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# Attention to central and peripheral visual space in a movement detection task: an event-related potential and behavioral study. II. Congenitally deaf adults

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(Accepted 22 July 1986)

*Key words:* Attention; Peripheral–central visual field; Event-related brain potential; Deafness; Motion perception; Hemispheric specialization; Development

We compared the effects of focussed attention upon event-related brain potentials (ERPs) to peripherally and centrally located visual stimuli in congenitally deaf subjects (Ss). The results were compared with those obtained from a group of normal hearing Ss in the same paradigm<sup>57</sup>. ERPs from deaf and hearing Ss displayed similar attention-related changes with attention to the centrally located stimuli. These included enhanced amplitudes of the N<sub>1</sub> component (157 ms) over the occipital regions of both hemispheres. By contrast, with attention to peripheral visual stimuli, ERPs from deaf Ss displayed attention-related increases that were several times larger than those from hearing Ss and different in scalp distribution. Whereas for hearing Ss the principal effects of attention to peripheral stimuli occurred over the contralateral parietal region, in deaf Ss the effects were also observed over the occipital regions of both hemispheres. In addition, lateral asymmetries in behavior and the ERPs indicated a greater role for the right hemisphere in this task in hearing Ss, but predominance of the left hemisphere in deaf Ss. These results suggest that auditory deprivation since birth has major effects on the development of the peripheral visual system. The specific pattern of group differences is discussed in relation to other studies of the effects of unimodal deprivation on the development of remaining modalities.

## INTRODUCTION

Philosophers and scientists have long debated the relative contributions of innate and environmental factors in the development of the sensory faculties<sup>6,17,43,64</sup>. One approach to this question has been to study the effects of sensory deprivation in one modality on the functions of remaining modalities. Early observers frequently concluded that when humans are deprived of stimulation through one or more senses compensatory increases in acuity are evident in the intact systems<sup>16</sup>. This point of view has also prevailed in the development of rehabilitative procedures designed to enhance and substitute an intact modality for a missing one<sup>3,75</sup>.

Several psychophysical studies of humans have attempted to verify experimentally the notion of 'inter-

modal compensation' (reviewed in ref. 9). Many such studies have measured sensory thresholds and acuity for simple stimuli. Taken as a whole, studies employing this type of test have not provided unambiguous evidence for compensatory enhancements following auditory or visual deprivation. Significantly, however, superiority of remaining modalities has been reported in studies that have required more complex processing, suggesting that the effects of sensory deprivation may be most marked on higher order perceptual and attentional processes of remaining modalities. For example, there are reports that attention to and localization of auditory, cutaneous and kinaesthetic information are superior in blind as compared to sighted individuals and psychoacoustic functions such as speech discrimination may be superior in the blind<sup>4,60,79</sup>. It is of interest to note that Diderot<sup>16</sup> at-

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tributed the apparently greater sensitivity to sounds demonstrated by the blind to superior attentional abilities.

While these behavioral data suggest that compensatory changes may occur primarily at higher levels of the nervous system, very little evidence is available concerning the neural mechanisms that might mediate such behavioral changes in humans. By contrast, over the past several years much has been learned about the changes in neural structures and functions following sensory deprivation in animals.

#### *Intramodal effects of sensory deprivation*

The morphological and physiological consequences of visual deprivation have been extensively studied beginning with the work of Wiesel and Hubel<sup>87,88</sup>. Following monocular deprivation for 3 months after birth most cells in area 17 of the cat are activated only by the experienced eye and the remainder display abnormal receptive fields. The important contribution of visual experience in the development of physiological properties of neurons in area 17 became further evident when studies of totally visually deprived animals revealed more binocularly driven cells with more normal receptive fields than were seen in monocularly deprived animals<sup>89,90</sup>. On the basis of these results it was suggested that one mechanism underlying the extensive neural reorganization following monocular deprivation might be competition between inputs from the two eyes for cortical synaptic sites<sup>41,89</sup>.

#### *Intermodal effects of sensory deprivation*

Extending this intramodal model of competition, other authors have proposed that a similar process of competition for neural connections between developing modalities might account for the effects of total visual deprivation on behavior. For example, Hyvarinen et al.<sup>35</sup> reported that in area 19 of visually deprived monkeys there is both a marked reduction of neurons responsive to visual stimulation and a significant increase in the number of cells responsive to somatic stimulation. They suggest this pattern of results may reflect the take-over of visual neurons by non-visual inputs in the absence of competition for synaptic space from visual inputs. Similar effects were observed in non-visual brain regions that receive polymodal inputs including parietal cortex (area 7)<sup>36</sup>. Ad-

ditionally, both superficial and deep layers of the superior colliculus display a reduction of visual responsiveness and increased responsiveness to auditory and somatosensory stimulation following visual deprivation<sup>15,68,85</sup>. A similar mechanism may underlie reports of abnormally large auditory evoked responses over visual cortex in blind mice<sup>6</sup> and of enhanced visual evoked responses over auditory cortex in congenitally deaf cats<sup>65,66</sup>.

The behavioral consequences of intermodal changes like these could take two main forms. First, decreased visual responsiveness of polymodal brain areas may account for the profound and apparently irreversible deficits in visual behavior that have been well documented following early visual deprivation in both humans and animals. Secondly, it is conceivable that the increased neural representation of remaining sensory modalities might underlie the reports of superior abilities within intact modalities observed in humans that have been blind or deaf since birth.

#### *Electrophysiological studies of blind and deaf humans*

Several studies have employed the EEG and event-related potential (ERP) techniques to study changes in cerebral organization following sensory deprivation in humans. Soon after Berger discovered the occipital  $\alpha$  rhythm of the EEG, Adrian and Matthews<sup>1</sup> observed that it was absent in blind subjects. They suggested that increased input from other modalities may desynchronize the EEG over the visual cortex in the blind. Their observation has since been replicated by several investigators<sup>30,61,62</sup>. Similarly, in deaf humans the EEG has been reported to show increases in photic driving over temporal brain regions<sup>62</sup>. A potentially more informative approach to the changes in intermodal organization accompanying sensory deprivation is to compare ERPs elicited by specific sensory or cognitive events in normal and unimodally deprived individuals. Numerous studies over the past two decades have documented the sensitivity of ERPs to the structural integrity of the nervous system and their power in elucidating the nature and timing of neural processes associated with specific aspects of information processing (reviewed in refs. 18, 32, 80).

In agreement with some of the psychophysical studies of blind humans, ERPs recorded to auditory

and somatosensory stimuli are reported to display shorter latencies in blind than sighted humans<sup>22,60</sup> and evoked responses to vibrotactile stimuli are larger and display shorter latencies in deaf than in hearing adults<sup>69</sup>. Neville et al.<sup>59</sup> presented further evidence for intermodal reorganization in deaf adults. They reported that over temporal and frontal brain regions the amplitude of the N<sub>150</sub> response of the ERP to visual stimuli was several times larger in congenitally deaf than in normally hearing Ss. The group differences were not observed in ERPs to visual stimuli presented to the fovea but were only apparent for stimuli presented in the peripheral visual fields. This suggested an increased reliance by deaf individuals on peripheral vision for the detection and localization of peripheral events. Another possibility, however, is that foveal input is less modifiable by experience than is that from the periphery. In support of this notion are studies showing that the Y cell system, which originates predominantly in the peripheral retina, develops later and is more sensitive to experience (i.e. displays more pronounced effects of visual deprivation) than are the X or W cell systems that arise primarily in the area centralis<sup>77,78</sup>. Moreover, since the Y cell system projects to extrastriate and parietal cortex these results are consistent with the reports showing marked effects of binocular deprivation in these cortical areas<sup>35,36</sup>.

These findings suggest that the behavioral consequences of early sensory deprivation might be more apparent on the processing of peripheral visual information and might be evident in measures of capacities like visual attention for which the integrity of the parietal cortex is essential. In support of this notion are studies showing that visual deprivation may affect visual attention more than visual acuity<sup>34,67,70</sup>. However, behavioral studies of humans or animals have not compared the effects of sensory deprivation on the processing of peripheral and central visual stimuli.

#### *ERP studies of visual attention*

A number of studies over the past decade have demonstrated the utility of ERPs in descriptive and analytic studies of selective attention to auditory, somatosensory and visual stimuli (reviewed in refs. 32, 33). However, a comparison of the effects of attention directed to peripheral vs central visual space had

not been reported. In Neville and Lawson<sup>57</sup> we report that in normal hearing Ss attention to peripheral and central regions of space in a task requiring the perception of direction of motion is associated with ERPs that have markedly different distributions over the scalp. During attention to the center of the visual field, the effects of attention were most marked in ERPs recorded over the occipital regions and were bilaterally symmetrical. In contrast, with attention to the periphery, the effects of attention were largest in ERPs recorded from over the parietal regions of the hemisphere contralateral to the attended visual field. In addition to these differences in anterior/posterior distribution, attention-related ERP changes displayed different lateral distributions for stimuli at different locations. While attention to the center produced bilaterally symmetrical attention effects, attention to both the left and the right visual fields produced attention effects that were larger from over the right than the left hemisphere. Thus, these results suggested that in normal hearing adults attention to peripheral and central regions of space are mediated by different neural systems that may include a greater role for the parietal cortex with peripheral attention, and a greater role for the occipital regions when attention is directed to foveated events. Additionally, these results suggested that the special role of the right parietal cortex in human spatial attention may be reserved for the processing of extrafoveal events.

In the present experiment we explored the hypothesis that in humans deaf since birth the systems that mediate attention are substantially modified and their capacities are enhanced when compared to normal hearing individuals.

## MATERIALS AND METHODS

### *Subjects*

Twelve deaf adults (6 male; mean age 21 years, range 17–26) with normal or corrected vision were paid to participate in the experiment. All but one subject (S) were right-handed. Each S was profoundly deaf, bilaterally, had been so since birth, and had at least one congenitally deaf relative. All Ss were free of other neurological disorders. The first language and major form of communication employed by these Ss was American Sign Language (ASL). Re-

sults from these Ss are compared with those from the 12 normally hearing Ss, reported in Neville and Lawson<sup>57</sup>.

#### *Stimuli, procedures and data analysis*

All methods were identical to those reported in the companion study of hearing Ss, except that the task instructions were presented in ASL. Briefly, the stimuli were white squares ( $0.6^\circ$ ) presented with an ISI of 280–480 ms  $18^\circ$  to the left (LVF) and right visual field (RVF) of a central fixation point (peripheral stimuli) and just above the fixation point (central stimuli). Eighty percent of the stimuli were single presentations of the squares for 33 ms ('standards'). Twenty percent of the stimuli 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 33 ms. The appearance of the second square produced a clear illusory movement in the direction of the second square (i.e. along the vertical, horizontal or diagonal axes).

During each of 6 blocks of trials Ss foveated the fixation point and focussed their attention on the stimuli in only one of 3 locations, in order to detect the direction of motion of the targets in that location. Ss kept their finger on the center button of a  $3 \times 3$  array and pressed one of 8 surrounding buttons to indicate the direction of motion of targets that occurred at the attended location. Half of Ss pressed with the left and half with the right hand. Scalp electrical activity was recorded from homologous points over left and right occipital, parietal, temporal, anterior temporal and frontal regions. Recordings from these electrodes and the vertical EOG recorded from the left inferior orbital ridge, were referred to the linked mastoids, and were amplified with a band pass of 0.01–100 Hz (time constant 8 s). The horizontal EOG was recorded between electrodes placed on the left and right external canthi, and was amplified with a DC amplifier and high-frequency half-amplitude cut-off of 60 Hz.

The EEG and EOG were digitized for 100 ms prior to and 924 ms following each stimulus presentation at a rate of 1 point/4 ms. Trials in which excessive eye movement or muscle artifact occurred were excluded (approximately 10% of all trials, range 2–15%). 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 as either peak or area amplitudes within a specified latency range. ERPs from deaf Ss were analyzed with a 5-way analysis of variance with repeated measures on the factors of location, attention, hemisphere and electrode. Comparisons of deaf and hearing Ss added group as a factor.

Behavioral measures of percent correct reaction time and  $d'$  and B were also scored by computer.

## RESULTS

### *Deaf subjects*

#### *Standards*

*ERP waveforms.* As seen in Fig. 1, the ERPs to the standard stimuli displayed a series of negative and positive components that varied in amplitude and latency both as a function of electrode position and attention condition. Over the posterior scalp two positive peaks at 100 and 230 ms ( $P_1$  and  $P_2$ ) were separated by a negative component ( $N_1$ ). After 250 ms the ERPs displayed broad shifts whose polarity depended on direction of attention.

*$P_1$  and  $P_2$ .* The amplitude of  $P_1$  was largest over the occipital regions for both central and peripheral stimuli (electrode central stimuli,  $P < 0.0001$ ; peripheral stimuli,  $P < 0.0001$ ). Focussed attention to both types of stimuli significantly enhanced  $P_1$  amplitude. These effects were largest over the occipital regions and were bilaterally symmetrical (attention  $\times$  electrode,  $P < 0.0001$ ). The amplitude of  $P_2$  to the central stimuli was largest from the occipital electrodes and was significantly enhanced with attention (electrode,  $P < 0.0001$ ; attention,  $P < 0.002$ ). Similarly, for peripheral stimuli  $P$  amplitude was increased with attention (location  $\times$  attention,  $P < 0.004$ ). This effect tended to be largest over the hemisphere ipsilateral to the attended periphery (location  $\times$  attention  $\times$  hemisphere,  $P < 0.01$ ).

*$N_1$ .* The amplitude of the  $N_1$  component was significantly increased when attention was directed to the eliciting stimuli as compared to when it was directed elsewhere. The magnitude and the distribu-

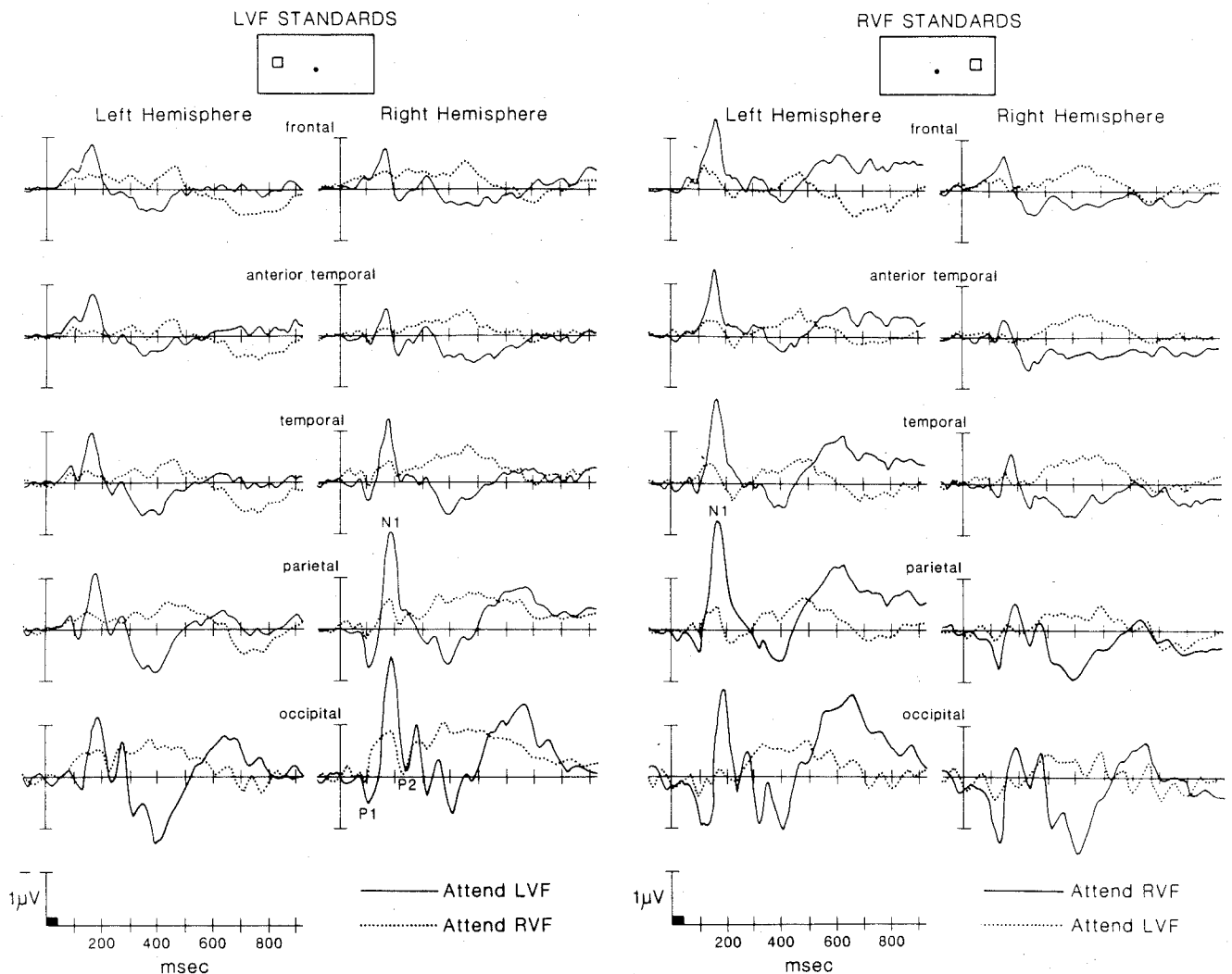


Fig. 1. ERPs averaged across 12 deaf subjects (Ss) to peripheral standards (presented to the left visual field (LVF) and right visual field (RVF)) when attended and inattended. Recordings from left and right frontal, anterior temporal, temporal, parietal and occipital regions.

tion of the attention-related increase on  $N_1$  was markedly different for the central and peripheral standards (location  $\times$  attention  $\times$  electrode,  $P < 0.0001$ ).

With attention to the center stimuli  $N_1$  was increased significantly over the occipital and parietal electrodes (attention,  $P < 0.0001$ ; attention  $\times$  electrode,  $P < 0.0001$ ). These effects were of equal amplitude over the two hemispheres (hemisphere, n.s.).

By contrast, attention to the peripheral stimuli was associated with significantly larger increases in  $N_1$  than for central stimuli (location  $\times$  attention,  $P < 0.0001$ ). Additionally, the distribution of the effects was different for the two types of stimuli (location  $\times$  attention  $\times$  electrode,  $P < 0.0001$ ). With attention to

the peripheral standards,  $N_1$  amplitude was increased over the temporal, parietal and occipital regions of the hemisphere contralateral to the stimulus (location  $\times$  attention,  $P < 0.0001$ ; location  $\times$  attention  $\times$  hemisphere  $\times$  electrode,  $P < 0.0001$ ). In addition, attended LVF stimuli also elicited large  $N_1$  responses over the ipsilateral (left) hemisphere (location  $\times$  attention  $\times$  hemisphere,  $P < 0.0004$ ; see Fig. 1).

Both the overall amplitude of  $N_1$  and the effects of attention on  $N_1$  were larger over the left than the right hemisphere (hemisphere,  $P < 0.02$ ; location  $\times$  attention  $\times$  hemisphere,  $P < 0.0004$ ). This asymmetry was evident at each of the electrode sites except the occipital regions where  $N_1$  was largest over

the hemisphere contralateral to the stimulus (hemisphere  $\times$  electrode,  $P < 0.001$ ; location  $\times$  hemisphere  $\times$  electrode,  $P < 0.0008$ ). Thus, as seen in Fig. 1, the contralateral distribution of  $N_1$  amplitude was much more pronounced for RVF than for LVF stimuli over the temporal and parietal sites (location  $\times$  hemisphere  $\times$  electrode,  $P < 0.0008$ ). As seen in Fig. 2, whereas with attention to the LVF  $N_1$  amplitude to all stimuli was similar over the left and right parietal regions, with attention to the RVF its amplitude was considerably larger over the left than the right hemisphere (attention  $\times$  hemisphere,  $P < 0.002$ ; attention  $\times$  hemisphere  $\times$  electrode site,  $P < 0.0001$ ).

*Area 300–600.* As seen in Fig. 1., ERPs to attended standards displayed a positive component peaking around 400 ms. By contrast ERPs to the same stimuli when inattended displayed a broad negativity from 300 to 600 ms (location  $\times$  attention,  $P < 0.0001$ ). Thus the effect of attention in this time region was the addition of a positivity (PD), which is evident in the difference ERPs (formed by subtracting ERPs to given stimuli when inattended from ERPs to the same stimuli when attended; see Fig. 3). PD was largest from over the occipital regions for both peripheral (electrode,  $P < 0.01$ ) and central (electrode,  $P < 0.005$ ) attention. Additionally, the overall amplitude of PD was larger with attention to peripheral than to central stimuli (location,  $P < 0.02$ ).

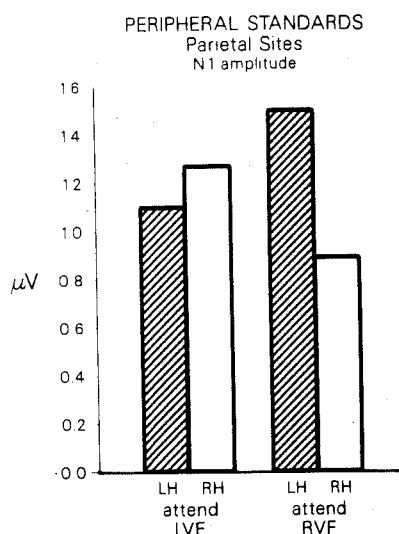


Fig. 2. Mean amplitude in  $\mu\text{V}$  of  $N_1$  across LHF and RVF stimuli from left (LH) and right (RH) parietal sites under attend LVF and attend RVF conditions.

*SW (area 600–900, difference ERPs).* Also evident in the difference waveforms (Fig. 3), following PD a broad negative wave was evident that was larger over the left than the right hemisphere both with attention to the central ( $P < 0.01$ ) and peripheral ( $P < 0.001$ ) standards.

#### Targets

ERPs to the target hits displayed a morphology similar to that of the attended standards, with the addition of a prominent negative peak around 270 ms ( $N_2$ ) and a large positivity peaking around 450 ms ( $P_3$ ) that was followed by a broad slow wave (SW).

*$P_1$  and  $P_2$ .*  $P_1$  was larger for targets than for standards (stimulus,  $P < 0.0001$ ). This increase was largest over the occipital regions for central stimuli, but over the frontal, temporal and parietal regions for peripheral stimuli (stimulus  $\times$  location  $\times$  electrode,  $P < 0.0001$ ). The amount by which  $P_1$  amplitude was increased with attention, however, was equivalent for standards and targets. Similarly  $P_2$  amplitude was larger for targets than for standards but the attention related increases in its amplitude were similar for the two types of stimuli.

*$N_1$ .* For central stimuli the increase in  $N_1$  amplitude with attention was larger for targets than standards over the parietal regions only (stimulus  $\times$  attention  $\times$  electrode,  $P < 0.0004$ ), while for peripheral targets the increase was apparent over more anterior regions as well (stimulus  $\times$  location  $\times$  attention,  $P < 0.05$ ).  $N_1$  amplitude was asymmetrical for peripheral but not central targets, similar to the effects observed in the ERPs to the standards, i.e. both the overall amplitude and the increase in amplitude with attention were larger from over the left than the right hemisphere (hemisphere,  $P < 0.004$ ; location  $\times$  attention  $\times$  hemisphere,  $P < 0.001$ ).

*$N_2$ .* The  $N_2$  to correctly detected targets was larger for peripheral than central hits (location,  $P < 0.01$ ), and was largest over the occipital and parietal regions for peripheral hits, but was largest over the parietal regions for central hits (attention  $\times$  location  $\times$  electrode,  $P < 0.0001$ ). Its amplitude was larger from over the hemisphere contralateral to the peripheral targets (location  $\times$  attention  $\times$  hemisphere,  $P < 0.003$ ).

*$P_3$ .* The  $P_3$  response was larger and peaked earlier for central than for peripheral targets over the parie-

## DIFFERENCE ERPs

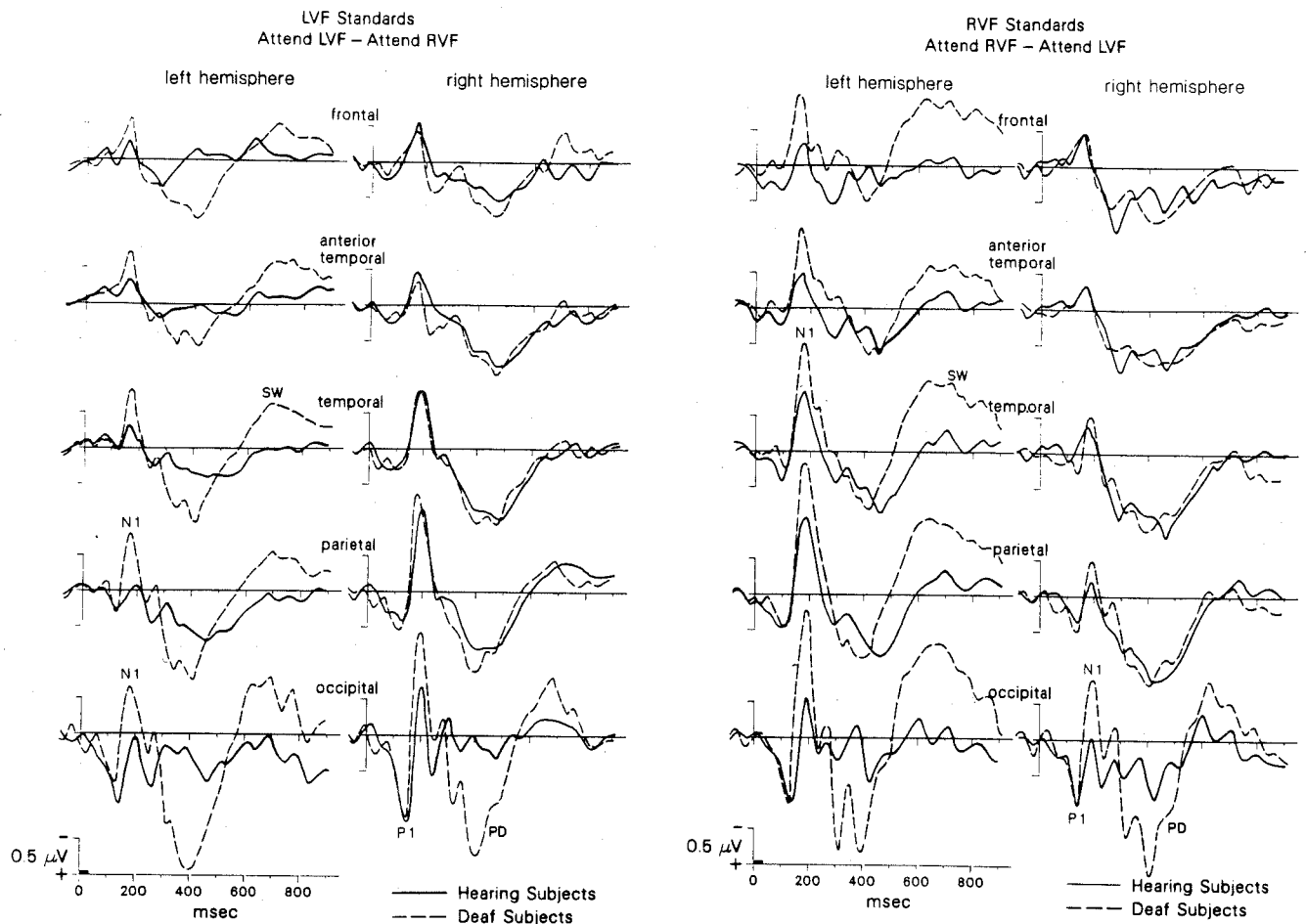


Fig. 3. Difference waveforms for LVF and RVF standards (formed by subtracting ERPs to inattended stimuli from ERPs to the same stimuli when attended) from 12 hearing (—) and 12 deaf (----) Ss. Recordings from left and right frontal, anterior temporal, temporal, parietal and occipital regions.

tal and occipital sites (location  $\times$  attention  $\times$  electrode,  $P < 0.0001$ ). For both peripheral and central targets  $P_3$  was largest from over the occipital regions (electrode,  $P < 0.0001$ ) and was of equivalent amplitude from the two hemispheres (hemisphere, n.s.).

*SW (area 700–900)*. Following  $P_3$ , a broad slow wave was evident in the ERPs to the target hits. This SW was more negative at the frontal than over the posterior and occipital regions (electrode,  $P < 0.002$ ). SW displayed a large (2–3  $\mu\text{V}$ ) asymmetry over the frontal, anterior temporal, temporal and parietal electrodes where it was consistently more negative from over the left than right hemisphere. This asymmetry was present in ERPs to both peripheral and central targets (location  $\times$  attention  $\times$  hemisphere  $\times$  electrode,  $P < 0.0001$ ).

#### Behavioral data

Deaf subjects were faster and more accurate at detecting direction of motion for central than peripheral targets ( $P < 0.0001$ ). For peripheral targets they

TABLE I

Mean latency  $P_1$  and  $N_1$  values (ms)

	Frontal	Anterior temporal	Temporal	Parietal	Occipital
$P_1$					
Hearing	106	104	95	99	105
Deaf	103	102	93	93	99
$N_1$					
Hearing	131	132	139	152	157
Deaf	136	140	145	157	167

TABLE II

Mean baseline to peak amplitude ( $\mu V$ ) of  $P_1$  and  $P_2$  components to stimuli at different locations under different attention conditions  
Values from left (LO) and right (RO) occipital sites, from hearing and deaf subjects.

	Location of stimulus					
	LVF		Center		RVF	
	LO	RO	LO	RO	LO	RO
<i>P<sub>1</sub> amplitude</i>						
Hearing Ss						
Attend LVF	0.8	1.0	1.5	1.7	0.4	0.4
Attend center	0.5	0.5	2.3	2.5	0.5	0.3
Attend RVF	0.2	0.4	1.3	1.4	1.1	0.8
Deaf Ss						
Attend LVF	0.7	1.1	1.9	2.1	0.9	0.8
Attend center	0.3	0.5	2.5	3.1	0.5	0.3
Attend RVF	0.2	0.5	1.8	1.9	1.6	1.7
<i>P<sub>2</sub> amplitude</i>						
Hearing Ss						
Attend LVF	0.8	0.9	0.8	1.1	0.6	0.4
Attend center	-0.1	0.1	1.9	2.2	0.3	-0.1
Attend RVF	0.2	0.4	1.1	0.9	0.9	1.2
Deaf Ss						
Attend LVF	1.0	0.6	1.2	1.5	0.6	0.6
Attend center	0.0	0.1	2.2	2.2	0.3	0.0
Attend RVF	0.2	0.2	1.1	1.0	1.2	1.4

tended to be more accurate in detecting the direction of motion when it occurred in RVF than LVF (percent correct,  $P < 0.08$ ).

#### Comparison of results from deaf and hearing Ss

##### Standards

*ERP waveforms.* The overall morphology of the ERPs was similar in deaf and hearing Ss and focussed attention altered the different components in similar ways in the two groups. However the magnitude and distribution of some of the attention-related changes were markedly different in deaf and hearing subjects.

*P<sub>1</sub> and P<sub>2</sub>.* The latencies, overall amplitudes and increases in amplitude with attention on both  $P_1$  and  $P_2$  were similar in deaf and hearing Ss (see Tables I and II).

*N<sub>1</sub>.* The latencies of  $N_1$  were similar in the two groups (see Table I). For the central standards the increase in amplitude of  $N_1$  with attention was of similar magnitude and displayed similar anterior-posterior distributions in deaf and hearing subjects. However, there was a tendency for the overall amplitude

of  $N_1$  to be larger from over the left than the right hemisphere in deaf subjects, but larger from the right than the left hemisphere in hearing subjects (group  $\times$  hemisphere,  $P < 0.02$ ).

In contrast to the results for central standards, for peripheral standards the magnitude of the attention related increase was considerably larger in deaf than in hearing Ss (group  $\times$  location  $\times$  attention,  $P < 0.001$ ; see Figs. 3 and 4). Moreover, with attention to the peripheral stimuli both the lateral distribution and the anterior posterior distribution of the attention effect were different in the two groups. As seen in Figs. 3-5, whereas hearing Ss displayed small at-

TABLE III

*N<sub>1</sub> amplitude ( $\mu V$ ) from left (LP) and right parietal (RP) sites to LVF and RVF standards while attending center*

	Stimulus			
	LVF		RVF	
	LP	RP	LP	RP
Hearing Ss	-0.6	-1.2	-0.9	-0.9
Deaf Ss	-1.2	-0.9	-0.9	-0.5



tention effects over the occipital regions deaf subjects displayed large attention-related increases over both left and right occipital regions (group  $\times$  location  $\times$  attention  $\times$  electrode,  $P < 0.001$ ). In addition, while over the right parietal and temporal regions the two groups displayed attention effects on  $N_1$  that were not significantly different, over the left parietal and temporal regions both the overall amplitude of  $N_1$  and the attention effects on  $N_1$  were larger in deaf than in hearing Ss (group  $\times$  hemisphere,  $P < 0.002$ ; group  $\times$  location  $\times$  attention  $\times$  hemisphere,  $P < 0.001$ ; see Figs. 5 and 6). As seen in Fig. 3, both the bilateral occipital increase in the deaf Ss and the amplitude increase in deaf Ss over the left hemisphere occurred irrespective of which lateral visual field was attended. The opposite patterns of lateral asymmetries in the two groups were also evident for unattended peripheral stimuli under conditions of attend center (see Table III).

*PD.* There were no group differences in the ampli-

tude or distribution of PD to central standards. For both deaf and hearing Ss PD was maximal over the occipital regions with attention to the center (electrode,  $P < 0.001$ ). With attention to both peripheral stimuli, however, the amplitude of PD was larger in deaf than in hearing Ss over the occipital regions of both hemispheres (group  $\times$  electrode,  $P < 0.01$ ; see Fig. 3).

*SW (area 700–900).* A slow negative component was evident from 700 to 900 ms in the difference ERPs over the left hemisphere in the deaf subjects (see Fig. 3). SW was significantly larger from the deaf than the hearing Ss for both peripheral and central stimuli over the anterior and posterior regions of the left hemisphere (peripheral stimuli, group  $\times$  hemisphere,  $P < 0.01$ ; central stimuli, group  $\times$  hemisphere,  $P < 0.006$ ).

#### Targets

ERPs to the targets whose direction of motion was

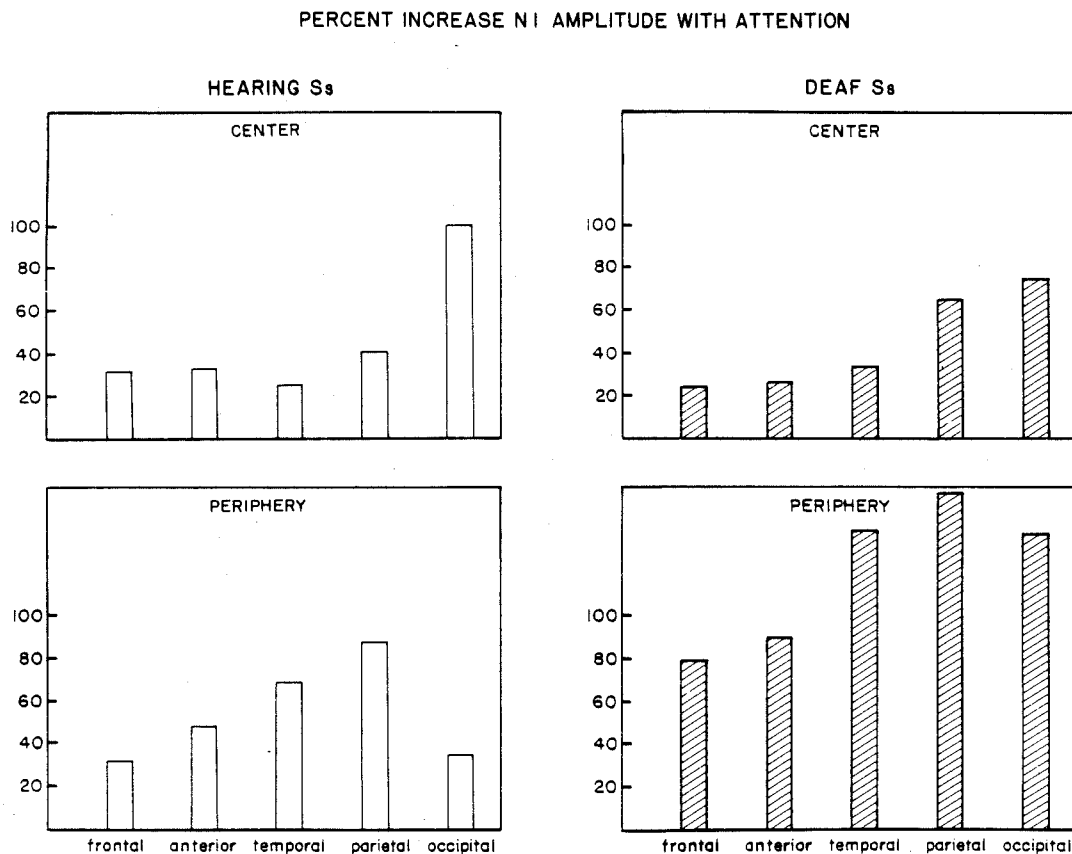


Fig. 4. Percent by which  $N_1$  amplitude was increased from inattend to attend conditions for hearing and deaf subjects. Top: center standards, mean of left and right frontal, anterior temporal, temporal, parietal and occipital sites. Bottom: peripheral standards, mean of contralateral frontal, anterior temporal, temporal, parietal and occipital sites.

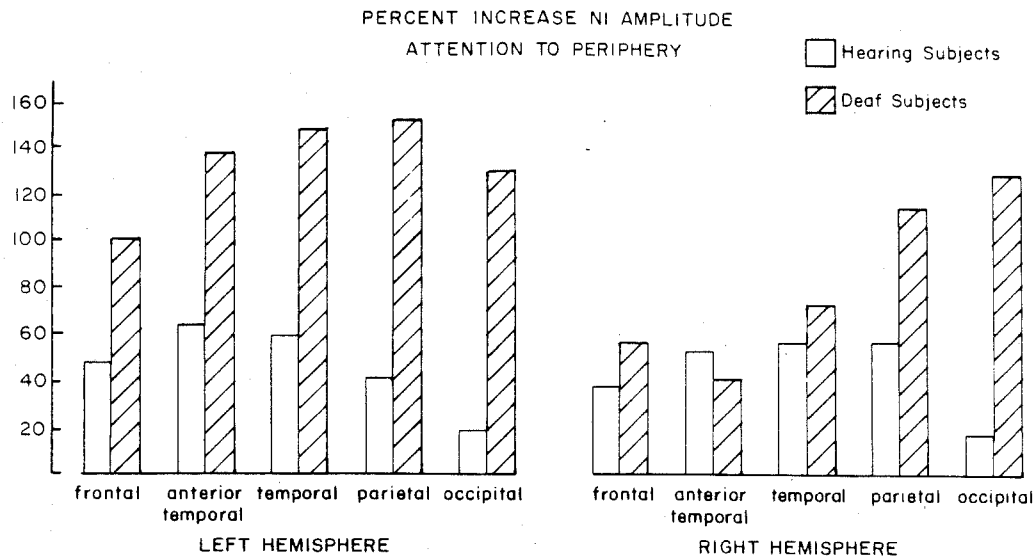


Fig. 5. Percent by which  $N_1$  amplitude to peripheral standards was increased from inattent to attend conditions for hearing and deaf Ss. Mean of responses to LVF and RVF stimuli.

correctly detected ('hits') displayed a similar morphology in deaf and hearing Ss. As for the standards, the  $P_1$  and  $P_2$  components were similar in the two groups. As seen in Fig. 7, the attention effects on  $N_1$  displayed group differences similar to those observed for the standards. The additional  $N_2$ ,  $P_3$  and SW components displayed group differences that were most marked over the left hemisphere.

$N_1$ . As for the central standards the effects of attention on  $N_1$  to the central targets were of similar magnitude and distribution in deaf and hearing Ss. For both groups the central targets elicited larger attention effects than the central standards over the pa-

rietal areas.

The group differences in the attention effects on  $N_1$  seen for the peripheral standards were also evident in the ERPs to the peripheral targets. Thus deaf and hearing Ss displayed similar  $N_1$  amplitudes over the right temporal and parietal regions, but deaf Ss displayed greater attention effects than hearing Ss over both occipital regions ( $P < 0.001$ ), and also over the left temporal and parietal electrodes (group  $\times$  location  $\times$  attention  $\times$  electrode  $\times$  hemisphere,  $P < 0.001$ ; group  $\times$  attention,  $P < 0.01$ ; see Fig. 7). Additionally, as for the standards, the overall amplitude of  $N_1$  was larger from the right than the left hemisphere in hearing Ss, but was larger from the left than the right hemisphere in deaf Ss (group  $\times$  hemisphere,  $P < 0.009$ ; see Fig. 6).

$N_2$ . While for central targets  $N_2$  was similar in the two groups, with attention to the periphery the  $N_2$  component peaked earlier and tended to be larger in deaf than hearing Ss in ERPs recorded from over posterior regions of the left hemisphere (latency, group  $\times$  attention,  $P < 0.003$ ; group  $\times$  location  $\times$  attention  $\times$  hemisphere,  $P < 0.03$ ; amplitude, group  $\times$  attention  $\times$  hemisphere  $\times$  electrode,  $P < 0.05$ ; see Fig. 7).

$P_3$ . For both central and peripheral targets  $P_3$  tended to occur earlier in deaf than hearing Ss over temporal and parietal regions of the left hemisphere (group  $\times$  location  $\times$  attention  $\times$  hemisphere  $\times$  electrode,  $P < 0.006$ ; see Fig. 7).

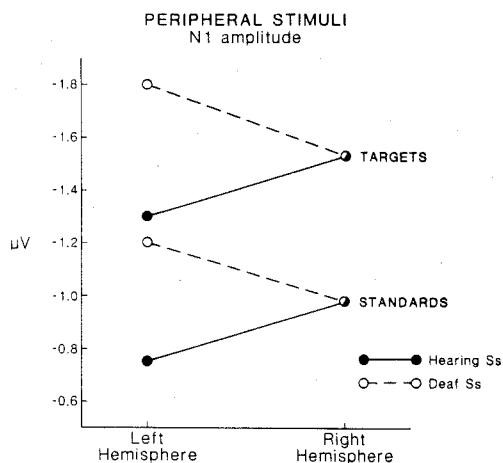


Fig. 6. Amplitude of  $N_1$  from the left and right hemispheres for hearing (—) and deaf (---) Ss. Mean amplitude across all conditions, for standards and targets separately.

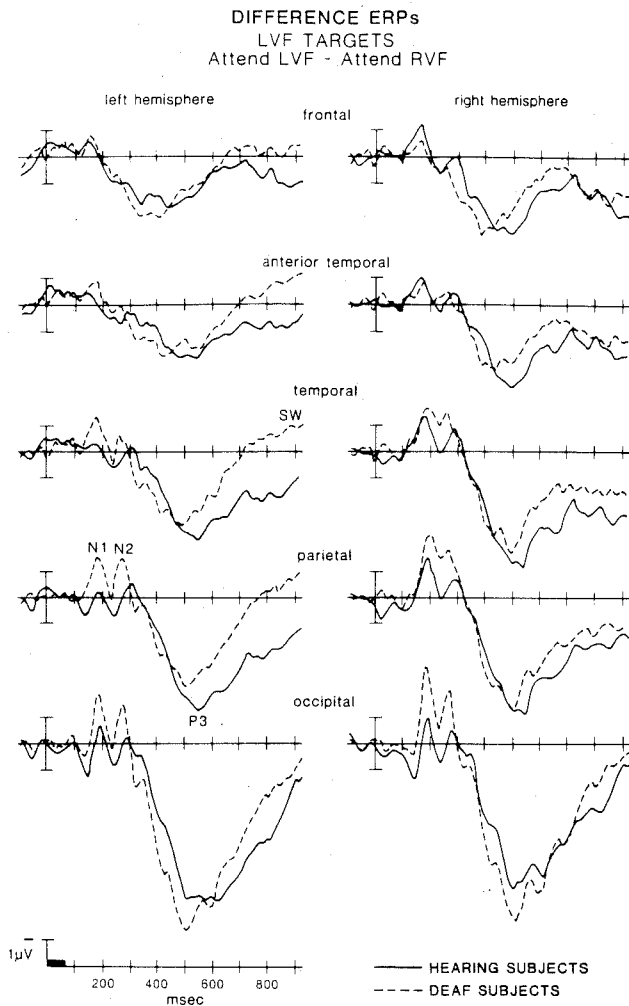


Fig. 7. ERPs from hearing (—) and deaf (---) Ss to LVF targets when attended and correctly detected, and when inattentive. Recordings from left and right frontal, anterior temporal, temporal, parietal and occipital sites.

$S_w$ . Following  $P_3$ , ERPs to the target hits remained positive in the hearing Ss, but displayed a negative slow wave in the deaf Ss. This group difference was apparent over both hemispheres for the central targets (group,  $P < 0.002$ ) but was greatest over the left hemisphere for the peripheral targets (group  $\times$  hemisphere,  $P < 0.003$ ; see Fig. 7).

#### Behavioral data

Whereas hearing subjects more accurately detected the direction of motion of targets in the LVF than the RVF, deaf subjects were more accurate in detecting direction of motion of RVF than LVF targets ( $d'$  group  $\times$  visual field  $F_{1,22} = 4.5$ ,  $P < 0.04$ ). As shown in Fig. 8, the two groups performed similarly for central targets and for LVF targets, but deaf Ss

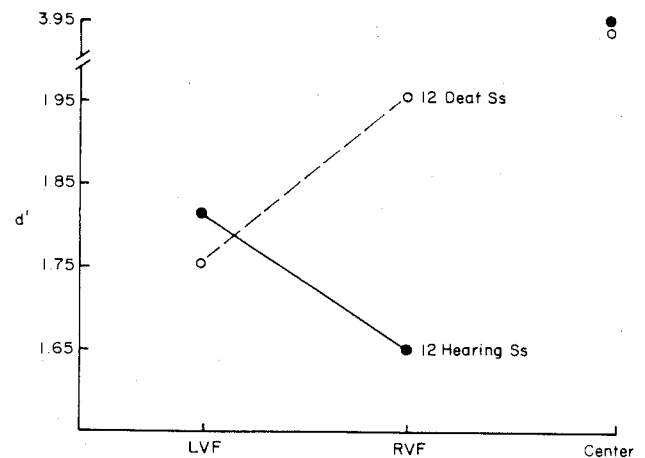


Fig. 8. Detection ( $d'$ ) of LVF, RVF and central targets for hearing (—) and deaf (---) Ss.

were more accurate than hearing Ss for RVF stimuli. A similar tendency was observed for measures of B (group  $\times$  visual field,  $F_{1,22} = 3.1$ ,  $P < 0.09$ ). Additionally, for peripheral stimuli deaf Ss responded on average 70 ms faster than hearing Ss ( $P < 0.04$ ).

#### DISCUSSION

These results support the proposal that the neural systems that mediate attention to visual space and perception of motion are different in normal hearing and congenitally deaf individuals. Moreover, they are in agreement with the hypothesis that while the processing of visual information presented to the foveal region is similar in deaf and hearing Ss, major differences occur in the cerebral systems that mediate perception and attention to peripheral visual information following auditory deprivation since birth.

As reported in Neville and Lawson<sup>57</sup>, ERPs from normal hearing Ss displayed distinct patterns of attention-related changes when attention was focussed on central as compared to peripheral space. With attention to the center, the amplitude of  $N_1$  was increased over the occipital regions of both hemispheres, while with attention to the periphery the major amplitude increase occurred over the temporal and parietal regions of the hemisphere contralateral to the attended periphery. These results were interpreted as in agreement with proposals that suggest peripheral and central information are processed by somewhat separate and parallel visual systems<sup>7, 73, 83, 84</sup>.

Like the hearing Ss, with attention to central space ERPs from deaf Ss also displayed increases in  $N_1$  amplitude that were largest over posterior regions bilaterally, and these were similar in magnitude to those seen in the hearing Ss. By contrast, attention to both LVF and RVF peripheral stimuli was associated with attention effects on the ERPs that were several times larger in deaf than in hearing Ss. Moreover the distribution of the attention effects for the peripheral stimuli displayed marked and specific group differences that occurred independently of which periphery was attended. Thus, while over right temporal and parietal regions deaf and hearing subjects displayed similar attention effects, group differences were of two types: (1) over both left and right occipital regions deaf Ss displayed attention effects that were 5–6 times larger than those observed in hearing Ss; and (2) over the left temporal and parietal regions deaf Ss displayed attention effects that were 2–3 times larger than those seen in hearing Ss.

These results can be compared with animal studies that have reported two major types of change following unimodal sensory deprivation since birth. First there is evidence for increased growth and activity in cortical structures associated with the remaining modalities — termed ‘compensatory hypertrophy’<sup>9,28,40,71</sup>. While very little is known about the possibility that similar changes might occur in humans under such circumstances, the data from the present experiment showing increased attention-related activity over the occipital regions in deaf Ss suggest that there may be compensatory increases in this type of visual activity following auditory deprivation since birth. Additionally, the behavioral data showing that deaf subjects detected the direction of motion faster and more accurately than hearing Ss indicate there are functional consequences of the increased physiological activity. The finding that the increases in ERP amplitudes and superior performance in the deaf were specific to the processing of the peripheral visual stimuli is consistent with an earlier study of the refractory period of visual ERPs in humans<sup>59</sup> and with research in animals (discussed above) showing that structures and functions associated with the ‘secondary’ visual system are more affected by sensory deprivation than is the geniculostriate system<sup>36,67,77</sup>.

The second major type of change observed in animals following unimodal sensory deprivation is that

neural structures that would normally process input to the deprived modality may instead mediate processing of information in remaining modalities — this has been termed ‘vicarious functioning’<sup>9</sup>. Thus, for example, in both cats<sup>65,66</sup> and humans<sup>60</sup> visual evoked responses recorded over auditory brain regions are larger than normal following auditory deprivation since birth. Additionally, visual cortex displays increased auditory responsiveness following visual deprivation<sup>6</sup>. Perhaps the present results, showing increased attention effects in ERPs over the left temporal and parietal regions in deaf Ss are also indicative of this type of functional reorganization. It may be, for example, that since our deaf Ss had not acquired speech, nor any auditory language skills, that regions of the left hemisphere which would normally mediate these functions, instead play a role in the type of visual spatial processing required in the present task.

#### *Possible mechanisms underlying intermodal changes*

There are several different mechanisms that might underlie both types of change observed in this study. Considerable evidence has accumulated which shows that substantial loss of neurons and synapses characterizes normal neural development (reviewed in ref. 14) and also that neuronal activity plays a major role in specifying the selective elimination and maintenance of cortical connections<sup>11,12,21,42,50</sup>. Moreover some evidence suggests that in the immature animal there is multimodal innervation of different cortical sensory areas<sup>26,37,45</sup> which is normally eliminated in early postnatal development. Conceivably, normal input through each sensory modality to the corresponding cortical area plays a role in the stabilization and/or maintenance of afferents in the appropriate modality and in the elimination of extramodal inputs. By this line of reasoning when auditory input is absent visual afferents to ‘auditory’ areas would be maintained. This would be in line with the intermodal cortical competition hypothesis, discussed above, and with the several lines of evidence showing the importance of patterned neural activity in determining the functional specializations of different neural populations.

A related possibility is that the major effect of sensory deprivation may be on those brain regions that receive multimodal input throughout life. For exam-

ple, there are reports of acoustically responsive cells in visual cortex that are selective for direction and display spatial selectivity<sup>23,48,49</sup>. Additionally, the multisensory nature of the superior colliculus has been well described<sup>47,81</sup>. Moreover, in unimodally deprived animals, cells in the superior colliculus (SC) shift their responsiveness in favor of remaining modalities<sup>15,68,85</sup>. Similarly, in extrastriate visual areas and in parietal cortex cells responsive to non-visual input increase in frequency following visual deprivation<sup>35,36</sup>. Another candidate structure for intermodal changes of this type is the superior temporal polysensory (STP) region in which almost half of the neurons are responsive to auditory, somesthetic and visual stimuli<sup>8,27</sup>. However, to our knowledge, this region has not been studied in unimodally deprived animals.

In each of these polysensory cortical structures and in the superior colliculus input from the Y cells in the retinal periphery is strongly represented<sup>82</sup>. Thus, the hypothesized increase of visual input in these areas following auditory deprivation might be greater for peripheral than foveal vision — in line with the present results showing the major group differences in visual ERPs to peripheral visual stimuli. Also in line with this proposal are the data showing that the retinal Y cells are more modified than the X cells following altered early experience<sup>77,78</sup>, and results showing that in normal development cells in the peripheral retina display more neuron loss than do cells in the central retina<sup>76</sup>.

Thus, the increased attention effects displayed in ERPs recorded from the left temporal and parietal regions and from over the left and right occipital regions in deaf Ss might be attributable to increased visual responsiveness in these areas due to lack of competition from auditory input. However alternative or additional possible mechanisms exist for both types of changes. For example, the increased responses in deaf Ss over the occipital regions might reflect increased growth or hypertrophy like that observed in cortical areas associated with remaining modalities in unimodally deprived animals. Another possible mechanism underlying the increased responses over the temporal regions in the deaf Ss could be the takeover by visual afferents of neurons that would normally be committed to auditory processing. The existence of transient retinal projections to the medial geniculate nucleus<sup>25</sup> and their stabilization and ex-

tension to auditory cortex following destruction of the principle targets of retinofugal axons in hamsters<sup>24,74</sup> shows that this type of change can occur.

These different possibilities are amenable to further investigation in anatomical studies of congenitally deaf animals and through the study of the time course of development of the group differences observed in this study. For example if there is early 'exuberant' multimodal cortical innervation in the human which is normally eliminated in the course of normal sensory stimulation, deaf and hearing neonates should display similar ERPs to visual stimuli initially and only later develop the distinct pattern of differences observed in this and other studies<sup>59</sup>.

#### *Lateral asymmetries*

In this task hearing Ss displayed larger amplitude attention related changes over the right hemisphere, and they more accurately detected the direction of motion of targets presented to the LVF. These results are consistent with considerable clinical data suggesting a greater role for the right hemisphere in visual attentional processes in normal hearing individuals<sup>31</sup>. In contrast, the behavior and ERPs from deaf Ss strongly imply a greater role for the left hemisphere in the present paradigm. As this task required skills that are critical in the perception of ASL, the native language of our deaf Ss, it is conceivable that the group differences in lateral asymmetries may have been in part attributable to the early acquisition of ASL. In sign discourse the eyes are typically focussed on the eyes and face of the signer so that much of the signed information falls outside of the foveal region. Lexical and syntactic information in ASL is transmitted by modulations of hand shape, location and motion<sup>39</sup>. If, as in spoken languages, the left hemisphere plays the major role in the perception of ASL (see refs. 5, 54, 63), then it may also, because of the temporal coincidence between language and motion, play a greater role in processing motion information critical to the production and perception of ASL, even in a non-language situation such as the present task. This would be analogous to the situation in hearing Ss where the perception of temporal order of rapidly presented non-language stimuli depends more on the left than the right hemisphere<sup>10, 19, 20, 29</sup>, perhaps because the perception of small differences in temporal patterning is an intricate part of

speech perception.

The hypothesis that functional asymmetries between the hemispheres are influenced by early language experience has received considerable support. Thus, for example, lateral cerebral specializations may be different in monolingual and bilingual individuals, in literate and illiterate populations, and in groups who have acquired an ideographic vs a phonetic script<sup>2,72,86</sup>. Additionally, several studies have reported that congenitally deaf individuals do not display the same pattern of left hemisphere specialization during reading English that characterizes hearing Ss<sup>38,44,46,55,56</sup>. Moreover, in line with the present results, there are other reports that show opposite patterns of hemisphere asymmetries in hearing and deaf Ss in the performance of non-language tasks<sup>13,51,52,54</sup>.

If the greater role of the left hemisphere in the deaf Ss in the present task is attributable to their acquisition of ASL and not to their auditory deprivation per se, then hearing Ss who learned ASL as their first language might also be expected to show this pattern of results. On the other hand, the bilateral increase in the attention effects over the occipital regions seen in the deaf Ss may be a reflection of compensatory increases in visual system activity secondary to audito-

ry deprivation since birth. Similar changes have been reported in other animals, and other bilaterally symmetrical differences in the anterior-posterior distribution of visual EPs have been reported in congenitally deaf Ss, but not in subjects who became deaf 4 years after birth, even though both types of subjects had acquired ASL<sup>53,59</sup>.

An important test of these hypotheses will be the study of normally hearing individuals who were born to deaf parents and thus do not have the altered sensory experience of the deaf Ss, but like them acquired ASL from their parents as a first language. According to the hypothesis above, they should not display the bilateral increase in occipital activity noted in the present task, nor the anterior expansion of the VEPs reported in Neville et al.<sup>59</sup>, but may display increased activity over the left temporoparietal regions. We report the results of such studies in Neville and Lawson<sup>59</sup>.

#### ACKNOWLEDGEMENTS

We are grateful to Dr. Steven Hillyard for helpful discussions of these data, to Debbie Crossman for secretarial help, and to NIH Grant NS14365 to H.J.N., for support of this research.

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