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Auditory attention in the congenitally blind: where, when and what gets reorganized?

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FUNCTIONAL reorganization of auditory attention was studied in 12 congenitally blind subjects and 12 controls using high-density event-related potentials during a highly focused dichotic listening task. Reaction times for the attend-ear intensity-deviant targets were markedly faster for the blind. Brain activity associated with sustained attention (N1 effect, Nd), and with the automatic detection of deviants in an unattended channel (MMN), did not exhibit reorganization. In contrast, marked plasticity changes were reflected in late auditory attentional processing (attend-ear targets), in the form of a prolonged negativity (200–450 ms post-stimulus) that was absent in the sighted subjects. The plasticity changes in the blind had a time course indicating progressive recruitment of parietal and then occipital regions, providing new evidence for cross-modal sensory reorganization in the blind. *NeuroReport* 9: 1007–1012

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Introduction

Animal studies of early sensory deprivation following severing of the primary auditory or visual afferent projections show compelling evidence for cross-modal sprouting and reafferentation of spared visual[1] and auditory pathways[2,3] at different levels of the central nervous system. A handful of functional imaging studies have attempted to demonstrate these phenomena non-invasively in humans with congenital deafness[4] and early or congenital blindness.[5–8]

Event-related potentials (ERP) were first employed in a study of functional reorganization of visual processing in congenital deafness using a task of motion discrimination. Both amplitude increases and changes in scalp topography were reported for the visual N1 wave in the deaf subjects. These changes were interpreted as suggesting recruitment of auditory areas for visual processing.[4] More recently, an ERP study of auditory selective attention to pitch changes was performed in early onset blindness.[5] A more posterior scalp distribution was reported for the processing negativity (PN), a slow negative wave associated with sustained attention to an auditory stimulus input channel,[9] as well as changes in the mismatch negativity (MMN) for unattended-ear stimuli.[5] The MMN is a negative wave elicited by deviant stimuli within a channel that peaks at around 200 ms and is thought to reflect the automatic detection of deviant stimuli in an unattended channel.[9–11]

Very recently, a second study from the same research group[6] did not replicate the previous findings of a more posterior distribution for the MMN in the blind, as studied during a reading task. However, a more posterior scalp distribution was reported for the N2b and P3 in response to the deviant stimuli in the attended ear (targets).

The present study aimed at clarifying the location, time course and stage of information processing of the components of auditory attention that undergo functional reorganization in the congenitally blind, by using a more demanding paradigm of highly focused auditory attention to intensity deviants, and by employing a high-density array of 64 electrical sensors.

Materials and Methods

Twelve subjects blind from birth (three men, nine women; eight right-handed, age 42 ± 8 years; no residual light perception; cause: retrolenticular fibrosis 11, glaucoma 1), and twelve sighted controls (six men, six women; 10 right-handed, age 25 ± 6 years) participated in the study. Subjects had no history of current or past neurological or psychiatric illness, and hearing function was normal. Informed consent was obtained from all subjects.

Subjects were presented with rapid sequences (ISI 120–320 ms) of 1000 Hz tone pipes delivered to one ear, and 3150 Hz tone pipes delivered to the other

ear, in random order.[10,12] In the Attend blocks, the task was to listen to the tones in one ear, and press a button upon detecting occasional (9% per ear) deviant tones (targets) of lesser intensity than the standards. All tones in the other ear were to be ignored. The standard/deviant intensity difference was adjusted for each subject to achieve a level of target detectability of around 70%. In the Read blocks, subjects had to ignore all tones and focus on normal reading (controls), or Braille reading (blind subjects).

Brain electrical activity was recorded using a 64 channel cap (Electrocap Inc.) referenced to the right mastoid (bandpass 0.01–100 Hz, gain 10^3, sampling rate 400 Hz, impedences $< 5\ k\Omega$). Eye movements artifacts were rejected off-line. ERPs were averaged for the 12 combinations of condition, ear, and type of stimulus for each subject, and grand-average ERPs were then obtained for each condition for the blind and sighted groups.

To examine the effects of sustained attention to an auditory stimulus channel we focused on the ERP to the standard tones, as sustained attention effects would be seen on all stimuli within that channel. ERP analyses were run on two early windows (20–50 ms; 60–100 ms) for the Attend-ear and Unattend-ear standards, and on the attentional difference waves of Attended-standard ERP minus Unattended-standard ERP in later sequential time windows.

To examine the effects of target-related processing, we analyzed the Attend-ear target ERP minus Standard ERP difference waves in sequential 50 ms time windows. To study the effects of deviance-related processing in the unattended ear, and during reading, we carried out an analysis on the targets and standards in these two conditions. We restricted the analysis to those electrode sites where a small MMN was appreciable in a 150–200 ms time window (three frontal electrode pairs).

For both difference waves analyses, repeated-measures ANOVAs were applied on the mean voltage amplitudes in each of the consecutive 50 ms time windows from 100 to 500 ms post-stimulus. Factors were group, ear, site, and hemisphere. For all analyses we employed a subset of 10 parasagittal electrode pairs covering the entire anteroposterior extent of the cap. In order to assess differences in scalp topography for the two difference waves, the ERP amplitudes were normalized separately for each subject and each ear using the root sum of squares method.[13] The p-value was set at 0.05, and corrected for deviations from sphericity (Greenhouse–Geisser epsilon method). In addition, to help the visualization of the changes of scalp distribution between the two groups, topographic maps were created using the spherical spline method[14] for the voltage data and for the group effect F-values (Fig. 2). Finally, mixed-design ANOVAs were employed for the following behavioral parameters: median reaction time (RT) to attended-ear targets (hits, 200–1000 ms), discrimination accuracy (percentage hit), and the target-standard intensity differences. Grouping factor was group (blind *vs* sighted), and within factor was attended ear (left *vs* right).

Results

Task performance: Discrimination accuracy and target-standard intensity differences were not statistically different between blind and sighted. In the RT analysis, the main factor group was highly significant ($F(1,22) = 8.75$, $p=0.007$). Blind subjects were on the average 91 ms faster than sighted subjects in discriminating targets in the attended ear (blind = 418 ± 38 ms, sighted = 509 ± 72 ms). Therefore, although accuracy of target detection was made to be similar in the two groups, blind subjects were much faster in signaling the occurrence of a target in the attended ear.

Event-related potentials: Figure 1A shows the grand average ERP waveforms for FCz (midway between Fz and Cz) and Pz for Attend-ear and Unattend-ear standards, and the Attended-standard minus Unattended-standard difference waves for the blind and the sighted groups. Figure 1B displays the ERPs to targets (thick line) and standards (thin line) in the Unattend-ear, Read and Attend-ear conditions and for the Attended-target minus Attended-standard difference waves for the blind and the sighted groups. The asterisk indicates a pronounced negativity at Pz in the blind, that is considerably attenuated in the sighted group.

Analyses on early components of the ERP to the standard tones (P20-50 and N1) replicated previously reported findings of enhancement of these components by sustained attention.[15] No significant amplitude or scalp topography differences of these effects were found in the blind group. This can be seen in the highly similar attentional difference waves for the two groups (Fig. 1A), as well as in Table 1a (left), which shows F values and probabilities for the site × group interaction for the raw data and normalized mean voltage amplitude values in the specified time windows. It is evident that there is no effect of blindness on the amplitude or scalp distribution in any of these latency windows from 100 to 500 ms. No higher-order interactions involving group reached significance either, and are therefore not reported.

In sharp contrast to the previous analysis, congenital blindness resulted in a dramatic change in scalp distribution of the target minus standard difference wave in the attended channel. Table 1 (right) shows

Table 1. Results from the sequential ANOVAs on sustained attention and target attention difference waves

	Sustained attention						Target attention					
	Group		Group × site				Group				Group × site	
Time (ms)	F	*p*	F	*p*	norm F	norm *p*	F	*p*	F	p	norm F	norm *p*
100–150	0.00	0.95	0.26	0.72	0.59	0.6	3.62	0.07	2.63	0.092	3.62	0.043*
150–200	0.12	0.73	0.22	0.82	0.33	0.77	0.25	0.62	0.8	0.62	1.51	0.24
200–250	0.58	0.45	0.08	0.92	0.24	0.76	6.04	0.02*	4.13	0.019*	1.92	0.17
250–300	0.38	0.54	0.26	0.74	1.05	0.36	4.13	0.054	7.09	0.0012**	5.15	0.0063**
300–350	0.44	0.51	0.48	0.64	0.56	0.57	0.60	0.45	4.37	0.0175*	4.72	0.0078**
350–400	0.32	0.58	0.95	0.41	0.82	0.45	0.00	0.97	1.92	0.16	2.16	0.13
400–450	0.26	0.63	0.67	0.55	0.54	0.68	0.00	0.99	1.32	0.28	0.66	0.49
450–500	0.15	0.70	0.27	0.72	0.36	0.79	0.56	0.46	0.67	0.53	0.22	0.75

Sustained attention: attended standard-tone ERP minus unattended standard-tone ERP; target attention: target-tone ERP minus standard-tone ERP in the attended ear: group main effect (df=1,22), unscaled values; group x site interaction (df=9,198), unscaled and normalized values. * = $p < 0.05$; **= $p < 0.01$.

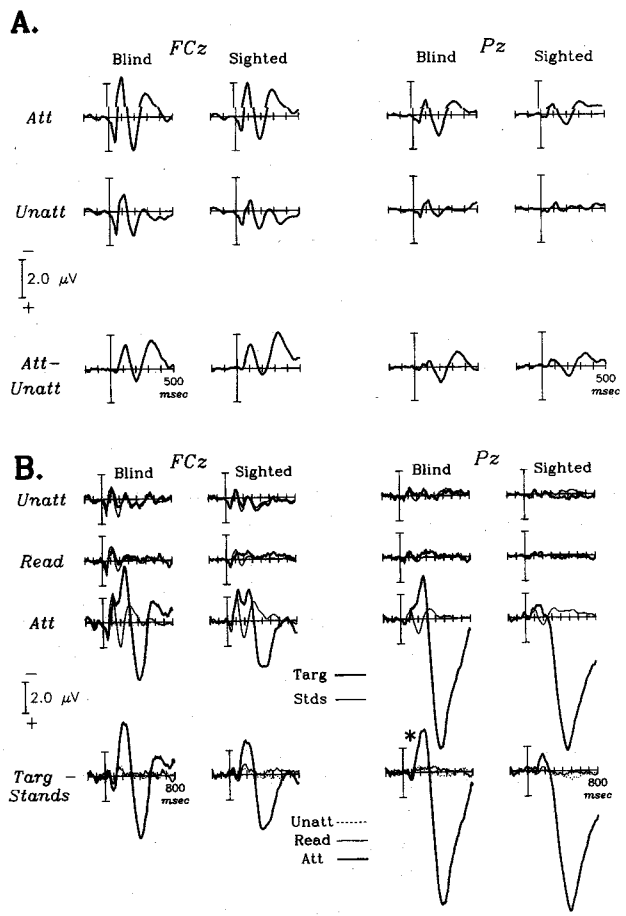

FIG. 1. Top: grand average ERPs at Fcz and Pz for attended and unttended standard tones, and attended minus unattended standard-tone difference waves. Bottom: grand-average ERPs at Fcz and Pz for all conditions, and target minus standard difference waves. Asterisk shows posterior distribution of DRN in the blind group.

that the group × site interaction was globally significant from 200 ms to about 350 ms, with a maximum effect between 250 and 300 ms. This was due to a more posterior distribution of a slow negative wave that extended in time beyond the classical fronto-central MMN in the blind subjects only (see also Fig. 1B, bottom). The top two rows of Fig. 3 show that in the both groups a MMN or deviance-related negativity (DRN) develops over fronto-central scalp around 150 ms, peaking around 200 ms. In the blind group only, however, a slow negative wave persists over time, with progressive topography shift toward more posterior scalp areas (see asterisk showing the center of mass of the DRN). It is evident from the bottom row of Fig. 2, that the scalp sites showing greater group differences are discrete areas in the parietal regions (P3i-P4i), and in occipital scalp regions (O1-O2), particularly on the left.

Substantially less deviance-related activity was seen in the Read and Unattend-ear blocks. A small but statistically significant MMN was present at frontal sites in both conditions, with no amplitude differences between the blind and sighted groups.

Discussion

In a task of highly focused attention to auditory tones, congenitally blind subjects were significantly faster in discriminating targets than sighted subjects. The ERP to standards in the attended ear, and the ERPs to both standards and targets in the unattended ear and during the reading task showed no amplitude or topography differences between blind and sighted groups. Similarly, the difference between Attended-ear standards and Unattended-ear standards, indexing

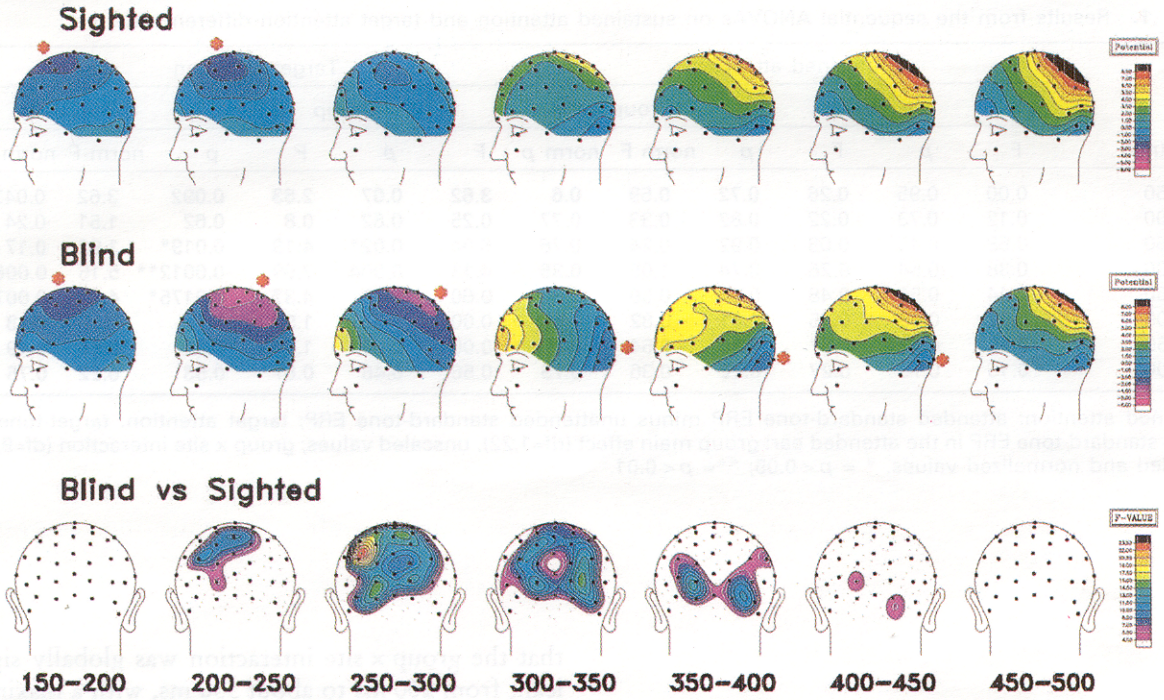

FIG. 2. Top two rows: topographical maps of the voltage amplitudes in the blind and sighted group for the Attended-ear target minus Standard difference wave. Asterisks show progressive posterior shift over time of the center of mass of the negativity. Bottom row: F-value topographical maps of the Group differences, $p < 0.05$ uncorrected.

sustained attention, showed no significant amplitude or topography differences. Thus, these results do not replicate earlier findings of a posterior distribution of a processing negativity between 200 and 350 ms in the early blind when analyzing a similar attended standard minus unattended standard difference wave, as well as the previously reported finding of a more posterior MMN for the unattended channel deviant minus standard difference wave.[5] We believe that both of the discordant results described above can be explained by a crucial difference in experimental paradigm. The previous study used a fixed ISI of 650 msec,[5] whereas our study employed random and much faster ISIs of 120–320 ms, making the focusing of attention on the attended ear far more demanding.[12] In the former case, it is quite plausible that with the slower and predictable ISI, subjects could orient to many of the tones in the unattended channel, while still maintaining adequate attention to the attended ear.[10,15] In order to further address the issue of processing of deviant tones outside the focus of attention, we employed the read condition, in which subjects focused on reading while listening to the auditory tones. We found no evidence of amplitude or topography changes in the MMN to deviant tones in this condition either. These results in the read condition are in agreement with very recent findings in early and late blind subjects, with no changes in MMN scalp distribution in both blind groups relative to the sighted group in a similar reading task[6] using a fixed and long ISI of 1 s. It is worth emphasizing that the latter results contradict the earlier report from the same group describing a posterior scalp distribution for the MMN to unattended deviants.[5] This combined evidence thus argues strongly against functional reorganization for the early mechanisms of sensory gating of auditory input in the congenitally blind.

No doubt the most striking effect in our study is the finding that the attend targets minus attend standards difference wave, indexing active target-specific processing, showed a marked difference in scalp topography in blind subjects. This change affected a slow negative wave between 200 and 450 ms, with the most significant between-group effect over parietal and occipital scalp regions between 250 and 350 ms post-stimulus (Fig. 2). Our results show that congenitally blind subjects recruit posterior cortical areas for the processing of task-relevant auditory information, and that such recruitment takes place in an ordered fashion over time. More specifically, the bulk of the MMN (peaking at 200 ms) appears distributed similarly to sighted subjects (fronto-centrally); at longer latencies in the blind, however, the deviance-related negativity to targets appears distributed predominantly over parietal scalp between 200 and 300 ms, and then over occipital scalp at a later stage, between 300 and 450 ms.

A very recent study reported a ERP topography change for the attended targets very similar to the one reported here. In both early and late onset blind subjects the N2b and P3 to attended targets, measured on the attend target minus attend standard difference wave, were posteriorly distributed relative to the sighted group.[6] Our temporal analyses suggest congenital blind subjects have a posteriorly distributed target-selective slow negative wave spanning at least 200 ms (200–400 ms). This slow wave overlaps the N2b and P3b. Whereas N2b may contribute to a variable extent to the posteriorly distributed effect, we found no support to the notion of a more posterior distribution of the P3b in blind subjects. It is evident from Fig. 2 that P3b has a similar scalp distribution in blind and sighted, with a maximum over Pz. The bottom row of Fig. 2 shows that beginning at 350 ms the significant group effect is a negativity focused over occipital scalp. At the peak of the P3b, around 500 ms, no group difference is present. This observation therefore argues against a contribution of P3b to the observed group effect, and suggests that the effect is is most likely due to a ongoing slow negative wave.

The finding of a topography change centered over the occipital lobe is consistent with recent PET reports of blood flow increases in or in the vicinity of striate cortex during Braille reading in the early blind,[7] and the disruption of Braille reading with transcranial magnetic stimulation over occipital cortex in the same group.[8] It is conceivable that our effects stem from reorganization in primary visual cortex. However, even if this were so, it would appear that these effects do not involve bottom-up changes due to subcortical visual reafferentation (e.g. at the thalamic level), since this would have resulted in topographical changes in the early sensory waves of the tone-evoked ERPs, which did not occur in our study. Rather, the long latency cross-modal reorganization appears to proceed in a top-down fashion through cortico-cortical connections, with auditory information reaching visual cortex after normally activating auditory cortex. However, the topography of our effects is not consistent with a striate source, which would tend to generate a midline voltage distribution. In addition, early visual attention effects in normals have been effectively localized to visual extrastriate cortex, with the striate cortex being rather insensitive to effects of strongly manipulated visual attention.[16] These results argue for a locus of plasticity situated in ventral extrastriate cortex, possibly recruiting the 'what' pathway involved in visual object recognition.

In addition to recruitment of occipital cortex, our results suggest that neuronal populations in parietal cortex also participate in the functional reorganization of auditory attention in blind subjects. Such parietal regions are a known substrate of visual attentional orienting and visuospatial processing.[17] Recent PET data have been reported for the importance of parietal neocortex for both object-centered reaching and recognition.[18] More importantly, recent PET evidence showed inferior parietal activation in auditory localization in both sighted and congenitally blind subjects, and significant correlations between CBF in parietal and occipital areas in the blind group only.[19]

A final point worth stressing is the left hemisphere predominance of the plasticity effects observed in the blind group. Both parietal and occipital activations were earlier over the left then right hemisphere, and the parietal activation was substantially more significant on the left side. A possible interpretation for this asymmetry is the left hemisphere superiority in the rapid parsing/sequential analysis of 'object-like', local *vs* global, or high-spatial frequency information, observed in the visual modality,[20] and the processing of high *vs* low temporal frequency information in the auditory modality.[21] Alternative possibilities are the recruitment of left-sided circuits involved in the sighted in visual image generation[22] and/or in visual object processing.[23]

Conclusion

Our study clarifies the issue of which component of auditory attention undergoes plastic changes in the congenitally blind. Such a component is late selection of auditory targets. The brain areas recruited for additional auditory processing in the blind are regions in the parietal cortex and occipital cortex, around 200–300 ms and 300–450 ms post-stimulus, respectively. These effects are stronger over the left hemisphere. The results reported here would not have been possible without the selective averaging capabilities provided by the ERP technique, allowing the extraction of the target-specific contribution to the plasticity changes, and without the high temporal resolution provided by ERPs, indicating the exact temporal course and the highly dynamic nature of these plasticity changes. In spite of our high-density array of sensors, the main limitation of this study is the relatively coarse spatial resolution of state-of-the-art ERP recordings. Thus, future work combining high-density ERPs with techniques such as dipole source modeling, PET and fMRI is required to clarify the exact localization within posterior cortex of these plasticity effects.

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