz by a minicomputer and stored along with behavioral responses on digital tape for off-line analysis.

The EEG was averaged off-line using an automatic artifact detection system that rejected trials with eye movements or blinks. The rejection criteria were adjusted for each subject on the basis of visual inspection of his or her single-trial wave forms. The different filter configurations were due to differences in the available settings on the amplifiers. These differences were isolated to the extreme ends of the bandpass range and should have little effect on the intermediate frequency ERP components that are of interest in the present study.
forms. Trials with incorrect behavioral responses were also excluded from the averages. Responses to targets were considered hits only if they occurred between 200 and 800 msec after stimulus onset.

**ERP measures**

The amplitudes of the ERP components were quantified in terms of mean voltage within a specified latency range (peak amplitudes were also measured and produced essentially identical results). The latency ranges were 75–125 msec for P1, 125–175 msec for N1, 175–225 msec for P2, 250–325 msec for N2, and 350–800 msec for P3. The data were analyzed with repeated measures analysis of variance (ANOVA); the P values were adjusted for heterogeneity of variance and covariance by the Greenhouse-Geisser epsilon coefficient (Jennings and Wood 1976). Multiple comparisons were controlled for familywise error by use of the Bonferroni test (Keppel 1982). ERPs to bilateral and unilateral stimuli were analyzed separately. Because the early components in this experiment appeared only at posterior sites, data from the frontal and central sites were only included for measures of the N2 and P3 components.

ERPs to bilateral stimuli that did not contain the target letter were analyzed with 4 factors: sequence type (all-bilateral vs. mixed bilateral and unilateral); attention direction (attend to the ipsilateral vs. contralateral visual field relative to the electrode location); hemisphere (left vs. right electrode placements); and electrode site (parietal vs. occipital vs. temporal). A fifth factor, target letter position (attended vs. unattended side), was added for analyses of stimuli containing the target letter. Unilateral ERPs were analyzed with 5 factors: sequence type (all-unilateral vs. mixed bilateral and unilateral); attention (stimulus in attended field vs. unattended field); contralaterality (recording site ipsilateral vs. contralateral to the stimulus); hemisphere (left vs. right); and electrode site (parietal vs. occipital vs. temporal). Separate ANOVAs utilizing these factors were conducted for stimuli that contained the target letter and for stimuli that did not.

**Sequential analysis**

An analysis of stimulus order effects on the ERPs was carried out on the unilateral stimuli from the mixed and all-unilateral sequences. Trials were sorted on the basis of whether the preceding stimulus was a unilateral on the same side, a unilateral on the opposite side, or a bilateral (this third category was obviously not present for all unilateral sequences). Trials preceded by stimuli containing the target letter were not included. Separate ANOVAs were conducted for the mixed and all-unilateral sequences because of the additional type of preceding stimulus possible for mixed sequences. The ANOVA design was identical to that described for unilateral stimuli above, except that the factor representing sequence type was replaced by a factor representing the type of preceding stimulus (same side, opposite side, or bilateral).

**Scalp distribution comparisons**

The scalp distributions of the P1 component and the attention effect in the P1 latency range were compared for bilateral stimuli in order to investigate whether the attention effect represents a modulation of the same generator source that produces the P1. Since the bilateral stimuli contained elements in both the attended and unattended visual fields, the amplitude at sites ipsilateral to the attended field was used as the measure of the ‘unattended’ P1, and the amplitude difference between the sites contralateral and ipsilateral to the attended field was used as the measure of the attention effect. These measures were analyzed with the same ANOVA factors as the bilateral ERPs.

The attention difference waves and the original ERP waves appeared to be differentially affected by the presence of overlapping components, and a different set of peak measures was therefore necessary for the above-described scalp distribution comparisons to reduce these distortions. There were 2 sources of overlap for the P1: the N1 that followed the P1, and unresolved activity from the preceding trial. The former was mitigated by measuring mean amplitude during the earliest phase of the P1 (60–100 msec post stimulus) and the latter
by using the interval immediately preceding P1 onset as the baseline \((0-40 \ \text{msec} \ \text{post stimulus})\).

A procedure similar to the method described by McCarthy and Wood (1985) was used to scale the amplitude values for the scalp distribution analysis. In particular, for each condition, the amplitude at each site was expressed as a \(z\) score: the mean for the condition was subtracted from each score, and the result was divided by the standard deviation. This scaling procedure necessarily eliminates any group differences, but allows an accurate test of interactions involving scalp distribution, which are multiplicative rather than additive (see also Hansen and Hillyard 1980).

**Results**

**Unilateral versus bilateral attention effects**

The ERPs elicited by unilateral stimuli not containing the target letter are plotted in Fig. 2 (except as noted, all figures and analyses presented here refer to stimuli that did not contain the target letter). As in previous spatial attention studies, the unilateral stimuli elicited larger P1 and N1 components when attended than when unattended, with the attention effects being largest at temporal and occipital scalp sites contralateral to the stimuli. This was reflected by significant attention \((P < 0.05)\) and attention \(\times\) contralaterality \((P < 0.005)\) effects for the P1 measure and a significant attention \(\times\) contralaterality effect for the N1 measure \(^2\) \((P < 0.05)\). There was also a broader, bilaterally symmetrical negative deflection beginning around 200 msec that was larger for attended than unattended stimuli at occipital and temporal sites; this resulted in an attention \(\times\) electrode site interaction in the 225–350 msec latency range \((P < 0.01)\). These results are highly similar to other studies of spatial attention that utilized unilateral stimuli.

\[^2\]The main effect of attention did not reach significance for the N1 measure, probably due to a small polarity reversal over the ipsilateral scalp sites in the all unilateral condition (Fig. 2). A separate ANOVA limited to the contralateral electrode sites did show a significant main effect of attention for the N1 measure \((F (1, 11) = 5.56, \ P < 0.05)\).

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Fig. 2. Grand-average ERPs elicited by unilateral non-target stimuli in all-unilateral sequences (top row) and mixed sequences (bottom row). ERPs for unattended stimuli are plotted with dashed lines and ERPs for attended stimuli are plotted with solid lines. The left column displays ERPs from temporal electrodes contralateral to the position of the stimulus and the right column displays ERPs from ipsilateral temporal electrodes.

The attention effects for bilateral stimuli, plotted in Fig. 3, were quite different. For both bilateral and mixed sequences, there was an enlarged positivity at scalp sites contralateral to the attended visual field extending from about 75 to 250 msec post stimulus. This attention-related positivity extended over the approximate latency range of the P1, N1, and P2 peaks. This effect was largest at occipital and temporal sites, smaller at parietal sites, and absent at central and frontal sites. The main effect of attention (i.e., the difference between sites ipsilateral versus contralateral to the attended side) was significant for this positivity in the latency ranges of the P1 (75–125 msec; \(P < 0.001)\), N1 (125–175 msec; \(P < 0.02)\), and P2 (175–225 msec; \(P < 0.05)\) waves; the interaction between attention and electrode site was significant in the P1 \((P < 0.002)\) and N1 \((P < 0.01)\) latency ranges. The attention effects for the N1 measure were, of course, caused by the attention-related positivity extending through the N1 latency range rather than an increase in N1 amplitude for attended stimuli. These results demonstrate that the broad, asymmetrical,
attention-related positivity observed by Heinze et al. (1990) for bilateral letter pairs can also be elicited by stimuli that produce the typical P1/N1 attention effects when presented unilaterally.

**Effects of sequence type**

The N1 wave for unilateral stimuli was significantly larger for the all-unilateral sequences than for the mixed sequences \( (P < 0.002) \), and the N1 attention effect was also significantly larger \( (P < 0.05) \) and more contralateral \( (P < 0.001) \). There was no significant effect of sequence type in the P1 latency range, however. Thus, the N1 attention effect was larger (more negative) in sequences with a higher proportion of unilateral stimuli, while the P1 attention effect was essentially unchanged.

A similar pattern of effects was evident for the bilateral stimuli. The N1 peak was generally larger for the mixed sequences than for the all-bilateral sequences (Fig. 3), resulting in a significant main effect for sequence type \( (P < 0.05) \) and a significant sequence type x scalp site interaction \( (P < 0.02) \). Moreover, the attention-related positivity was considerably reduced in the N1 latency range, resulting in a significant interaction between sequence type and direction of attention \( (P < 0.05) \) and a significant interaction of those two factors and electrode site \( (P < 0.05) \). However, the attention effects were not altered by sequence type in the P1 or P2 latency ranges. This pattern of results appears to indicate the emergence of an N1 attention effect for bilateral stimuli when they were interspersed with unilateral stimuli, resulting in a diminution of the attention-related positivity in the N1 latency range.

**Sequential analysis**

Fig. 4 shows the ERP wave forms sorted as a function of stimulus sequence in the all-unilateral condition. Each ERP wave form is labeled by a letter pair (e.g., U.A), where the second letter

\[
\begin{align*}
\text{Contralateral} & \quad \text{Ipsilateral} \\
\text{---} & \quad \text{-----} \\
0 & \quad 200 & \quad 400 & \quad 1.0 \mu V
\end{align*}
\]

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![Fig. 4](image)

Fig. 4. Grand-average ERPs from contralateral temporal scalp sites for the all-unilateral sequences, grouped according to stimulus sequence. The solid lines represent ERPs to attended stimuli and the dashed lines represent ERPs to unattended stimuli. A: ERPs to attended preceded by attended (A.A) stimuli overlapped with ERPs to unattended preceded by unattended (U.U) stimuli. B: ERPs to attended preceded by unattended (U.A) stimuli overlapped with ERPs to unattended preceded by attended (A.U) stimuli. The wave forms are collapsed over left and right electrode sites.
designates the evoking stimulus as attended (A) or unattended (U) and the first letter similarly designates the immediately preceding stimulus. The ERPs in Fig. 4 are plotted so that attended and unattended wave forms for the same physical stimulus order are overlapped; that is, the stimuli and their order of occurrence were identical for attended preceded by attended (A.A) and unattended preceded by unattended (U.U) stimuli. A similar equivalence was maintained for attended preceded by unattended (U.A) and unattended preceded by attended (A.U) stimuli. This method of comparison was used in order to avoid the confounding of sequential effects with refractory effects.

The attention effect for the A.A versus U.U stimuli was very similar to the attention effect observed for bilateral stimuli, a positivity extending from the latency range of the P1 into the latency range of the P2, with no enhancement of the N1 wave. The attention effect for the U.A versus A.U stimuli, however, was dominated by a large N1 enhancement, while the P1 attention effect was eliminated. These effects resulted in significant stimulus order × attention × electrode site interactions for both the P1 measure \( (P < 0.02) \) and the N1 measure \( (P < 0.01) \) and an interaction of these factors with contralaterality for the N1 measure \( (P < 0.05) \).

A similar pattern of results was obtained for unilateral stimuli in the mixed sequences, shown in Fig. 5. Only an N1 enhancement was present for A.U compared to U.U stimuli, whereas a broad positivity was elicited by A.A compared to U.U stimuli. An attention-related positivity was also observed when the preceding stimulus was bilateral. These effects produced significant atten-
tion \times stimulus order \times electrode site interactions for the P1 (P < 0.05), N1 (P < 0.02), and P2 (P < 0.02) measures. These data indicate that the N1 attention effect is reduced when the previous stimulus contained elements in the same visual field.

Because the sequential analysis required a subdivision of the stimulus events, the ERP averages were derived from a fairly small number of trials and hence have relatively low signal-to-noise ratios. In particular, the P1 wave appeared to be distorted by the presence of baseline variations during the first 100 msec. In order to determine the reliability of the stimulus order effects described above, we conducted a sequential analysis using a more extensive data set from an experiment by Mangun (1987). These data were collected under conditions virtually identical to the all-unilateral condition of the present experiment, except that electrode sites halfway between the temporal and occipital sites were utilized instead of T5 and T6, and larger numbers of stimulus presentations and subjects were used.5

The wave forms from this additional data set are presented in Fig. 6. As in the sequential analysis of the data from the present experiment, the N1 attention effect was larger when the preceding stimulus occurred on the opposite side, resulting in a significant attention \times stimulus order \times contralaterality interaction (P < 0.001) and an interaction of these factors with electrode site (P < 0.001). Additional analyses indicated that the attention \times contralaterality and attention \times contralaterality \times electrode site interactions were significant for the U.A versus A.U comparison (P < 0.001), but not for the A.A versus U.U comparison (P > 0.30). Unlike the previous sequential analysis, however, the P1 attention effect was not significantly larger when the preceding stimulus was on the same side, and was actually somewhat larger when the preceding stimulus was on the opposite side. The inconsistent results for the P1 wave indicate that the effects of stimulus order on the P1 attention effect must be considered unreliable and/or subject to subtle unknown factors that distinguished the two experiments. However, the effect of sequential order on the N1 attention effect was clearly replicated in these data.

**Scalp distributions**

In order to test the hypothesis that the early portion of the attention-related positivity for bilateral stimuli represents a modulation of the exogenous P1 component, the scalp distribution of the P1 attention effect (i.e., the difference between contralateral and ipsilateral sites in the P1 latency range) was compared to the scalp distribution of the 'unattended' P1 wave (i.e., the P1 measure at ipsilateral sites). When expressed as a percentage of occipital amplitude, the P1 attention effect was 42% at parietal sites and 73% at temporal sites, while the ipsilateral P1 amplitude was 33% at parietal sites and 75% at temporal sites (averaging

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5 The study of Mangun (1987) had 5 attention conditions: attend 100% left; attend 75% left and 25% right; attend 50% left and 50% right; attend 25% left and 75% right; and attend 100% right. Only the attend 100% left and attend 100% right conditions were analyzed for sequential effects here. Sixteen subjects were used (compared to 12 in the present study), and each ERP average in the sequential analysis was derived from approximately 200 stimuli (compared to approximately 125 in the present study). The latencies of P1 and N1 were longer in the Mangun study, so slightly different measurement windows were used: 85–135 msec for P1; 155–205 msec for N1.
over left and right electrode pairs). The corresponding interaction between attention and electrode site was not significant \((P > 0.40)\), consistent with the hypothesis of a single generator source for both the P1 and the early positive attention effect. Additional evidence for a common source was provided by the principal components analysis (see Appendix), in which the P1 wave and the early phase of the attention effect were represented by a single component and the late phase of the attention effect was represented by a separate component.

**ERPs to target stimuli**

ERPs to bilateral stimuli that contained the target letter in either the attended or unattended visual field are compared with non-target ERPs in Fig. 7. The ERPs elicited by arrays containing the target letter in the unattended field were essentially identical to the ERPs elicited by non-targets. In contrast, the ERPs elicited by bilateral arrays containing an attended-field target were similar to non-target arrays only during the P1 and N1 latency ranges; an N2 wave began to emerge at about 200–250 msec in the target ERPs at posterior scalp sites contralateral to attended field. This lateralized wave, elicited specifically by attended-field targets, resulted in a significant interaction between attention, contralaterality, and electrode site for both bilateral \((P < 0.05)\) and unilateral \((P < 0.02)\) targets. Attended-field targets also elicited A, large P3 component was also elicited by stimuli containing the target letter in the attended field, but no P3 activity was evident when the target letter occurred in the unattended field, resulting in significant main effects of attention for both bilateral \((P < 0.001)\) and unilateral \((P < 0.001)\) stimuli. There were no significant interactions involving contralaterality for the P3 measure.

**Behavioral performance**

In order to assess the relationship between the ERP attention effects and behavioral responses, 3 measures of target detection performance were calculated: reaction time relative to target onset; target detection accuracy (quantified as the \(d'\) measure of sensitivity); and response bias (quantified as the beta measure of decision criterion). The

<table>
<thead>
<tr>
<th>Sequence type</th>
<th>Bilateral stimuli</th>
<th>Unilateral stimuli</th>
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<tbody>
<tr>
<td></td>
<td>RT</td>
<td>(d')</td>
</tr>
<tr>
<td>All bilateral</td>
<td>501</td>
<td>2.2</td>
</tr>
<tr>
<td>Mixed</td>
<td>493</td>
<td>2.4</td>
</tr>
<tr>
<td>All unilateral</td>
<td>–</td>
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**TABLE II**

Behavioral performance in the mixed and unilateral sequences as a function of the preceding stimulus.
mean performance results are presented in Table I. For bilateral stimuli, subjects were significantly more accurate ($P < 0.001$) and nearly significantly faster ($P < 0.06$) in the mixed sequences than in the all-unilateral sequences, but there were no significant effects for response bias. For unilateral stimuli, subjects were faster ($P < 0.002$) and had a lower criterion ($P < 0.05$) during the all-unilateral sequences than during the mixed sequences, but accuracy was not significantly affected by sequence type. In general, subjects were faster and/or more accurate as the proportion of bilateral stimuli within the sequence decreased.

A sequential analysis of detection performance was also conducted, as summarized in Table II. In the mixed sequences, detection accuracy was higher ($P < 0.0001$) and decision criterion was lower ($P < 0.02$) when the preceding stimulus was unattended. Reaction time was also faster, but this effect did not approach significance. In the all-unilateral sequences, detection accuracy was also higher ($P < 0.002$), decision criterion lower ($P < 0.01$), and reaction time faster ($P < 0.05$) when the preceding stimulus was unattended. Detection accuracy was reduced by about the same amount for targets preceded by an attended-field stimulus or a bilateral stimulus.

Discussion

*Effects of attention on the P1 wave*

The results of this and the preceding study (Heinze et al. 1990) indicate that spatial selective attention acts early visual processing in a similar fashion whether the attended and unattended elements are presented together within single stimulus arrays or separately in a randomized sequence. In both cases, attended stimulus elements elicit an enlarged positivity over the contralateral posterior scalp that begins between 75 and 100 msec after stimulus onset and lasts 60 msec or longer.

For bilateral stimuli, the early phase of this positivity has approximately the same scalp distribution as the P1 wave and may, therefore, represent increased activity within the same neural populations. This is consistent with the hypothesis that visual-spatial attention acts to enhance the stimulus-evoked neural activity reflected in the exogenous P1 wave (Hillyard and Mangun 1987; Mangun and Hillyard 1988). The attention-related enhancement of the exogenous P1 has been interpreted as reflecting a facilitation of sensory processing of items at the attended location (Hillyard and Mangun 1986; Heinze et al. 1990). Heinze et al. (1990) showed that this P1 enhancement occurred for unilateral ‘probe’ stimuli that were similar to the task-relevant stimuli and also for very dissimilar probes, suggesting that spatial attention may select stimuli on the basis of location before all relevant features have been processed. These results therefore support ‘early selection’ theories of visual-spatial attention (e.g., Bashinski and Bacharach 1980; Johnston and Dark 1986; Downing 1988).

The proposal that the early positive attention effect represents a modulation of the P1 component was also supported by a principal components analysis (see Appendix). A component corresponding to the P1 wave was found to vary in magnitude with attention and was dissociable from a second component that corresponded to the later phase of the attention-related positivity. This suggests that the attention-related positivity may be composed of multiple attentional processes rather than a single long-duration process. However, given the controversial assumptions inherent in principal components analysis (cf., Rössler and Manzey 1981; Wood and McCarthy 1984), further evidence would be needed to be confident in these conclusions.

*Effects of attention on the N1 wave*

In previous studies of spatial selective attention wherein sequences of unilateral stimuli were presented in random order to attended and unattended locations, the N1 component was enlarged for stimuli that were attended relative to when they were unattended (Eason et al. 1969; Eason 1981; Harter et al. 1982; Hillyard and Münte 1984; Mangun et al. 1986, 1987; Mangun and Hillyard 1987, 1988, 1990). The present studies have shown that this N1 enlargement is reduced according to the proportion of bilateral stimuli within the stimulus sequence. Heinze et al.
(1990) observed no attention-related N1 enlargement for either unilateral or bilateral stimuli in sequences composed primarily (62%) of bilateral stimuli. The present study replicated this result for bilateral stimuli in sequences composed entirely of bilateral stimuli and demonstrated an increased negativity in the N1 latency range when only 33% of the stimuli in the sequence were bilateral. The N1 attention effect for unilateral stimuli was also shown to be larger in sequences with a higher proportion of unilateral stimuli. Thus, the N1 attention effect for both unilateral and bilateral stimuli appears to be affected by the proportion of bilateral stimuli within the sequence.

Several hypotheses have been forwarded to account for the reduction of the N1 attention effect in sequences containing bilateral stimuli (Heinze et al. 1990). First, this reduction may be a result of simple physiological refractoriness due to stimulus repetition. Since bilateral stimuli contain elements at both attended and unattended locations, the effective rate of stimulus presentation at a given location increases as the proportion of bilateral stimuli increases. This factor alone might reduce the amplitude of the N1. However, refractoriness would reduce N1 amplitude for both attended and unattended stimuli and would not necessarily eliminate the modulation of N1 by attention. Moreover, the P1 would also be expected to exhibit this refractoriness. Thus, although refractoriness may play a role in the reduced N1 attention effect for sequences containing bilateral stimuli, it cannot completely account for these results.

A second hypothesis proposes that the N1 represents the engagement or orienting of attention to a task-relevant location. The presentation of a unilateral stimulus on the unattended side may automatically attract attention away from the attended location briefly such that a subsequent attended unilateral stimulus requires a re-orientation of attention back to the attended location. Indeed, several studies have shown that unilateral irrelevant stimuli can automatically attract attention to their location (e.g., Jonides 1981; Posner and Cohen 1984). In addition, given that the attended field remains blank during the presentation of an unattended-field stimulus, the attentional focus may simply dissipate independently of any distraction caused by the unattended-field stimulus. When a bilateral stimulus containing both attended and unattended elements is presented, however, the presence of attended-field elements presumably allows attention to remain engaged at the attended location. Accordingly, this hypothesis predicts that the orienting process and its manifestation in the N1 component should be reduced in sequences containing bilateral stimuli.

**Stimulus order effects**

Further evidence in support of the above hypothesis was provided by the sequential analysis of unilateral stimuli, which showed that the N1 attention effect was evident only when the preceding stimulus was presented on the opposite side. The prior opposite-field stimulus may have attracted attention to its location and/or allowed attention to dissipate at the task-relevant location, thereby necessitating a re-engagement of attention to the next attended stimulus. When an attended stimulus was preceded by an attended or bilateral stimulus such that the need for re-orienting was reduced, the N1 enhancement was diminished, leaving only the attention-related positivity.

The sequential effects are also consistent with another hypothesis, however, namely that the N1 enhancement indexes a limited capacity process that cannot operate effectively when the time between its successive activations is short. The time between successive attended-field stimuli was shorter when the preceding stimulus was on the attended side rather than the unattended side, which may have reduced the available capacity for the process indexed by the N1. Unfortunately, sequential order was necessarily confounded with the amount of time between successive attended-field stimuli in the present design, so this hypothesis could not easily be differentiated from the re-orienting hypothesis.

The behavioral results provide some support for this alternative hypothesis. Target detection was slower and/or less accurate when more bilateral stimuli were present in the sequences and when the previous stimulus was on the same side; these were the same conditions under which the
N1 attention effect was small, consistent with limits in processing capacity. However, this decrement in target detectability may have been caused by some other factor, such as sequential masking effects occurring when the preceding stimulus contained elements at the attended location. Further experiments are needed to determine the specific cognitive processes indexed by the N1 attention effect and the relationship between these effects and detection performance.

Although these interpretations must be considered tentative, the present results do indicate that the P1 and N1 attention effects reflect distinctly different kinds of attentional processes. The N1 effect appears to correlate well with the engagement or orienting of attention to the relevant location, triggered by the occurrence of a stimulus at that location. In contrast, the P1 appears to reflect a facilitation of early sensory processing that is preset prior to stimulus onset, perhaps representing a tuning or facilitation of the visual pathways (cf., Eason 1981; Harter and Aine 1984).

Higher levels of selection

We have proposed that the attention effects manifested in the P1 and N1 components are related to early levels of selection based on stimulus location. Higher levels of selection were reflected in the N2 component (onset at 200 msec) that was present at scalp sites contralateral to the visual field containing an attended target. This component, which was also prominent in the experiments of Heinze et al. (1990), appears to belong to the family of negative ERP waves associated with stimulus evaluation processes, including the components labeled N2, N200, mismatch negativity, and selection negativity (Renault et al. 1982; Ritter et al. 1983; Harter and Aine 1984; Näätänen and Picton 1987; Wijers et al. 1987). Simson et al. (1977) initially demonstrated the modality specificity of the N2 wave associated with infrequent target detections: visual targets elicited an N2 that was largest over occipito-temporal cortical areas while the N2 following auditory targets had an anterior, midline scalp maximum. These authors proposed that the N2 is a ‘generic component’ reflecting discriminative processing and stimulus classification within modality- and task-specific cortical areas (Simson et al. 1977; Ritter et al. 1983). This processing may predominate in the right or left cerebral hemisphere depending upon whether the stimulus classification task involves semantic or spatial attributes (Ritter et al. 1983; Harter and Aine 1984).

In the present studies, the N2 associated with visual target detection also had an occipito-temporal scalp maximum as reported by Simson et al. (1977). In addition, a sizeable lateral asymmetry was also evident, with much larger N2 amplitudes over the hemisphere contralateral to the visual field in which the attended target occurred. This suggests that the discriminative processing leading to target classification is carried out preferentially in the hemisphere that directly receives the sensory information, perhaps in the occipito-temporal pathway that mediates object recognition in primate visual cortex (Ungerleider and Mishkin 1982; Desimone et al. 1985; Haxby et al. 1988).

Like the P1 and N1 components, the lateralized N2 component depended upon the location of the stimulus and the task instructions. However, while the P1 and N1 waves were essentially equivalent for stimulus arrays that contained the target compared to those that did not, the N2 was specifically elicited by targets. Heinze et al. (1990) proposed that the levels of processing represented by these components have a hierarchical relationship such that early selection on the basis of location (reflected in larger P1 and/or N1 amplitudes for attended-field stimuli) controls the flow of perceptual information to the higher levels of discriminative processing reflected by the N2 and P3 components (cf., Hillyard and Münte 1984). Such a scheme would allow the level of selection in a particular task to be determined by the complexity of the required discrimination, a much more efficient means of controlling access to perceptual resources than either early or late selection alone.

Appendix

In order to determine whether the attention-related positivity was a unitary component or included independent subcomponents (perhaps overlapped P1 and P2 waves), a principal compo-
ments analysis (BMDP-4M) was conducted on the ERP wave forms elicited by the non-target stimuli at parietal, occipital, and temporal sites. Consecutive time points were averaged together to reduce the number of variables, and the samples were taken from 100 msec prestimulus to 400 msec poststimulus for a total of 64 samples per wave form. The ERPs from all non-target stimuli in all experimental conditions were entered into the PCA, for a total of 864 wave forms. This analysis included ERPs elicited by both bilateral and unilateral stimuli.

Varimax rotation is generally conducted after initial component extraction in PCA studies of ERP components. However, since Varimax rotation attempts to produce components that are highly loaded on a small number of time points, it was suspected that this rotation method might spuriously divide the attention-related positivity into several short duration components. Quartimax rotation, the other common orthogonal PCA rotation method, provides a solution in which each time point is highly loaded on a small number of components, which tends to produce a small number of components each highly loaded on a large number of time points. This method was considered likely to produce an erroneous solution opposite to that produced by Varimax rotation, creating a single broad component from a small number of overlapped components. In order to minimize any biasing of the results, both rotation methods were used and the unrotated solution was computed as well. The first 6 components were examined in each PCA.

Varimax and Quartimax rotations produced components that were nearly identical, although the order of extraction was somewhat different. The first 4 components from the Varimax rotation and the corresponding components from the Quartimax rotation are plotted in Fig. 8. There were 3 components in the latency range of the attention-related positivity, corresponding approximately in latency to the P1, N1, and P2 peaks (note that the polarity of the PCA factor loadings does not indicate the polarity of the corresponding ERP peaks). The fourth component plotted in Fig. 8 may represent the late, slow negativity present for attended unilateral stimuli.

![Fig. 8. PCA factor loadings from the Quartimax (top) and Varimax (bottom) rotations. The order of extraction is indicated by the numbers at the peak of each component.](image)

The factor scores associated with these PCA components were compared with the area amplitude measures for each of the peaks, and the correlation coefficients are presented in Table III. The strong correlation between mean amplitude and factor scores provides additional evidence for the correspondence between the PCA components.

<table>
<thead>
<tr>
<th>Rotation</th>
<th>Factor</th>
<th>P1</th>
<th>N1</th>
<th>P2</th>
<th>N2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quartimax</td>
<td>1</td>
<td>0.1763</td>
<td>0.1349</td>
<td>0.3959</td>
<td>0.9816</td>
</tr>
<tr>
<td>Quartimax</td>
<td>2</td>
<td>0.3486</td>
<td>0.9168</td>
<td>0.1968</td>
<td>0.0398</td>
</tr>
<tr>
<td>Quartimax</td>
<td>3</td>
<td>0.0062</td>
<td>0.3289</td>
<td>0.8575</td>
<td>0.0799</td>
</tr>
<tr>
<td>Quartimax</td>
<td>4</td>
<td>0.8340</td>
<td>0.0756</td>
<td>0.1575</td>
<td>0.0334</td>
</tr>
<tr>
<td>Varimax</td>
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<td>0.1307</td>
<td>0.0684</td>
<td>0.2769</td>
<td>0.9235</td>
</tr>
<tr>
<td>Varimax</td>
<td>2</td>
<td>0.3369</td>
<td>0.9234</td>
<td>0.2089</td>
<td>0.0755</td>
</tr>
<tr>
<td>Varimax</td>
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<td>0.9176</td>
<td>0.1279</td>
<td>0.1237</td>
<td>0.1137</td>
</tr>
<tr>
<td>Varimax</td>
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<td>0.0388</td>
<td>0.3253</td>
<td>0.8868</td>
<td>0.1444</td>
</tr>
<tr>
<td>Unrotated</td>
<td>1</td>
<td>0.5951</td>
<td>0.6755</td>
<td>0.7243</td>
<td>0.8086</td>
</tr>
<tr>
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<td>0.6227</td>
<td>−0.0231</td>
<td>−0.5272</td>
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<td>0.5218</td>
<td>−0.2617</td>
<td>−0.4277</td>
<td>0.1792</td>
</tr>
<tr>
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<td>−0.2825</td>
<td>0.1687</td>
<td>0.2129</td>
<td>0.0572</td>
</tr>
</tbody>
</table>

Table III: Correlations (Pearson r) between factor scores for the first 4 factors and mean amplitudes for the P1, N1, P2, and N2 peaks. All correlations have 862 degrees of freedom.
Fig. 9 shows the effects of the attentional manipulations on factor scores for the P1-, N1-, and P2-related components from the Quartimax rotation. The effects of attention were attributed largely to the P1- and P2-related components for the bilateral stimuli, whereas attention affected the P1- and N1-related components for unilateral stimuli. PCA has many limitations (Rösler and Manzey 1981; Wood and McCarthy 1984), but this analysis is consistent with the hypothesis that the attention-related positivity was not a single ERP component, but was instead composed of overlapping P1 and P2 peaks with no intervening N1 peak.

This work was supported by an NSF Graduate Fellowship to S.I.L., a grant from the Deutsche Forschungsgemeinschaft to H.J.H., and NIMH Grant MH-25594 and O.N.R. Contract N00014-86-K-029 to S.A.H.

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