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# Attention to central and peripheral visual space in a movement detection task: an event-related potential and behavioral study. I. Normal hearing adults

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The effects of focussed attention to peripherally and centrally located visual stimuli were compared via an analysis of event-related brain potentials (ERPs) while subjects detected the direction of motion of a white square in a specified location. While attention to both peripheral and foveal stimuli produced enhancements of the early ERP components, the distribution over the scalp of the attention-related changes varied according to stimulus location. The attention-related increase in the amplitude of the  $N_1$  wave (157 ms) to the peripheral stimuli was greater over the parietal region of the hemisphere contralateral to the attended visual field. By contrast, the largest effects of foveally directed attention occurred over the occipital regions where the increase was bilaterally symmetrical. Additionally, the effects of attention on the ERPs were significantly larger for moving than for stationary stimuli, and this effect was greater for peripheral than for central attention. A long-latency positive displacement component (300–600 ms) was larger over the right than the left hemisphere during attention to the lateral visual fields, but was symmetrical in amplitude when central stimuli were attended. These results suggest that different pathways are modulated when attention is deployed to different regions of the visual fields. Further, they suggest that the special role of the right hemisphere in spatial attention may be limited to analysis of information in the visual periphery.

## INTRODUCTION

Several lines of investigation have led to the proposal that there exist two distinct modes of analysis of visual information. One is primarily concerned with the discrimination of contours and figural properties of stimuli and is hypothesized to mediate the identification of details of objects (the 'focal' or 'what' system)<sup>18,25,38,53,57,59</sup>. The other is concerned with orienting towards events in visual space and the processing of information about stimulus location (the 'ambient' or 'where' system). This functional distinction has been linked to the differential sensitivities of the central and peripheral areas of the retina. Thus the higher acuity of the foveal region is clearly specialized for resolving the details of visual objects, while the greater sensitivity to movement of the peripheral retina is hypothesized to mediate shifts of at-

tention toward potentially important stimuli in the periphery.

Considerable anatomical evidence in animals has been interpreted as support for the functional distinction between the focal and ambient systems<sup>28,51,56</sup>. The pathway from the retina to the lateral geniculate, striate and inferior temporal cortex is critical in pattern discrimination and identification, while lesions to the pathway from the retina that includes the superior colliculus and projects to extrastriate cortical regions including parietal cortex lead to deficits in orientation towards and localization of peripheral visual stimuli<sup>6,23,26,53,57,59</sup>.

Neuropsychological studies of visual perception following selective damage to the visual pathways have been interpreted as showing that this distinction may apply to the human visual system as well. Thus, whereas damage to the occipitotemporal pathway is

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associated with deficits in the recognition of visual objects, lesions to the parietal cortex produce impairments in spatial attention and the ability to perceive spatial layout<sup>16,38,46,47</sup>. In addition, reports that target localization and visually guided attention are preserved after lesions to striate cortex have been interpreted as evidence that these functions rely on the retinocollicular-extrastriate visual system<sup>42,43,45,61,65</sup>. However considerable controversy surrounds these claims, in part due to the methods whereby evidence for 'blindsight' has been obtained, and in part due to the difficulty in assessing the extent of cortical damage in human patients<sup>4</sup>.

Psychophysical evidence from neurologically intact humans also lends support to the notion that there are two parallel and complementary visual systems associated with peripheral and central regions of the retina<sup>2,27</sup>. For example, Paillard and his colleagues<sup>39-41</sup> on the basis of several types of studies, provide evidence for two distinct channels or modes of analysis of visual information. The first, termed 'static', includes the central retina (up to 10-15° eccentricity), is sensitive primarily to stable or slow moving stimulus features including object shape, pattern and contour, and displays sustained reactivity. The second or 'kinetic' mode includes the peripheral retina, detects high velocities (greater than 10 degrees/s), is specially tuned for movement and velocity coding, and displays transient reactivity. The authors note that the distinction between the sustained (X) and transient (Y) retinal ganglion cells corresponds with their behavioral observations, and that response properties of single neurons in the inferior parietal lobe, including their sensitivity to direction of motion and foveal sparing<sup>32,33</sup>, are in agreement with the notion that this structure plays an important role in 'kinetic' vision.

Consistent with these proposals is a report by Zihl et al.<sup>66</sup> of a patient displaying a selective deficit in the perception of motion in the peripheral field, with preservation of the perception of slow movement in central vision (up to 15° eccentricity). The lesions in this patient included the periventricular segment of temporoparietal and occipital white matter, bilaterally, a region which the authors suggest may correspond to MT in the monkey<sup>64</sup>.

Other data suggest that different cortical areas may mediate attention to central and peripheral visu-

al space. Several studies in monkeys have reported that neurons in posterior parietal cortex show increased activity with attention to the peripheral visual fields, while neurons in striate cortex may not<sup>3,10,33,62</sup>. Likewise, in humans, the parietal cortex has been strongly implicated in spatial attention to the periphery of the visual field<sup>7,15</sup>. Parietal lesions, especially to the right hemisphere, often lead to marked inability to attend to stimuli in the visual field contralateral to the lesion. On the other hand, Singer et al.<sup>54</sup> report data which suggest that lesions to striate cortex in humans may interfere with the ability to attend to the center but not the periphery of visual space.

A complementary approach to the study of the organization of the visual system in humans has been to record from the scalp the electrical responses elicited by visual stimuli (visual evoked responses, VEPs) in patients with damage to the visual cortical areas. The results of such studies suggest that the activity of pathways to striate and extrastriate visual regions may be associated with different VEPs<sup>1,5,48,55</sup>. Similarly, the study of VEPs elicited in neurologically intact humans may also bear on these proposed functional and anatomical distinctions. Several investigators have reported differences in the amplitude, scalp distribution and refractory period of VEPs to peripheral and foveal stimuli that appear to be consistent with hypotheses concerning the relevance of different cortical areas in the processing of information projected to different retinal areas<sup>11,35,44,49</sup>. However, since in each of these studies subjects were not required to differentially process the visual stimuli, these results may simply reflect the different cortical representations of peripheral and central retinal projections rather than functional differences between the two visual systems.

In the present experiment we employed the event-related brain potential (ERP) technique to explore the possibility that the spatial focussing of attention may operate differently for stimuli presented to the central and peripheral visual fields. The neurophysiology of attention in humans has been investigated by comparing ERPs elicited by stimuli when they are attended as compared to when attention is directed away from them. The analysis of ERPs recorded during selective attention to auditory, visual and somatosensory stimuli has contributed important informa-

tion about the nature and timing of attentional processes in humans (for review see refs. 13, 19, 21, 22, 34). For example, several studies have converged on the conclusion that attentional processes are hierarchically ordered with identification of elementary stimulus properties occurring earlier than the selection for their combinations. Moreover, these studies suggest that mechanisms of attention may include both gating of the sensory ('exogenous') responses as well as the addition of attention-specific ('endogenous') processes. Studies of attention to the spatial location of visual stimuli have revealed attention-related increases in the amplitude of ERP components beginning around 80 ms post-stimulus<sup>14,20,60</sup>. These studies have employed peripheral stimuli (range 5–20° lateral to fixation) and reported that attention-related changes in ERPs are generally larger over the scalp contralateral to the attended stimulus. In view of the literature reviewed above, it is conceivable that attention to the central visual field might be associated with a different pattern of attention-related responses than has been reported for peripheral attention. Therefore in the present experiment ERPs to peripheral and foveal stimuli were recorded from over several positions between the two hemispheres while subjects focussed their attention on different locations in the visual field in order to detect the direction of motion of target stimuli at the attended location.

## MATERIALS AND METHODS

### *Subjects*

Twelve young adults (6 male, 6 female; mean age 20 years, range 18–23) were paid to participate in the experiment. All but one subject (S) were right-handed. All had visual acuity (Snellen) of 20/40 or better.

### *Stimuli*

The stimuli were white squares (5 × 5 mm) presented in 3 positions on a dark video monitor controlled by a microcomputer. The 'peripheral' stimuli were presented 14.7 cm to the left and right of a black dot which subjects fixated. The 'center' stimulus appeared in the center of the monitor just above the fixation point. The monitor was 45.7 cm from the S, so that the peripheral stimuli occurred 18° laterally, and

the stimuli subtended a visual angle of 0.6° square. Eighty percent of the stimuli were single presentations of the squares for 33 ms ('standards'). The remaining 20% consisted of one 33-ms presentation of a square in the same position as the standards, followed immediately by the illumination of one of 8 adjacent squares for an additional 33 ms. The appearance of the second square produced a clear illusory movement in the direction of the second stimulus (i.e. along vertical, horizontal or diagonal axes).

### *Procedure*

Ss were seated comfortably in a copper-shielded, sound-attenuating room and were given instructions describing the task along with 4 practice sessions. Each of 6 blocks of trials consisted of 960 stimuli, 320 in each of the 3 display locations (256 standard flashes and 64 targets — 8 in each direction). The order of presentation of the standards and targets across all positions was randomized, with the constraint that at least one standard occurred between any two targets occurring in the same location. The stimuli were presented at intervals between successive stimuli that varied randomly from 280 to 480 ms (mean = median = 384 ms), regardless of where they appeared on the screen. Ss were instructed to keep their eyes fixated on the center throughout each recording block. Before each block of trials, Ss were told to focus their attention to only one of the 3 locations, in order to detect the direction of motion of the targets at that location. Thus each position was attended twice. The order in which Ss attended the 3 locations was counter-balanced across all Ss. Ss kept their finger on the center button of a 3 × 3 array and were told to press one of the 8 surrounding buttons to indicate the direction of motion of targets that occurred at the attended location. Half of the Ss responded with their left and half with their right hand. Each block lasted approximately 6 min. Ss were given a 1-min break in the middle of each block, as well as a longer break half way through the experiment.

### *ERP recording*

Scalp electrical activity was recorded with Ag/AgCl electrodes from homologous positions over left and right occipital (O<sub>1</sub>, O<sub>2</sub>), parietal (30% of the interaural distance lateral to a point 13% of the nasion–inion distance posterior to Cz), temporal (33%

of the interaural distance lateral from Cz), anterior-temporal region (50% of the distance from  $F_{7(8)}$  to  $T_{3(4)}$ ), and frontal regions ( $F_7$ ,  $F_8$ ). Recordings from these electrodes and the vertical EOG recorded from the left inferior orbital ridge were referred to the linked mastoids. The horizontal EOG was recorded between electrodes placed on the left and right external canthi. Electrical activity from the scalp and the vertical EOG was amplified with a bandpass of 0.01–100 Hz (time constant 8 s). The horizontal EOG was amplified with a DC amplifier and a high-frequency half-amplitude cut off of 60 Hz. The EEG was digitized on-line on a PDP 11/34 computer.

#### Data analysis

The averaging program sampled the EEG for 100 ms prior to and 924 ms following each stimulus presentation at a rate of 1 point/4 ms. Trials in which ex-

cessive eye movement or muscle artifact occurred were excluded from the average (approximately 2–15% of all trials). ERPs were averaged separately for standards and targets at each location (3), attention condition (3), hemisphere (2) and electrode site (5). ERP 'difference waves' were formed by subtracting, point by point, ERPs recorded during different attention conditions.

ERP component amplitudes were quantified by computer with reference to the 100-ms prestimulus baseline. Peak amplitudes (the maximum negative or positive point in a specified time window) and mean amplitudes (within the same window) were measured according to the following criteria:  $P_1$  was defined as the most positive deflection between 50 and 175 ms post-stimulus;  $N_1$  as the most negative deflection between 75 and 225 ms;  $P_2$  as the most positive deflection between 175 and 300 ms;  $N_2$  between 250 and

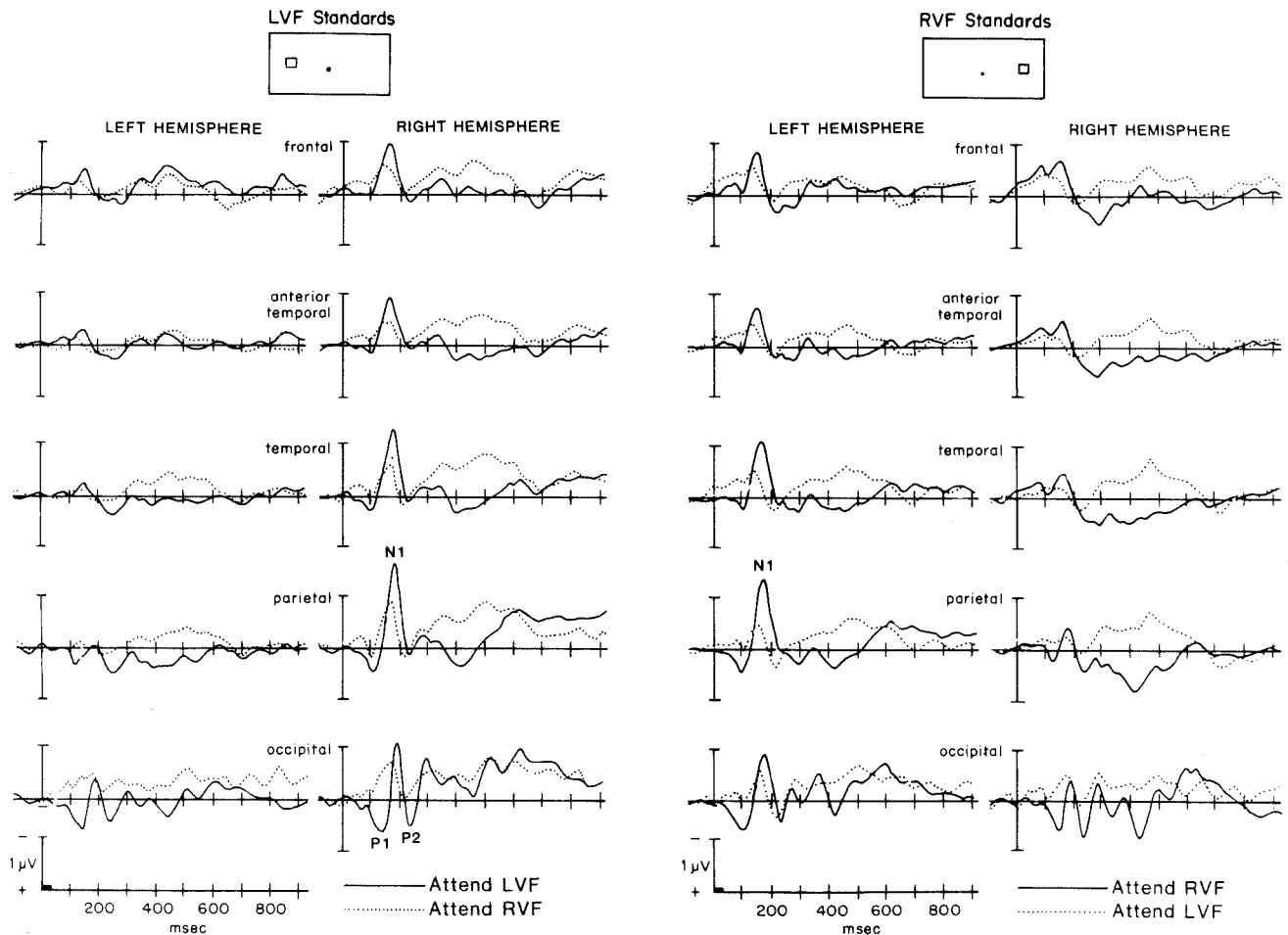


Fig. 1. ERPs averaged across 12 subjects (Ss) to peripheral standards (left visual field (LVF) and right visual field (RVF)) when attended and inattended. Recordings from left and right frontal, anterior temporal, temporal, parietal and occipital regions.

375 ms;  $P_3$  between 250 and 700 ms; PD (positive difference) between 300 and 600 ms; and SW (slow wave) between 700 and 900 ms. Statistical analysis of the standard and target ERP data was performed with a 5-way analysis of variance with repeated measures on 3 levels of stimulus location, 3 levels of attention, two levels of hemisphere and 5 levels of electrode. Comparisons of the standards and targets added stimulus as a factor. Subanalyses of variance were performed to further clarify significant interactions.

Behavioral measures of reaction time (RT) and target detection were also scored by computer. On the basis of pilot data a hit was defined as a correct button press (i.e. the direction of target motion was correctly indicated) that occurred within 300 to 1900 ms following each target in the attended location. All responses which fell outside this window were classed as false alarms.

Hit and false alarm probabilities were obtained and used to calculate the signal detection parameters  $d'$  and  $B$  for each of the 3 attention conditions.  $P$  (hit) was defined as the ratio of the number of hits to the number of attended targets presented. The probability of a false alarm was estimated as the ratio of false alarms/number of attended standards.

## RESULTS

### Standards

*ERP waveforms.* As seen in Fig. 1, the visual stimuli elicited ERPs displaying a series of positive and negative deflections that differed in latency and amplitude as a function of electrode position. Over the posterior scalp two positive peaks were evident at 100 and 230 ms ( $P_1$  and  $P_2$ ) and a negative component occurred around 157 ms ( $N_1$ ). The negative peak occurred significantly earlier (at 131 ms) from anterior

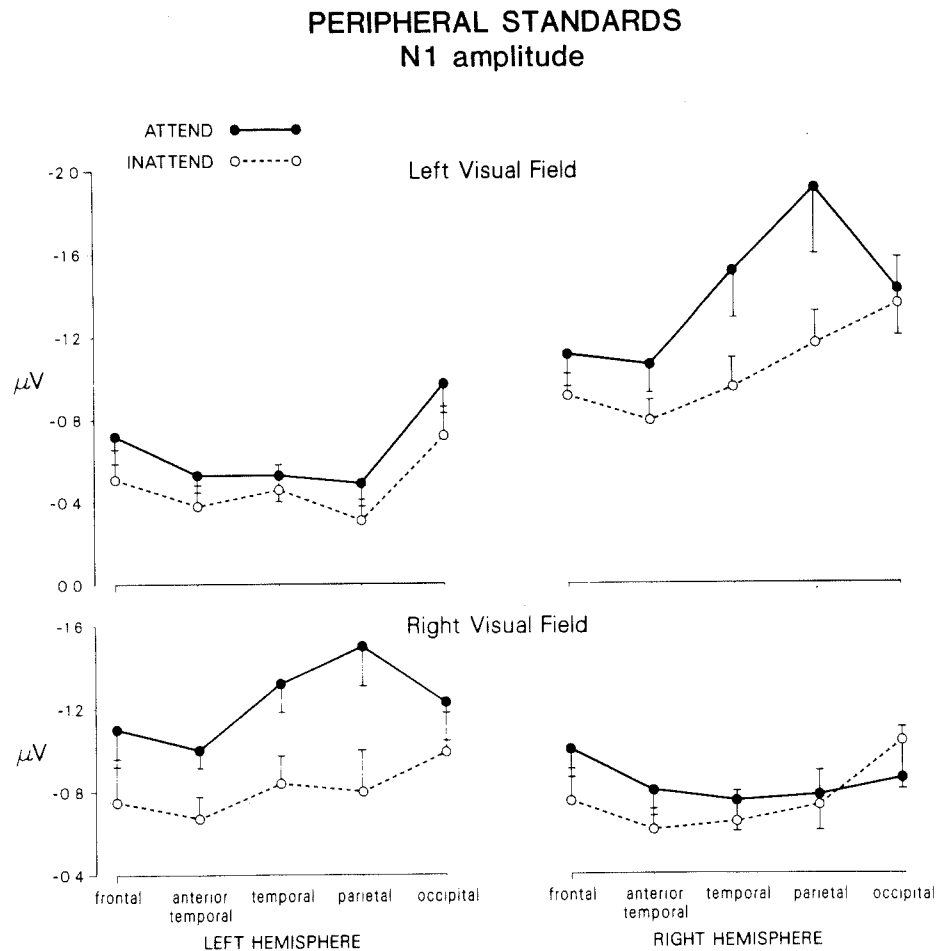


Fig. 2. Mean amplitude of  $N_1$  ( $\mu V \pm S.E.M.$ ) across 12 Ss to LVF and RVF standards when attended and inattended (mean of two inattent conditions), from left and right frontal, anterior temporal, temporal, parietal and occipital electrode sites.

than posterior sites (electrode  $F_{4,44} = 16.0$ ,  $P < 0.0001$ ). After 250 ms the ERPs displayed broad shifts in amplitude, the polarity of which depended upon direction of attention.

$P_1$  and  $P_2$ . The amplitudes of both  $P_1$  and  $P_2$  to the peripheral stimuli were enhanced and their latencies were increased when attention was directed toward them as compared to when attention was directed either to the center or to the other periphery. This attention-related increase in amplitude was largest over the occipital regions and was of equal amplitude over the two hemispheres for  $P_1$  (attention  $\times$  location  $\times$  electrode,  $P < 0.00001$ ), but tended to be larger over the hemisphere ipsilateral to the peripheral stimulus for  $P_2$  (location  $\times$  attention  $\times$  hemisphere,  $P < 0.002$ ; see Fig. 1). While the overall amplitude of  $P_1$  and  $P_2$  was larger for central than for peripheral stimuli (location,  $P_1$ ,  $P < 0.0001$ ;  $P_2$ ,  $P < 0.0005$ ), central stimuli displayed effects of attention similar to peripheral stimuli. Thus, with attention to central stimuli the amplitudes of both  $P_1$  and  $P_2$  were increased bilaterally over the occipital regions ( $P_1$ , attention  $\times$  electrode,  $P < 0.00001$ ;  $P_2$ , attention  $\times$  electrode,  $P < 0.04$ ).

$N_1$ . The amplitude of  $N_1$  displayed different patterns of attention-related changes for peripheral and central stimuli.

For both left and right field stimuli the amplitude

of  $N_1$  was larger when Ss directed their attention toward them than when they attended to the center or the opposite side (location  $\times$  attention,  $P < 0.002$ ). This increase in  $N_1$  amplitude with attention was largest in ERPs recorded over the temporal and parietal regions of the hemisphere contralateral to the stimulus (location  $\times$  attention  $\times$  hemisphere  $\times$  electrode site,  $P < 0.01$ ). This can be seen in Figs. 1 and 2.

The central stimuli elicited  $N_1$  components of larger overall amplitude than the peripheral stimuli ( $P < 0.0001$ ), and the attention-related changes showed a different distribution over the scalp. As seen in Fig. 3, the major attention-related increase in  $N_1$  amplitude occurred bilaterally over the occipital regions (attention  $\times$  electrode site,  $P < 0.0004$ ). This increase in amplitude over the occipital regions was on average 95% of the inattended amplitude. There was also a small tendency for  $N_1$  amplitude to central standards to be increased slightly over the right parietal area (attention  $\times$  hemisphere  $\times$  electrode,  $P < 0.06$ ).

Thus, while the major effects of attention to central stimuli occurred bilaterally over the occipital regions (attention,  $P < 0.001$ ), with attention to the peripheral stimuli the amplitude of  $N_1$  was not significantly increased over the occipital sites (attention  $\times$  location,  $P = 0.74$ ) but was increased by 60–90% over the temporal (location  $\times$  attention,  $P < 0.0001$ ;

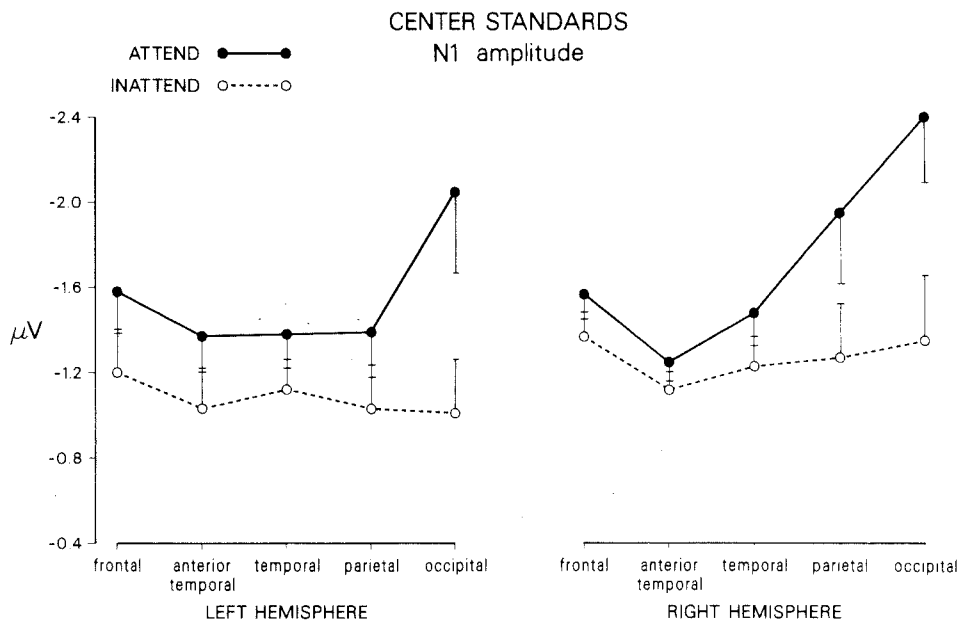


Fig. 3. Mean amplitude of  $N_1$  (12 Ss) to central standards when attended and inattended (mean of two inattend conditions from left and right frontal, anterior temporal, temporal, parietal and occipital electrode sites).

location  $\times$  attention  $\times$  hemisphere,  $P < 0.01$ ) and parietal (location  $\times$  attention,  $P < 0.001$ ; location  $\times$  attention  $\times$  hemisphere,  $P < 0.04$ ) regions of the contralateral hemisphere. Fig. 4 displays the attention effects for peripheral and central stimuli in different individual subjects. The different scalp distributions of the attention-related increase in  $N_1$  amplitude for peripheral and center stimuli was highly reliable (location  $\times$  attention  $\times$  hemisphere  $\times$  electrode,  $P < 0.0001$ ).

The contralateral distribution of  $N_1$  to both attended and inattended peripheral stimuli interacted with a tendency for its amplitude to be larger from the right than the left hemisphere across all conditions and electrode sites (hemisphere,  $P < 0.04$ ). Thus, the contralateral distribution of  $N_1$  was more pronounced for left (LVF) than right visual field (RVF) stimuli (location  $\times$  hemisphere,  $P < 0.001$ ), everywhere except over the occipital regions (location  $\times$  hemisphere  $\times$  electrode site,  $P < 0.001$ ; see Figs. 1 and 2). Thus, as seen in Fig. 5, while during attention to the LVF  $N_1$  amplitude to all stimuli was larger over the right than the left parietal region, with attention to the RVF, its amplitude over the two parietal regions was identical (attention  $\times$  hemisphere,  $P <$

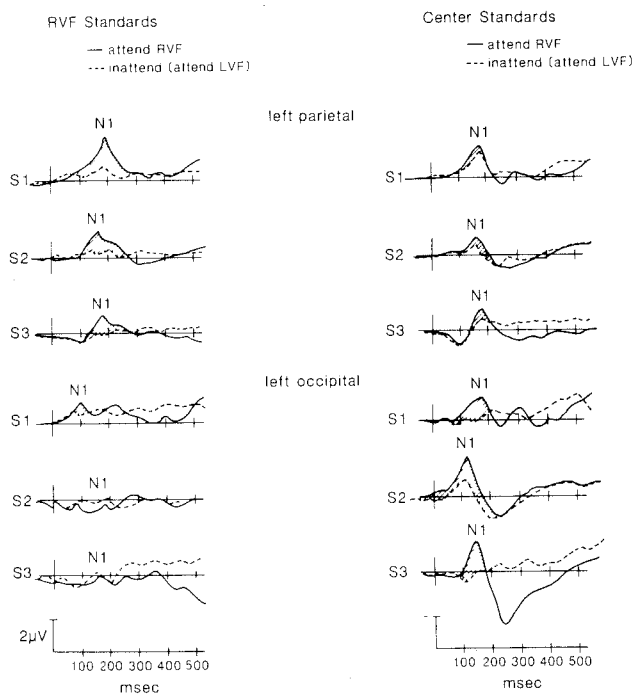


Fig. 4. ERPs from individual subjects (S1, S2, S3) to RVF and center standards when attended and inattended. Recordings from left parietal and occipital regions.

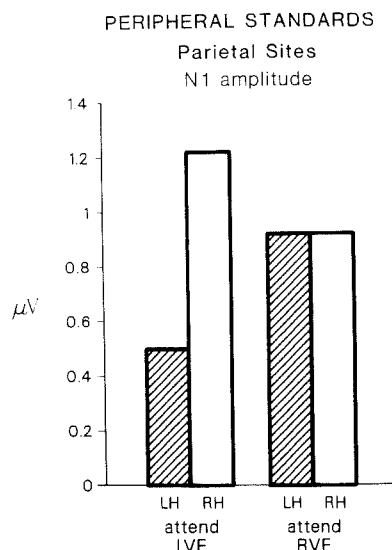


Fig. 5. Mean amplitude in  $\mu\text{V}$  of  $N_1$  across LVF and RVF stimuli from left (LH) and right (RH) parietal sites under attend LVF and attend RVF conditions.

0.0003). Similar results were observed at the temporal electrodes (attention  $\times$  hemisphere,  $P < 0.004$ ). In contrast to these results, for central stimuli both  $N_1$  amplitude and the attention-related increase in its amplitude were of equal amplitude bilaterally over the occipital regions (attention  $\times$  hemisphere, n.s.; see Fig. 3).

**Area 300–600.** As seen in Fig. 1, ERPs to *inattended* stimuli displayed a broad negative wave beginning at around 300 ms and returning to baseline around 700 ms. By contrast, ERPs to the same stimuli when they were attended were at baseline or slightly positive in this time region (location  $\times$  attention,  $P < 0.00001$ ). Thus, as seen in the difference ERPs (Fig. 6), formed by subtracting the ERP to given stimuli when inattended from the ERP elicited by the same stimuli when attended, directed attention was associated with the addition of a positive displacement (PD) of maximum amplitude between 400 and 500 ms. For the peripheral stimuli over the occipital sites PD amplitude was larger over the hemisphere ipsilateral to the attended visual field. In contrast, over the temporal and parietal regions PD amplitudes were larger from over the right than the left hemisphere during attention to both the left and the right peripheral stimuli (see Fig. 7; hemisphere effect,  $P < 0.01$ ; location  $\times$  electrode site  $\times$  hemisphere,  $P < 0.0003$ ).

ERPs to the central stimuli also displayed a nega-

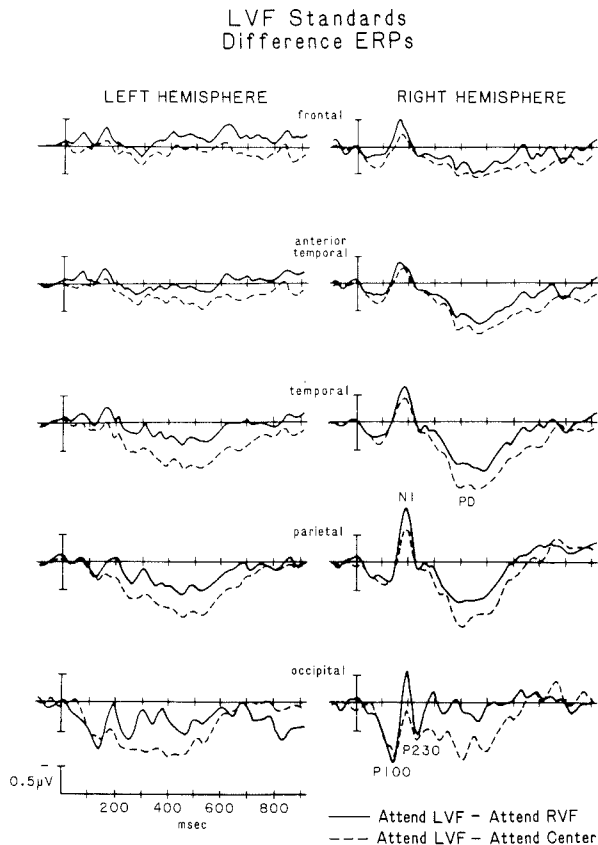


Fig. 6. Difference ERPs for LVF stimuli formed by subtracting ERPs to LVF stimuli when inattended (i.e. under attend center (---)) and attend right (—) conditions) from ERPs to attended LVF stimuli. Recordings from left and right frontal, anterior-temporal, temporal, parietal and occipital electrodes.

tive displacement between 300 and 600 ms when inattended, and a positive shift when attended. The PD wave associated with attention to the center was largest over the posterior scalp (electrode site,  $P < 0.05$ ), and, in contrast to the results for peripheral stimuli, was symmetrical from over the two hemispheres (hemisphere, n.s.). In addition, with attention to the center, PD was larger over the occipital regions while with attention to the periphery it was larger over temporal and parietal regions (attention  $\times$  electrode site,  $P < 0.02$ ).

In ERPs to *inattended* peripheral stimuli the amplitude of the area from 300 to 600 ms was more negative when attention was directed to the center as compared to when it was directed to either periphery ( $P < 0.005$ ). Thus for peripheral stimuli PD was significantly larger during attention to the center than with attention to the other periphery (see Fig. 6; attention effect,  $P < 0.008$ ).

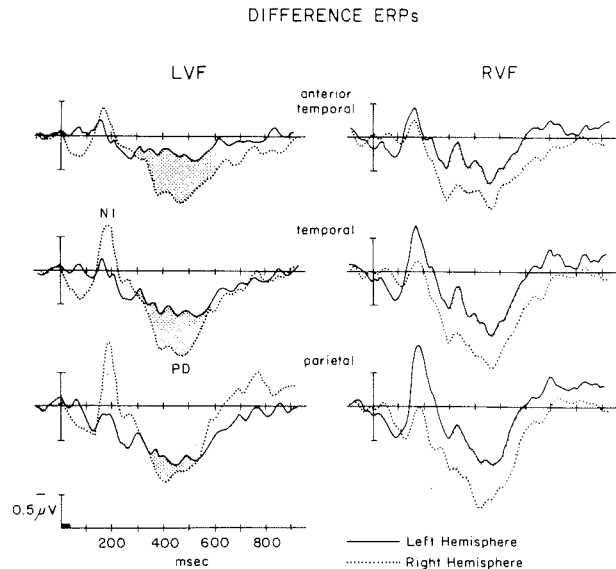


Fig. 7. Difference ERPs for LVF and RVF stimuli from anterior-temporal, temporal and parietal electrodes over the left and right hemispheres.

#### Target stimuli

**ERP waveforms.** As seen in Fig. 8, prior to 250 ms the morphology of the ERPs to the target stimuli was similar to that elicited by the standards. However, following 250 ms ERPs to correctly detected targets (i.e. those whose direction of motion was accurately perceived, 'hits') displayed an additional negative component at 289 ms ( $N_2$ ) followed by a large positive component at 493 ms ( $P_3$ ). ERPs to unattended targets displayed a broad negative shift.

**$P_1$  and  $P_2$ .** The overall amplitudes of the  $P_1$  and  $P_2$  components were larger to the targets than to the standard stimuli and this effect was equivalent for central and peripheral stimuli (stimulus effect,  $P_1$ ,  $P < 0.0001$ ;  $P_2$ ,  $P < 0.00001$ ). Moreover the targets displayed a similar pattern of attention-related changes as seen for the standards:  $P_1$  amplitude was increased bilaterally over the occipital region for peripheral and central targets (location  $\times$  attention  $\times$  electrode,  $P < 0.0008$ ), and  $P_2$  displayed larger amplitude increases over the ipsilateral hemisphere for the peripheral targets, and bilaterally symmetric increases over the occipital regions with attention to the center (location  $\times$  attention  $\times$  hemisphere,  $P < 0.001$ ; location  $\times$  attention  $\times$  electrode,  $P < 0.00001$ ).

**$N_1$ .** In contrast to the results for the standards, where  $N_1$  to central stimuli was larger than for pe-



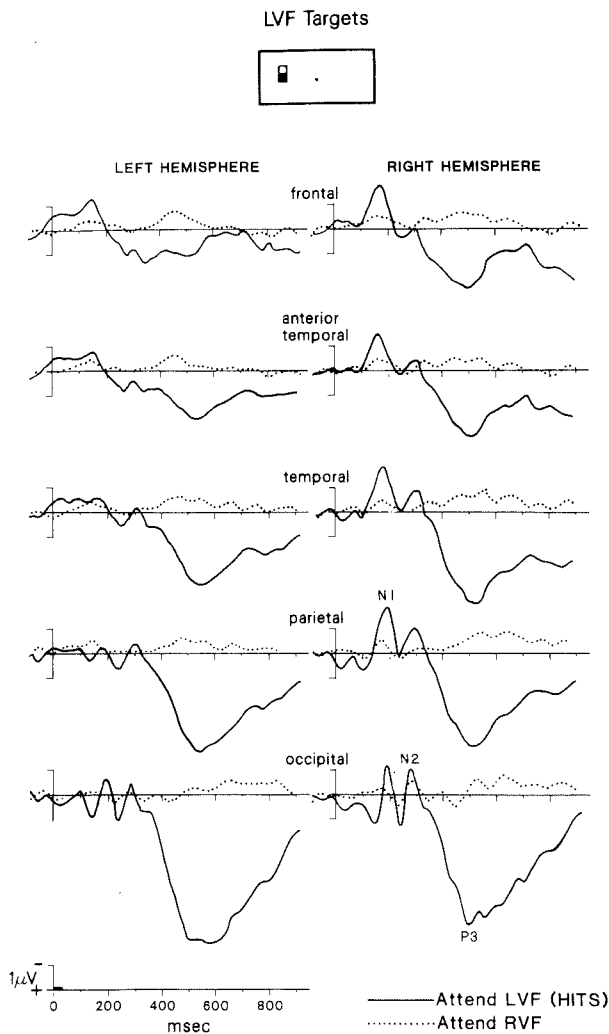


Fig. 8. ERPs to LVF targets when attended and correctly detected, and when inattended. Recordings from left and right frontal, anterior-temporal, temporal, parietal and occipital sites.

peripheral stimuli,  $N_1$  to the target stimuli was of similar amplitude for peripheral and central stimuli (location effect, n.s.). This result was due to a large increase in  $N_1$  amplitude to *peripheral* targets as compared to peripheral standards (targets,  $-1.42 \mu\text{V}$ ; standards,  $-0.86 \mu\text{V}$ ) at each electrode site (stimulus effect  $F_{1,11} = 83.4$ ,  $P < 0.00001$ ). This difference in amplitude increase between standards and targets for peripheral as compared to central stimuli was highly reliable (stimulus effect  $\times$  location  $\times$  electrode,  $P < 0.00001$ ).

The effect of attention on  $N_1$  amplitude to center targets displayed a similar distribution over the scalp as for center standards: i.e. the increase with attention was largest over right parietal and bilateral occi-

pital regions (attention effect,  $P < 0.001$ ; attention  $\times$  electrode,  $P < 0.001$ ; attention  $\times$  hemisphere  $\times$  electrode,  $P < 0.0001$ ). Additionally, for central stimuli, the overall magnitude of the attention-related increase in  $N_1$  amplitude was not different for the targets and standards (stimulus  $\times$  attention, n.s.). On the other hand, for peripheral stimuli the increase in  $N_1$  amplitude with attention was 2–3 times larger for the target than for the standard stimuli over the temporal, parietal and occipital sites (stimulus  $\times$  attention  $\times$  location,  $P < 0.001$ ; stimulus  $\times$  location  $\times$  attention  $\times$  electrode,  $P < 0.007$ ). This differential increase in the attention effect for peripheral as compared to central targets is displayed in Fig. 9 (stimulus  $\times$  location  $\times$  attention  $\times$  electrode,  $P < 0.00001$ ).

$N_2$ . ERPs to correctly detected targets contained a prominent  $N_2$  component largest over posterior scalp sites. For peripheral stimuli  $N_2$  displayed a tendency to be larger from the hemisphere contralateral to the

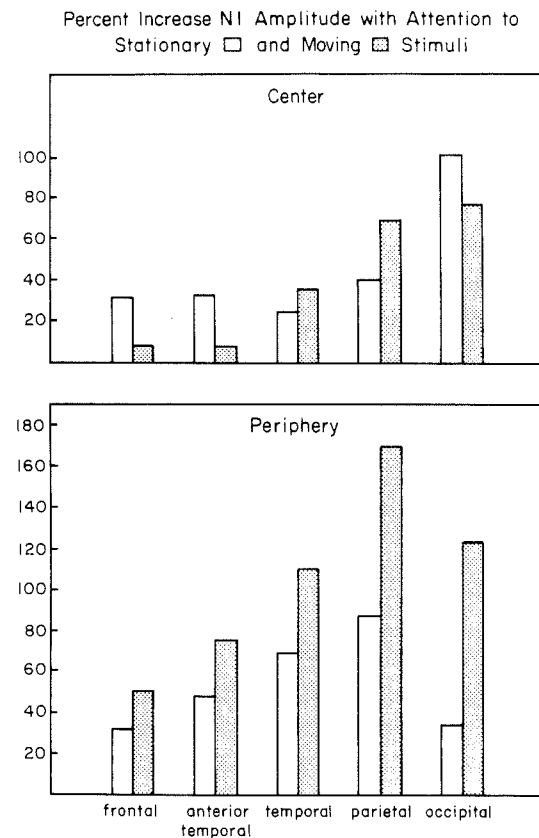


Fig. 9. Percent increase in  $N_1$  amplitude with attention. Top: center standards and targets (mean of left and right hemispheres). Bottom: peripheral standards and targets (mean of contralateral hemisphere).

TABLE I

*Behavioral data*

	<i>LVF</i>	<i>RVF</i>	<i>Center</i>
<i>d'</i>	1.8	1.6	3.9
<i>B</i>	9.0	4.8	10.0
% Correct	53.2	53.0	90.0
RT (ms)	1046	1018	911

stimulus (location  $\times$  attention  $\times$  hemisphere,  $P < 0.11$ ), while for central stimuli it was symmetrical from the two hemispheres.

$P_3$ . The large positive component in ERPs to correctly detected targets ( $P_3$ ) occurred on average 87 ms earlier and was larger for central than peripheral target hits (location  $\times$  attention, latency,  $P < 0.0003$ ; peak amplitude,  $P < 0.00001$ ). The amplitude of  $P_3$  was largest over the occipital regions for both peripheral and central hits. Additionally, at sites anterior to the occipital region,  $P_3$  tended to be larger from over the right than the left hemisphere for both peripheral and central hits (location  $\times$  attention  $\times$  electrode  $\times$  hemisphere,  $P < 0.01$ ).

#### *Behavioral data*

As shown in Table I, subjects detected the direction of motion of the targets more accurately when they occurred in the center than in the periphery ( $P < 0.0001$ ). Performance tended to be more accurate for the left than the right visual field targets ( $P < 0.09$ ). The Beta scores showed a similar visual field asymmetry ( $P < 0.08$ ). The percent correct detection scores were also higher for central than peripheral stimuli ( $P < 0.0001$ ), but did not exhibit visual field asymmetries. Reaction times were faster for central than for peripheral stimuli ( $P < 0.0001$ ).

#### DISCUSSION

The attention-related changes in the ERP displayed different distributions over the scalp when attention was directed towards the periphery as compared with towards the center of the visual field. In general, attention to the (stationary) standards in the periphery elicited effects in the ERPs that were largest from over temporal and parietal brain regions of the contralateral hemisphere, or that were larger from over the right hemisphere. By contrast, atten-

tion to standards in the center of the visual field elicited bilaterally symmetrical effects that were largest over the occipital regions. The attention-related changes in ERPs to the moving targets were 2–3 times larger for peripheral as compared to central stimuli. Attended targets in both central and peripheral visual fields elicited ERP components that were larger over the right than the left hemisphere. Each of these points is discussed below.

#### *The effects of attention: standards*

Two major effects of spatially directed attention were evident in the ERPs. The first was an increase in the amplitude of early (<250 ms) ERP components that were elicited by both attended and inattended stimuli ('exogenous components'). These results are similar to those reported in other studies of visual spatial attention and are consistent with the hypothesis that one of the mechanisms underlying spatial attention may be the modulation or gating of the sensory response to visual stimuli<sup>8,9,20–22</sup>. On the other hand, after 250 ms the ERPs displayed markedly different morphologies depending on the direction of attention. ERPs to inattended stimuli displayed a prolonged negativity whereas those to attended stimuli displayed a positive shift. Thus these results suggest that the mechanism of spatial attention also includes the addition of a new, 'endogenous' process, manifest in the PD component of the ERP. Studies in the auditory modality also report the addition of an endogenous component with spatially directed attention. However the ND or processing negativity associated with attention to auditory stimuli displays an anterior distribution, and is bilaterally symmetrical<sup>12,34</sup>. The different polarities and distributions of the ND and PD components suggest that different neural mechanisms contribute to spatial attention in the auditory and visual modalities.

#### *Comparison of attention effects for peripheral and central standards*

Aspects of both the exogenous and the endogenous attention effects displayed different distributions over the scalp when attention was directed to the central as compared to the peripheral visual standards. With attention to the center the enhancement of the amplitude of  $N_1$  was most pronounced over the occipital regions and was of equal amplitude over the

two hemispheres. By contrast, with attention to the periphery, the major increase in  $N_1$  amplitude occurred over the temporoparietal region of the hemisphere contralateral to the stimulus. These results suggest that attention to peripheral and central space is associated with modulation of activity in different neural pathways. Moreover, the pattern of results is compatible with the hypothesis that attention to the center of the visual field modulates activity in the retinogeniculate pathway that projects to striate cortex while attention to the visual periphery is associated with activity in the visual pathway that includes projections to parietal cortex of the contralateral hemisphere.

This distributional difference could arise in part from inputs being gated preferentially into the more posterior portions of the striate cortex that contain the representation of the central visual fields during foveally directed attention. The enlarged parietal response for laterally directed attention is also consistent with the evidence that parietal areas are concerned more with the processing of peripheral than central events<sup>59</sup>. Considerable data from animal studies of single neurons in parietal cortex support the notion that neural systems in parietal cortex are specialized to direct attention to stimuli in the contralateral visual field. Yin and Mountcastle<sup>63</sup> described 'visual space neurons' in parietal area 7 that increased their rate of discharge when visual stimuli were presented at the peripheral edge of the (usually contralateral) receptive field. Moreover, the average latency of the discharge was 79 ms, comparable to the onset of the earliest attention-related changes observed in this study. Of interest in view of the present findings is the report that activity in visual space neurons was suppressed if the animal directed a saccade toward the visual stimulus.

The present results showing the largest attention effects over occipital regions with attention to the center suggest that animal studies of single units may observe that neurons in striate cortex increase their activity during attention to the fovea (whereas, in agreement with the present results, they apparently do not show consistent changes in activity with attention to the periphery)<sup>62</sup>. Certain clinical studies of brain-damaged humans can also be interpreted as support for a greater parietal cortex involvement for peripheral attention and occipital mediation of cen-

tral attention. The phenomenon of hemi-inattention to contralateral (usually left) space following parietal lesions occurs in the presence of intact ability to attend to and process information that is foveated (reviewed in refs. 7 and 15).

While other ERP studies of visual attention have utilized different paradigms and electrode sites<sup>13,20,60</sup> these studies provide some evidence that the eccentricity of the peripheral stimuli was an important factor in producing the pattern of results observed here. Thus, for example, Mangun et al.<sup>29</sup> observed larger attention effects on  $N_1$  at parietal than occipital electrodes with attention to stimuli at 30° eccentricity, but Hillyard and Munte<sup>20</sup> utilizing stimuli of 5° eccentricity, produced attention effects of similar magnitude at the parietal and occipital electrode sites.

The endogenous PD component displayed a more widespread distribution than did the attention effects on  $N_1$ . Its amplitude was large over temporal and parietal regions for both peripheral and central attention. Thus the endogenous activity associated with attention may be more similar with attention to the center and periphery of the visual fields than are the exogenous processes reflected in  $N_1$ . However, PD amplitude during attention to the center was larger over the occipital regions than with attention to the periphery, suggesting that posterior brain regions are more active under conditions of attention to central as compared to peripheral space.

The amplitude of PD was considerably larger when Ss attended the center as compared to the peripheral stimuli. This effect was due to the greater amplitude of the negativity ( $N_{300-600}$ ) to *inattended* peripheral stimuli with attention to the center than to the other periphery. If  $N_{300-600}$  indexes a process related to the suppression of inattended input, these data suggest that suppression of peripheral stimuli may be more effective when attention is directed to the fovea than when the foveal region itself must be suppressed. The behavioral data showing faster RTs and higher  $d'$  for detection of central than peripheral targets suggest the suppression of irrelevant peripheral targets may indeed have been more effective than the suppression of irrelevant central targets.

*Hemispheric asymmetries.* With attention to the *peripheral* stimuli both the amplitude of the  $N_1$  component and the amplitude of the PD component were larger from temporoparietal regions of the right than

the left hemisphere. These asymmetries, together with the behavioral data indicating that detection of the direction of motion tended to be more accurate for LVF than RVF targets, suggest the right hemisphere played a greater role than the left in this task. These data are consistent with proposals, developed on the basis of the different effects of lesions to the left and right hemispheres, that the right parietal areas contribute more to attentional processes than do homologous areas of the left hemisphere<sup>15,17,30,31</sup>. More specifically, the data from this experiment appear to support a modified form of the hypothesis that the greater role of the right hemisphere may be attributable to its ability to attend to both left and right hemispace, whereas the left hemisphere may attend only to the contralateral (right) side of space<sup>17</sup>. The current results suggest that when subjects attend to the left visual field,  $N_1$  amplitudes from the right hemisphere to *all stimuli* are considerably larger than those from the left hemisphere, but that both hemispheres respond equivalently under conditions of attending the right visual field. These effects on  $N_1$  further suggest that the specialized functions of the right hemisphere come into play at a relatively early stage in the processing of peripheral stimuli (i.e. around 100 ms).

The asymmetry of the later PD component with attention to the periphery suggests that the later stages of attentional processing also display a similar lateral specialization. Harter et al.<sup>14</sup> have observed a similar pattern of asymmetries with peripheral attention. In contrast to these results, the attention effects in ERPs to the central standards were bilaterally symmetric over the occipital regions. These data suggest that both hemispheres play a role in the deployment of attention to the objects and events in the center of the visual field, while the specialized mechanisms of the right parietal cortex are primarily concerned with the deployment of attention to the peripheral visual fields. These data are in agreement with clinical evidence from humans showing that lesions to the parietal cortex, especially of the right hemisphere, do not impair the ability to focus attention on foveated objects but markedly interfere with the ability to shift attention to stimuli falling outside the foveal region, in the contralateral hemispace.

*ERPs to targets.* The early (<250 ms) components of the ERPs to target hits displayed morphologies

and attention-related changes similar in several respects to those observed in ERPs to the standards. However the addition of motion differentially affected the ERPs to peripheral and central targets. The overall amplitude of the  $N_1$  component and its attention-related changes were markedly increased at each of the electrode sites for the *peripheral* targets as compared to the peripheral standards. In contrast, the  $N_1$  to *center* targets was of similar amplitude to that of the center standards. These results are in agreement with several different lines of evidence showing that sensitivity to motion, whether real or apparent, is greater in peripheral than in central visual fields<sup>58,66</sup>. The increase in the attention effect on  $N_1$  to moving as compared to stationary *peripheral* stimuli was largest over the temporal, parietal and occipital areas. This distribution is of interest in view of the reports that neurons in parietal and striate cortex are sensitive to motion of low velocities like those used in the present study. Additionally, a recent case study observed a selective disturbance of the perception of movement in the peripheral visual fields following a bilateral lesion affecting the posterior part of the middle temporal gyrus and the lateral occipital gyri and the right angular gyrus<sup>66</sup>. The current results are in agreement with the suggestion that these areas play an important role in the perception of movement in the visual periphery, and further suggest that they may be important in mediating the processes that underlie the deployment of attention to moving peripheral stimuli.

While at most electrode sites the amplitude of  $N_1$  to the *center* targets was similar to that of the center standards, separate comparisons at each of the electrode sites revealed that over the parietal area  $N_1$  and the attention-related increase in its amplitude were increased for central targets as compared to standards. These data suggest that parietal cortex may participate in the perception of and attention to motion in the center as well as the periphery of the visual fields. The suggestion is in agreement with studies of monkeys that report there are directionally selective neurons in parietal area 7 that are active during foveal tracking of moving targets<sup>24,50,52</sup>.

Following 250 ms ERPs to the target hits displayed a prominent negative peak followed by a large positivity. Both components were largest over the posterior scalp and probably correspond to the  $N_2$ - $P_3$  or

P<sub>300</sub> complex elicited in conjunction with the decision that a stimulus was a target (i.e. displayed motion) and the decision concerning its direction of motion. The larger amplitude and earlier latency of P<sub>3</sub> to central than peripheral targets is in agreement with the behavioral data showing superior and faster detection of direction of motion for central than peripheral targets. Moreover, the asymmetry showing P<sub>3</sub> larger from over the right than the left hemisphere is consistent with the behavioral data showing that the detection of motion direction tended to be more accurate for targets in the left than the right visual field.

In summary, the results from this experiment suggest that attention to peripheral and central space may be mediated by non-identical neural systems. The data suggesting more activity of the contralateral temporoparietal cortex for peripheral attention, but greater attention effects over the occipital region for central attention might be seen as in agreement with unit data from research with monkeys and with human clinical data showing that lesions to parietal and occipital areas differentially affect attention to central and peripheral visual events. Similarly the results showing the addition of motion to the attended stimuli substantially increased ERPs associated with peripheral attention, but had smaller and more circumscribed effects on ERPs associated with central at-

tention, is compatible with the animal and human clinical literature. The timing and distribution of the attention effects suggest that specialized systems in the right temporoparietal region come into play early when attention is directed to peripheral space. The fact that ERPs are sensitive to the mechanisms of attention that apparently are different for peripheral and central space suggests this approach may be useful in the study of the normal development and the role of early experience in the development of the two visual systems. We have previously reported that early auditory deprivation may have more pronounced effects on sensory processing of peripheral as compared to central visual stimuli<sup>35</sup>. In companion papers we report on the effects of early auditory deprivation and the acquisition of a visual language on aspects of intra- and interhemispheric organization during attention to peripheral and central space<sup>36,37</sup>.

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