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Attention to central and peripheral visual space in a movement detection task. III. Separate effects of auditory deprivation and acquisition of a visual language

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We employed event-related brain potentials (ERPs) and measures of signal detectability to compare attention to peripheral and central visual stimuli in normal hearing subjects who were born to deaf parents (HD Ss) and whose first language was American Sign Language (ASL). The results were compared with those obtained from normal hearing Ss⁴² and congenitally deaf Ss⁴³ in the same paradigm. Task performance and ERPs during attention to the foveal region were similar in the 3 groups. In contrast, with attention to the peripheral stimuli the deaf Ss displayed attention effects over the occipital regions of both hemispheres that were several times larger than those in the hearing and the HD Ss. However, both HD and deaf Ss displayed lateral asymmetries in behavior and ERPs that were opposite in direction to those of the hearing Ss. Whereas hearing Ss detected the direction of target motion better when it occurred in the left visual field, deaf and HD Ss performed better for right visual field targets. Consistent with these results, the amplitude of the attention-related increases in the ERPs were larger from temporal and parietal regions of the right than the left hemisphere in hearing Ss, but were larger from the left than the right hemisphere in both the HD and the deaf Ss. These results suggest that auditory deprivation and the acquisition of a visual language have marked and different effects on the development of cortical specializations in humans.

INTRODUCTION

Two decades of research on animals have documented the marked effects of early sensory experience on the physiology and anatomy of brain regions primarily associated with the altered sensory modality^{49,63,64}. Most of this research has been conducted within the visual modality, where many of the deficits in visual behavior following binocular or monocular deprivation have been attributed to specific structural and functional changes observed in subcortical and cortical visual areas. It also seems likely that, in an animal reared in a complex environment, visual deprivation would result in other types of altered experiences, each of which may impact the development of functions and/or structures of relevant brain regions. For example, following deprivation in one sen-

sory modality there may be increased functional demand on and concomitant increased activity of intact modalities. In support of this notion are a few studies that have reported heightened electrical activity and hypertrophy in brain areas associated with remaining sensory modalities in congenitally deaf or blind animals^{23,32,45,50}. Moreover, the effects of altered early experience are apparently not limited to the development of the sensory systems. For example, the physiology of parietal cortex and the structure and metabolism of motor cortex are altered following sensory deprivation^{8,20,28}, and both enriched and isolated rearing environments have been shown to impact the structure and metabolism of several different brain regions^{22,48}. Thus, it appears from this large literature that early experience plays an important role in specifying the functional properties of

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several different cortical areas. However, often in this work the functional consequences of the different early experiences have not been linked to changes in particular brain regions.

In contrast, while the anatomical and physiological consequences of sensory deprivation in humans have not been well documented, the effects on behavior are apparent and have been extensively studied. For example, in addition to the severe and lasting deficits that early blindness produces on the development of visual functions, there are several reports that suggest certain auditory and somatosensory skills may be superior in blind individuals^{3,4,47}. Similarly, there are reports that congenitally deaf individuals show enhanced visual and tactile perceptual skills compared to normal hearing persons^{6,11,13,51}. One of the most profound consequences of congenital blindness or deafness in humans occurs on the acquisition of one or more forms of language. Thus, blind individuals often come to rely on tactile transmission of written information presented via Braille or the Optacon system⁵³. Many deaf individuals acquire a visual signed language in which grammatical and lexical information is conveyed through modulations of the shape, location and movement of the hands (American Sign Language or ASL)³¹.

It seems reasonable that the primary sensory deficit, secondary alterations in intact modalities and alterations in the course of language acquisition each might affect different aspects of neural development in unimodally deprived humans. However, while behavioral studies of sensory and language functions in congenitally blind and deaf humans abound, little is known about the impact of their altered experiences on different cortical specializations. One method that has been employed to study this question is the comparison of event-related brain potentials (ERPs) in normal and unimodally deprived individuals. For example, Feinsod et al.¹⁶ report that ERPs to simple somatosensory stimuli display earlier latencies in blind than in sighted individuals. While these results could reflect compensatory increases in somatosensory functions in the blind, the authors note that their blind subjects had received extensive training in tactile skills including Braille reading, which may have been a factor in producing the group differences.

A distinctive aspect of cerebral organization relevant to language functions is the functional speciali-

zations of the two hemispheres, whereby the left hemisphere usually plays a greater role in language production and comprehension and the right hemisphere is dominant for certain aspects of non-language cognitive functions²¹. By contrast, many aspects of simple sensory functioning appear to be organized symmetrically in the two hemispheres. It may be, therefore, that the effects of abnormal sensory experience on sensory functions may occur primarily through changes in brain areas that are organized symmetrically in the two hemispheres, while abnormal language experience may predominantly affect the development of lateral functional asymmetries between the hemispheres. Several studies have reported abnormal patterns of lateral cerebral specializations in blind and deaf subjects^{27,34-36,65}. However, some authors have attributed these results to the sensory deficits of their subjects while others attribute them to altered language experience. Similarly, alterations in sensory thresholds and ERPs have been variously interpreted as arising from abnormal sensory or language experience. For example, Neville et al.⁴⁴ reported that the amplitude of ERPs to peripherally located visual stimuli were significantly larger over frontal and anterior temporal brain regions in congenitally deaf than in normally hearing subjects. The observed group differences were of equal magnitude over the two hemispheres. These results were interpreted as evidence for changes in the organization of the visual system secondary to auditory deprivation since birth. In a study of ERPs during reading of English, Neville et al. observed marked differences in lateral asymmetries between deaf and hearing Ss and attributed these to their different early language experiences^{40,41}.

In order to dissociate the influences of altered sensory and language experience on these ERP measures, further data are needed. Neville and Lawson⁴³ compared ERPs and behavior of congenitally deaf and normal hearing adults in a task requiring focussed attention to different regions of visual space in order to detect target motion. As in the Neville et al.⁴⁴ study, while attention to the fovea produced similar results in the two groups, major differences between deaf and hearing Ss occurred in the processing of peripheral visual stimuli. Deaf Ss displayed attention-related increases in the amplitude of ERP components that were several times larger than those

of hearing Ss, and the distribution of the attention effects was different in the two groups. Moreover, whereas hearing Ss displayed lateral asymmetries in behavior and in the ERPs that indicated a greater role for the right hemisphere in this task, the deaf subjects displayed an opposite pattern of lateral asymmetries. As discussed in Neville and Lawson⁴³ intergroup differences over the occipital regions of both hemispheres may have indexed increased activity or compensatory hypertrophy of brain regions associated with an intact (in this case visual) modality, as has been reported in other unimodally deprived animals. Similarly, the increased responsiveness over left temporal and parietal regions in deaf Ss may have resulted from reorganization or 'functional reallocation' of brain areas that would normally process auditory information for the processing of information from remaining modalities. Evidence for this type of change has also been reported in other animals^{7,46}. However it is also conceivable that the increased activity over the left hemisphere in the deaf Ss was a consequence of the acquisition of a visual language rather than to the absence of auditory input per se. The major group differences occurred when Ss were required to detect motion of peripherally placed stimuli, skills that are critical in the perception of American Sign Language. If, as in spoken languages, the left hemisphere plays a greater role in processing ASL than the right (see refs. 5 and 39 for evidence on this), the temporal coincidence between motion perception and language processes may result in left hemisphere specialization for the perception of peripheral motion in non-language tasks as well.

In the present experiment we attempted to dissociate the effects of auditory deprivation and the acquisition of a visual language on the differences between deaf and hearing Ss by testing a third group of subjects who, like the deaf Ss, had acquired ASL as a first language, but who had not experienced any auditory deprivation.

MATERIALS AND METHODS

Subjects

Twelve normal hearing adults (6 male; mean age 22 years; range 18–25) with normal or corrected vision were paid to participate in the experiment. Each

subject (S) had been raised by either one or two deaf parents whose major form of communication was ASL, and each S had acquired ASL as a first language, at the normal age for language acquisition. Results from these Ss (termed hearing Ss with deaf parents or HD Ss) are compared with those from the 12 normally hearing Ss and the 12 congenitally deaf Ss reported in Neville and Lawson^{42,43}.

Stimuli, procedures and data analysis

All methods were identical to those reported in the companion study of hearing Ss, except that, as for the deaf Ss, the task instructions were presented in ASL. Briefly, the stimuli were white squares (0.6°) presented with an ISI of 280–480 ms, 18° 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 at that location. Ss kept their finger on the center button of a 3 × 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 the 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

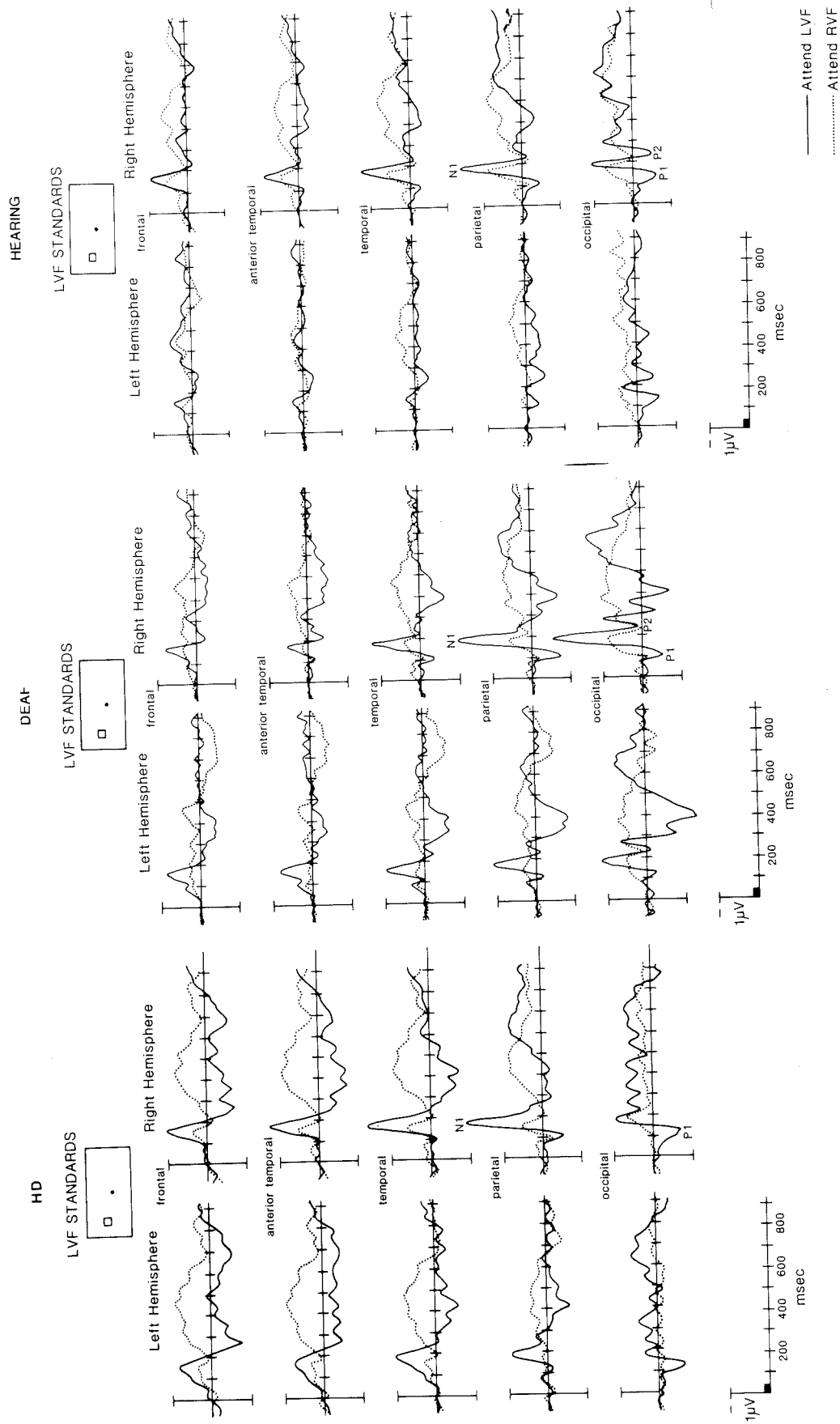


Fig. 1. ERPs averaged across 12 HD subjects (left panel), 12 deaf Ss (center panel) and 12 hearing Ss (right panel) to standard stimuli presented to the left visual field (LVF) when attended (attending LVF) and when inattended (attending RVF). Recordings from left and right frontal, anterior temporal, temporal, parietal and occipital cortex.

TABLE I

Mean latency P_1 and N_1 values (ms) for HD subjects

	Frontal	Anterior temporal	Temporal	Parietal	Occipital
P_1	108	100	92	95	101
N_1	140	144	149	158	154

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 0–15%). 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 hearing Ss with deaf parents (HD Ss) were analyzed with a 5-way analysis of variance with repeated measures on the factors of location, attention, hemisphere and electrode. Comparisons of hearing, deaf and HD Ss added group as a factor.

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

RESULTS

Standards

ERP waveforms. As seen in Fig. 1, the morphology of the ERPs from the HD Ss was similar to that seen in ERPs from both hearing and deaf Ss. All groups displayed early positive and negative components (P_1 , P_2 and N_1) followed by broad shifts in amplitude whose polarity depended on direction of attention. Major differences between the groups oc-

TABLE II

Percent increase N_1 amplitude. Attention to center

	Frontal	Anterior temporal	Temporal	Parietal	Occipital
Hearing	30	30	20	45	92
Deaf	22	25	30	70	84
HD	18	16	10	77	104

curred in the distribution of the effects of attention on the N_1 and PD components.

P_1 and P_2 . The amplitude, latency and attention effects on P_1 and P_2 were similar in the hearing, deaf and HD Ss.

N_1 . The latency of N_1 in the HD Ss was similar to that of the other two groups (see Table I). As seen in Fig. 1, in the HD Ss, as in the normal hearing and in the deaf Ss, the amplitude of N_1 was significantly increased when attention was focussed on the eliciting stimuli as compared to when it was directed elsewhere (location \times attention, $P < 0.0001$). With attention to the central stimuli the increase in N_1 amplitude for the HD Ss was similar in magnitude and distribution to that seen in the deaf and hearing Ss (group \times location \times attention, n.s.; see Table II).

With attention to the peripheral stimuli all 3 groups of Ss displayed large increases in N_1 over the parietal region of the hemisphere contralateral to the attended periphery. Over the right temporal and parietal regions the attention effects were of similar magnitude in all 3 groups (see Figs. 1 and 2).

However, in contrast to the deaf Ss in whom N_1 attention effects were large over the left and right occipital regions, the HD Ss, like the hearing Ss, displayed small attention effects over the occipital regions when attending the peripheral stimuli (group \times location \times attention \times electrode, $P < 0.001$) (Figs. 1 and 3).

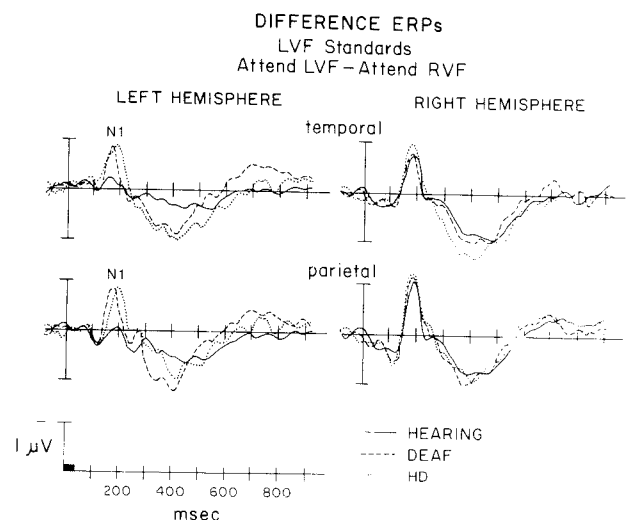


Fig. 2. Difference ERPs, formed by subtracting ERPs to inattentive LVF stimuli from ERPs to the same stimuli when attended, from hearing, deaf and HD Ss. Recordings from left and right temporal and parietal regions.

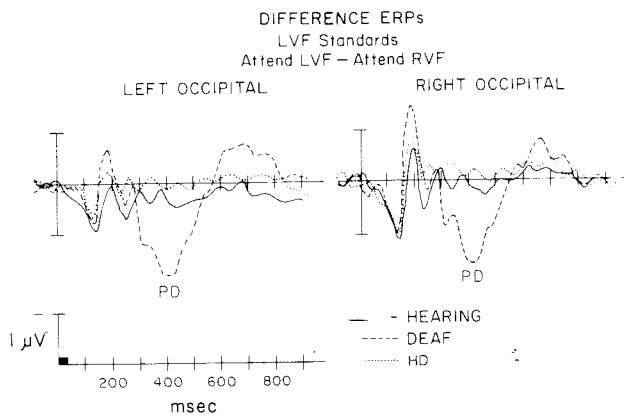


Fig. 3. Difference ERPs for LVF standards from hearing, deaf and HD Ss, recorded over left and right occipital regions.

On the other hand, whereas hearing Ss displayed absent or small attention effects over temporal and parietal regions of the ipsilateral, left hemisphere with attention to the LVF, HD Ss like the deaf Ss, displayed large attention-related increases in N_1 over these regions (Figs. 1 and 2). Similarly, with attention to the RVF the attention-related increase in N_1 amplitude over the left temporoparietal regions was larger in HD and deaf Ss than in hearing Ss (group \times location \times attention \times hemisphere \times electrode, $P < 0.001$).

Area 300–600 ms (PD). As seen in Fig. 1, in all groups ERPs to inattended stimuli displayed a broad negative component while ERPs to the same stimuli when attended were positive in the same time region. Thus, in the difference waveforms (formed by subtracting the ERP to stimuli when inattended from ERPs to the same stimuli when attended), it is evident that attention adds a large positivity (PD) to this region of the ERP.

The 3 groups displayed similar amplitudes and distributions of the PD component with attention to the central stimuli. However, with attention to the periphery the HD Ss, like the hearing Ss, displayed larger amplitude PD from over frontal, temporal and parietal regions than from the occipital sites. This result is in contrast to the results for the deaf Ss, in whom PD amplitude was largest over the occipital regions. Over both occipital sites PD amplitude was significantly larger in deaf than in hearing and HD Ss (group \times electrode, $P < 0.001$; see Figs. 3 and 4).

SW. The slow negative potential (area 600–900 ms) evident in the difference ERPs in the deaf Ss was of somewhat reduced amplitude in both the HD and

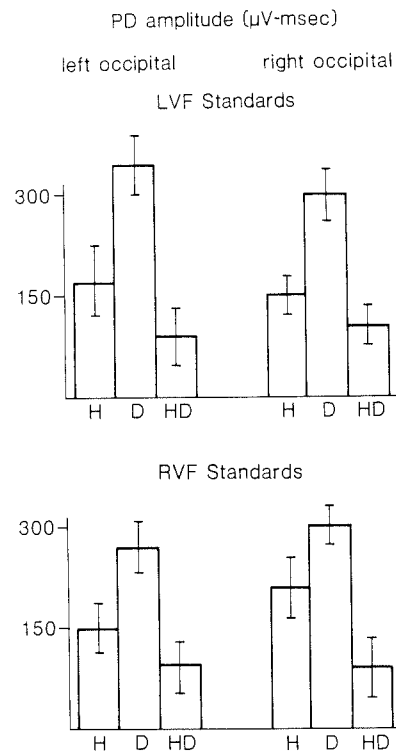


Fig. 4. Amplitude of PD in the difference ERPs during attention to the LVF standards (attend LVF minus attend RVF) and RVF standards (attend RVF minus attend LVF) from left and right occipital electrode sites for hearing, deaf and HD Ss.

the hearing Ss (group, $P < 0.05$). However SW amplitude tended to be asymmetrical in the same direction (i.e. left hemisphere more negative) in the deaf and HD Ss (group \times hemisphere, $P < 0.04$).

Targets

In all 3 groups ERPs to the targets whose direction of motion was correctly detected displayed similar morphologies which included the early components seen in ERPs to the standards as well as the addition of a prominent negative peak around 280 ms (N_2) and a large positive component around 450 ms (P_3). The attention effects on the N_1 to targets displayed similar group differences as seen for the standards. Thus, for the peripheral stimuli deaf Ss displayed larger N_1 effects over the bilateral occipital regions that did the HD or the hearing Ss ($P < 0.01$). Over the left temporal and parietal regions the HD and deaf Ss displayed larger attention effects than did the hearing Ss (group \times attention \times electrode, $P < 0.02$). The N_2 component was larger in the deaf Ss than in the hearing or HD Ss over the temporal and parietal sites (group \times electrode, $P < 0.01$). There were no signifi-

cant group differences in the amplitude or latency of P_3 . As was observed in ERPs to the standards, SW elicited by targets was larger in deaf than HD or hearing Ss ($P < 0.01$), and deaf and HD displayed a similar asymmetry (left greater than right) in the amplitude of SW (group \times hemisphere, $P < 0.02$).

Behavioral data

The HD Ss, like the deaf Ss, detected the direction of target motion more accurately in the RVF than LVF (visual field $P < 0.01$). Hearing Ss displayed an opposite pattern of lateral asymmetries (see Fig. 5) (group \times visual field, $P < 0.04$). The RTs of HD Ss were similar to those of the hearing Ss, i.e. approximately 70 ms slower than those of the deaf Ss.

Refractory period of the visual evoked response

We previously reported⁴⁴ that deaf Ss display larger visual evoked response (VEP) amplitudes than do normal hearing Ss to peripheral visual stimuli presented in a passive recovery cycle paradigm. In order to test the hypothesis that those group differences were evidence for alterations in visual processing secondary to auditory deprivation, against the alternative possibility that the acquisition of ASL played a role in the pattern of results, we tested 8 of the HD Ss from the current study and compared their data with those of the hearing and deaf Ss described in Neville et al.⁴⁴ (except that data from 4 additional deaf Ss have been added).

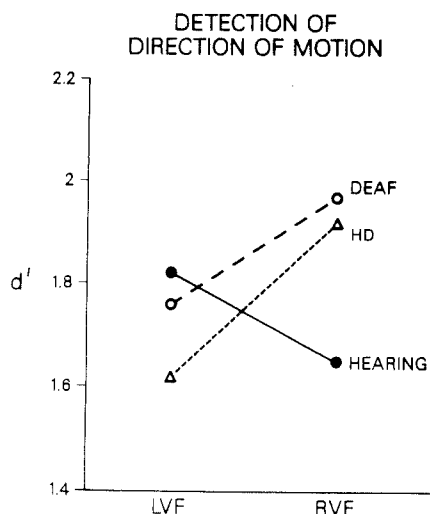


Fig. 5. Detection (d') of motion of targets in the left and right visual fields (LVF and RVF) for hearing (—), deaf (----) and HD (....) Ss.

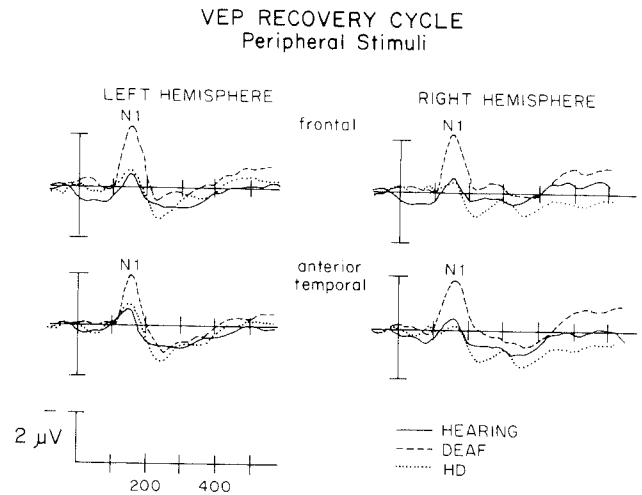


Fig. 6. ERPs to peripheral visual stimuli (summed across LVF and RVF) in the paradigm described in Neville et al.⁴⁴. ERPs from hearing (—), deaf (----) and HD (....) Ss recorded over frontal and anterior temporal regions of the left and right hemispheres.

Briefly (described more completely in ref. 44), ERPs were recorded to a white rectangle ($1.2 \times 0.6^\circ$) presented 8.3° in the LVF or RVF or to the fovea (100 ms duration). The ISI was either 0.5, 1.0 or 3.0 s, randomly intermixed. Subjects foveated a central fixation point during six 3-min blocks of 200 trials each. The ERPs from all groups displayed a negative component around 150 ms (measured as the peak negativity between 100 and 200 ms) and by a positive component around 230 ms (maximum positivity between 180 and 300 ms). The N_1 response in ERPs recorded from over frontal and anterior temporal regions was similar in all 3 groups in response to the foveal stimuli (group effect, n.s.). However, the N_1 to the peripheral stimuli was significantly larger in the deaf than in HD or the normal hearing Ss (group, $P < 0.001$). As seen in Fig. 6, this group difference was equivalent over the left and right hemispheres.

DISCUSSION

These results suggest that auditory deprivation since birth and the early acquisition of a visual (sign) language have marked and different effects on aspects of cerebral function brought into play in the present paradigm. The similarity between deaf and HD subjects in the pattern of lateral asymmetries in this task suggests that their different early language experience (i.e. acquisition of ASL) may have been

the factor that produced a pattern of hemispheric specialization different from that seen in the normal hearing Ss. On the other hand the similarity in the anterior/posterior distribution of ERPs in HD and hearing Ss suggests that the alterations in this aspect of cerebral organization observed in the deaf Ss may be attributable to their early auditory deprivation.

Lateral asymmetries

While a large literature has described the asymmetries in the functional specializations of the two hemispheres in the adult, rather little is known of the ontogeny of this distinguishing feature of the human brain. There is evidence that cerebral asymmetries may be present at or before birth and may therefore be strongly determined (reviewed in ref. 30). However, several lines of evidence also suggest that aspects of the final pattern of hemispheric asymmetries depend on specific parameters of early language experience. For example, individuals who acquire an ideographic script may rely more on structures of the right hemisphere during reading than do those who have acquired a phonetic script^{15,24,25}, bilinguals may display less asymmetrical cerebral organization than monolinguals^{1,58,59} and individuals who acquire language later than normal may display abnormal patterns of asymmetries between the hemispheres¹². As noted in the Introduction, alterations in asymmetries during language processing have been observed in deaf and blind humans, however the possibly different roles of sensory deprivation and abnormal language experience in producing these effects have not been separately assessed.

The effects of early language experience on cerebral asymmetries during non-language cognitive processing have been less well-studied. However, in hearing individuals the left hemisphere plays a greater role in the perception of temporal order of rapidly presented non-language auditory information, a result that may be attributed to the fact that the perception of fine differences in temporal order is critical for the perception and production of speech^{2,9,14,33,57}. Additionally, some evidence suggests that certain cognitive skills which depend more on the right hemisphere in hearing subjects who speak English, are mediated by the left hemisphere in individuals who have acquired a language whose lexicon or grammar makes use of those skills. For example, whereas

English speakers display either right hemisphere or bilateral involvement in pitch discrimination, speakers of Thai, Chinese and Vietnamese, languages in which differences in pitch are linguistically significant, display a greater role for the left hemisphere on such tasks^{26,38,60,61}. Similarly, deaf Ss who have acquired ASL, a language in which hand location and facial expression provide grammatical and lexical information, display evidence of an increased role of the left hemisphere during dot localization and the recognition of faces, tasks on which hearing Ss without knowledge of ASL show right hemisphere predominance^{10,39}. The present results, showing left hemisphere specialization for the perception of peripheral motion in both deaf and hearing individuals who have acquired ASL, a language in which motion is significant, are compatible with these studies. These results, in conjunction with the data that suggest the left hemisphere is specialized for the processing of both spoken and signed languages^{5,39,62}, suggest that the left hemisphere is initially biased to serve as the substrate for the acquisition of language, but that critical parameters of the language play a role in specifying other functions that the left hemisphere will mediate, and those which the right hemisphere subserves. Thus these data are similar to many other results in neurobiology which suggest that aspects of the final pattern of cortical specializations are influenced by relevant aspects of early experience.

Anterior-posterior differences

The results showing that with attention to the periphery deaf subjects displayed increases in N_1 and PD amplitudes over both occipital regions that were several times larger than those of the hearing and HD Ss indicates that this effect is not attributable to the acquisition of ASL and is likely a consequence of auditory deprivation since birth. Similarly, the bilaterally symmetric increase in the N_1 of deaf Ss compared to hearing and HD Ss in the recovery cycle paradigm may also be interpreted as evidence for compensatory alterations in the visual system secondary to auditory deprivation.

Taken together, these results suggest that early auditory deprivation impacts the development of aspects of the visual system which are organized symmetrically in the two hemispheres. The specific

changes appear to include both increased attention-related activity of posterior visual areas, and increased visual activity over anterior brain regions.

Possible mechanisms

Studies of experimental animals with early unimodal deprivation as in congenital deafness or early enucleation have reported increased growth and activity of cortical areas associated with remaining sensory modalities^{23,45,50}. The bilateral increase of attention-related ERP activity observed over the occipital areas in deaf Ss could be a reflection of this type of change. A related possibility is that cells responsive to auditory input, which have been observed in posterior visual areas^{17,37,55}, are taken over by visual afferents when auditory input is absent. The increased visual activity over the anterior temporal regions may also reflect one of several possible underlying changes. It could be that a novel projection from the retina to subcortical and cortical auditory structures is formed when auditory input is absent — similar to changes observed in the visual system by Schneider⁵² and Frost^{18,19} following structural damage. Alternatively, it may be that auditory deprivation permits the maintenance and/or elaboration of normally transient visual input to auditory or multimodal areas in temporal cortex. In support of this hypothesis, a recent study has shown that in the newborn kitten there are projections between auditory and visual cortices that are eliminated in the course of normal development²⁹. Perhaps these would be maintained in a unimodally deprived animal.

Similar mechanisms could underlie the group differences in lateral cortical specializations seen in this study, which apparently were due to early language experience. Perhaps in the human neonate each

hemisphere has the capacity to develop or to maintain the structural and functional organization necessary to subservise aspects of both language and non-language cognitive skills. The data showing that many aspects of language and non-language cognitive skills can develop normally following early hemispherectomy are compatible with this hypothesis⁵⁴. It may be that early in development characteristics of the language to which the child is exposed determine which specific activities each hemisphere will maintain and which will be eliminated. A similar mechanism may underlie the large differences in aspects of speech perception in individuals who have been exposed to different linguistic experience early in development⁵⁶. Similarly, perhaps, the critical interplay and temporal coincidence between spatial location, motion and facial expression in a linguistic context may bring aspects of these cognitive functions into the province of the left hemisphere in individuals who acquire ASL early in development. It will be of interest to determine whether the acquisition of sign language at later stages also impacts the development of the specializations of the two hemispheres. Similarly, studies of postnatally deafened individuals may contribute information about possible sensitive or critical periods when the development of the visual system can be altered by auditory deprivation.

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