

Auditory Spatial Tuning in Late-onset Blindness in Humans

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Abstract

■ Blind individuals who lost their sight as older children or adults were compared with normally sighted controls in their ability to focus auditory spatial attention and to localize sounds in a noisy acoustic environment. Event-related potentials (ERPs) were recorded while participants attended to sounds presented in free field from either central or peripheral arrays of speakers with the task of detecting infrequent targets at the attended location. When attending to the central array of speakers, the two groups detected targets equally well, and their spatial tuning curves for both ERPs and target detections were highly similar. By contrast, late blind participants were significantly more accurate than sighted participants at localizing sounds in the periphery. For both groups, the early N1 amplitude to peripheral standard stimuli displayed no significant spatial tuning. In contrast, the amplitude of the later

P3 elicited by targets/deviants displayed a more sharply tuned spatial gradient during peripheral attention in the late blind than in the sighted group. These findings were compared with those of a previous study of congenitally blind individuals in the same task [Röder, B., Teder-Sälejärvi, W., Sterr, A., Rösler, F., Hillyard, S. A., & Neville, H. J. Improved auditory spatial tuning in blind humans. *Nature*, 400, 162–166, 1999]. It was concluded that both late blind and congenitally blind individuals demonstrate an enhanced capability for focusing auditory attention in the periphery, but they do so via different mechanisms: whereas congenitally blind persons demonstrate a more sharply tuned early attentional filtering, manifested in the N1, late blind individuals show superiority in a later stage of target discrimination and recognition, indexed by the P3. ■

INTRODUCTION

For centuries, anecdotes have abounded about individuals who have lost one of their perceptual senses and compensate with superior abilities in the remaining senses (James, 1890, pp. 509–510). Recently, behavioral, electrophysiological, and neuroimaging studies have documented cross-modal compensation and plasticity after sensory deprivation (for reviews, see: Röder & Rösler, 2004; Bavelier & Neville, 2002; Kujala, Alho, & Näätänen, 2000; Rauschecker, 1995). The vast majority of these studies have focused on individuals who were deaf or blind from birth. Less is known about the extent to which people who become deaf or blind as older children or adults are able to improve the capabilities of their intact modalities or whether cross-modal compensation in such “late blind” individuals is mediated by the same neuronal mechanisms as in congenitally deaf or blind individuals. To investigate these questions, we compared late blind and sighted individuals in their

ability to localize and focus attention upon sounds in a noisy, free-field environment. The underlying neural mechanisms were investigated by recording event-related potentials (ERPs). The results were compared with previously reported findings from congenitally blind individuals performing in the same task paradigm (Röder, Teder-Sälejärvi, et al., 1999).

Numerous studies have shown that congenitally blind individuals are equally good or better at localizing sounds than sighted individuals (Abel, Figueiredo, Consoli, Birt, & Papsin, 2002; Zwiers, Van Opstal, & Cruysberg, 2001; Weeks et al., 2000; Röder, Teder-Sälejärvi, et al., 1999; Rauschecker & Kniepert, 1994; Rice, 1970). Using a paradigm identical to that of the present study, Röder, Teder-Sälejärvi, et al. (1999) found that congenitally blind individuals were superior to sighted controls in localizing and focusing attention upon infrequent targets from far lateral speakers (72°–90° azimuth). By contrast, both groups were equally precise for targets from frontal speakers (0°–18° azimuth). The N1 amplitude decreased with increasing distance from the attended speaker in both groups. However, although congenitally blind and sighted participants had equivalent N1 gradients when attending the central speaker, when attending the peripheral

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speaker, congenitally blind individuals displayed a steeper decline in N1 amplitude than sighted participants reflecting a sharper tuning of spatial attention. Moreover, they had a more posterior scalp distribution of the N1 attention effect compared to sighted controls. Therefore, Röder, Teder-Sälejärvi, and colleagues concluded that a reorganization of multisensory brain areas (i.e., a takeover of visual areas by the auditory modality), similar to that previously demonstrated in visually deprived cats (Korte & Rauschecker, 1993; Rauschecker & Korte, 1993), might have contributed to the performance advantage of the congenitally blind participants. Consistent with this idea, Weeks et al. (2000) used positron emission tomography to demonstrate activation of the ventral occipital cortex during an auditory localization task in congenitally blind but not in sighted participants.

Past research on auditory localization abilities with late blind individuals reported that they were slightly more precise than sighted individuals, whereas congenitally blind participants were clearly superior to both groups (Rice, 1970). Recent studies have suggested more clearly that late blind individuals can develop an advantage over normally sighted individuals (Abel et al., 2002; King & Parsons, 1999) and, in some cases, may even surpass congenitally blind individuals (Abel et al., 2002). The present experiment employed the same auditory attention paradigm as Röder, Teder-Sälejärvi, et al. (1999) to investigate possible adaptive changes related to auditory spatial attention and localization abilities in late blind participants. Based on animal studies that have shown a decrease in minimum audible angles in adult ferrets after a short time of visual deprivation (King & Parsons, 1999), a specific advantage of late blind individuals was predicted for peripheral sound sources. Concurrent ERP recordings allowed assessment of whether any behavioral superiority that might be observed in late blind participants was mediated by improved tuning of early attention mechanisms, as was found for congenitally blind individuals (Röder, Teder-Sälejärvi, et al., 1999), or whether different adaptive mechanisms, perhaps reflected in longer latency ERPs, were utilized by the late blind group.

METHODS

Participants

Eleven late blind adults participated in the experiment. Data from two participants were excluded from the final analyses because of too many ocular and muscle artifacts in the electroencephalogram (EEG) recordings. The age of the remaining nine late blind participants (6 women, 3 men) ranged from 27 to 64 years ($M = 46.6$ years, $SD = 11.7$). Participants lost their vision between the ages of 9 and 52 ($M = 28.0$ years, $SD = 13.5$), leading to an average of 18.6 years of visual deprivation ($SD = 13.4$; Min = 5 years, Max = 46 years). Blindness was due to

glaucoma (4 participants), gradual loss of vision because of retinopathy of prematurity (1 participant), development of cataracts (1 participant), optic nerve atrophy (2 participants), and an accident which destroyed the optic nerve and detached the retina (1 participant). Three participants reported diffuse light perception without pattern vision; all others were completely blind. One participant had received a Master's degree, four had graduated from college (BA/BS), and four had graduated from high school.

Nine adults with normal or corrected-to-normal vision matched in age ($\pm 15\%$), sex, and handedness served as a control group (6 women, 3 men; age: Min = 33, Max = 62, $M = 46.0$ years, $SD = 9.0$). Seven of the sighted participants had graduated from college, one from high school, and one did not finish high school.

All participants reported having normal hearing in both ears (which was confirmed in a subsample with a hearing test), being right-handed and free of neurological impairments. All participants gave informed consent and received monetary compensation for their participation.

Material

Eight matched speakers were mounted on a horizontally oriented metal hoop at the height of the participant's head at a distance of 1.2 m. The four central speakers were situated at 0° , 6° , 12° , and 18° azimuth and the peripheral ones to the right at 72° , 78° , 84° , and 90° (Figure 1).

Stimuli were bursts of broadband pink noise of two different bandwidths. Noise bursts with a bandwidth of 500–5000 Hz served as standards, whereas deviants had an increased bandwidth of 500–15000 Hz (duration of both types of stimuli: 83 msec, including 10 msec rise and fall time; intensity: 76 dB SPL). Stimuli were presented in a randomized sequence and were equally

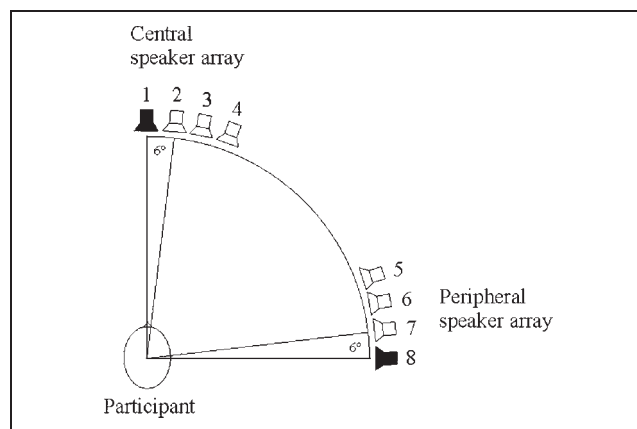


Figure 1. Central and peripheral speaker arrays. In separate conditions, participants had to detect deviants at Speaker 1 (attend-center) or Speaker 8 (attend-periphery).

likely to occur at each of the eight speakers. For each speaker, standards occurred with a probability of .84, whereas deviants were less frequent (.16).

Head movements were monitored by a narrow beam of infrared light that was reflected from a small head-mounted mirror. Its sensitivity was 4° of angle for vertical and 2° of angle for horizontal head movements (see Teder-Sälejärvi, Hillyard, Röder, & Neville, 1999 for a detailed description of the equipment used).

Procedure

Sitting in a sound-attenuating chamber, participants were instructed to attend to Speaker 1 (0° azimuth) in half of the blocks and to Speaker 8 (90° azimuth) in the other half of the blocks. They were instructed to press the response button when they detected a deviant at the attended speaker only (not at adjacent speakers). The response hand was counterbalanced across participants. They were asked to respond as quickly as possible, but to regard accuracy as more important than speed. Sighted participants were blindfolded.

Participants were familiarized with the stimuli and speaker configuration as well as with the task before the experiment. Before each block started, participants were instructed as to which speaker to attend. Each block consisted of a random sequence of 960 noise bursts with an average ISI of 180 msec (varying between 90 and 270 msec, rectangular distribution). Each block lasted two and a half minutes, and participants received feedback about their hit and false alarm rate after each block. The two conditions (attend-center, attend-periphery) were tested with 12 blocks each. Participants had a 10-min break halfway through the experiment. A complete session required 3 to 4 hr including the electrode cap application and removal.

Recording of Event-related Potentials

ERPs were recorded from 41 tin electrodes mounted in an elastic cap (Electro-Cap International). Scalp sites were standard (International 10/20 System) and non-standard positions: frontal sites: Fp1, Fp2, F7, F3, Fz, F4, F8; fronto-central: FC5, FC1, FC2, FC6; temporal and central sites: T3, CT5, C5, C3, C1, Cz, C2, C4, C6, CT6, T4; central and parietal sites: P3, CP1, Pz, CP2, P4; temporo-occipital sites: IN5, T5, TO1, IPz, TO2, T6, IN6; parieto-occipital sites: PO1, PO2; and occipital sites: O1, O2, IN3, Inz, IN4. The right mastoid was used as reference. The recordings were re-referenced off-line to an average left/right mastoid reference. Vertical eye movements were recorded using an electrode below the left eye. The voltage difference between electrodes at the outer canthi was used for monitoring horizontal eye movements (bipolar recording). In order to reduce eye movements overall, participants were asked to put their thumb and index/middle finger of the nonresponding

hand on the blindfold over their closed eyes. This strategy provided immediate feedback about eye movements and helped participants to keep their eyes still.

Electrophysiological recordings were amplified with a band pass of 0.1–100 Hz. The EEG and electrooculogram (EOG) were recorded continuously and digitized at a rate of 250 Hz.

Data Analysis

For the behavioral data, response rates and reaction times were determined off-line. A button press within 200–800 msec after a deviant at the attended speaker was categorized as a hit. False alarms were defined as responses within a 200–800 msec time interval after deviants at any of the adjacent speakers. Response rates were calculated as the number of responses to deviants divided by the actual number of deviants at a particular speaker.

All trials, regardless of the correctness of the participant's response, were included in the ERP analysis. Thus, trials with incorrect responses to nontarget deviants (false alarms) and incorrect failures to respond to target deviants (misses) were included in the deviant ERPs as well. Trials with excessive eye movements or muscle artifacts were rejected off-line with an automated artifact rejection algorithm. All amplitude measures of the ERPs were determined with respect to a 100-msec prestimulus baseline. The mean amplitude of the N1 to standards was measured within the time window of 100–200 msec poststimulus in accordance with previous studies (Röder, Teder-Sälejärvi, et al., 1999; Teder-Sälejärvi et al., 1999). The mean amplitude of the P3 to deviants was measured within a 300–500 msec poststimulus interval. The signal-to-noise ratio was inadequate to permit analysis of the N1 to deviants. Difference waves were computed for ERPs to both standard and deviant sounds: ERPs to stimuli from Speaker 1 when it was not attended (in the attend-periphery condition) were subtracted from ERPs to the same stimuli when Speaker 1 was attended (in the attend-center condition), and similarly for Speaker 8 in the attend-periphery condition. The effects of attention on the N1 amplitude to standard stimuli and on the attended minus unattended N1 difference wave (Nd) were by and large equivalent; accordingly, only the N1 amplitudes to stimuli on the attended side were analyzed here to assess gradients of attention (as in Röder, Teder-Sälejärvi, et al., 1999). The scalp topographies of the attention effects for the N1 to standards and the P3 to deviants were analyzed for their anterior–posterior distributions at the midline electrodes (Fz, Cz, Pz, IPz, and Inz) and for laterality at the off-midline electrodes (F3–4, C3–4, P3–4, and O1–2). Hierarchical ANOVAs were performed separately for the different dependent variables using the program package SAS. Group was considered as a between-participants factor, and all other factors were defined

as within-participant factors. Further analyses were carried out separately for the two groups of participants in order to demonstrate group differences or similar trends in the two groups. Nonsphericity of the data was corrected by adjusting the significance levels according to the method suggested by Huynh and Feldt (1970).

RESULTS

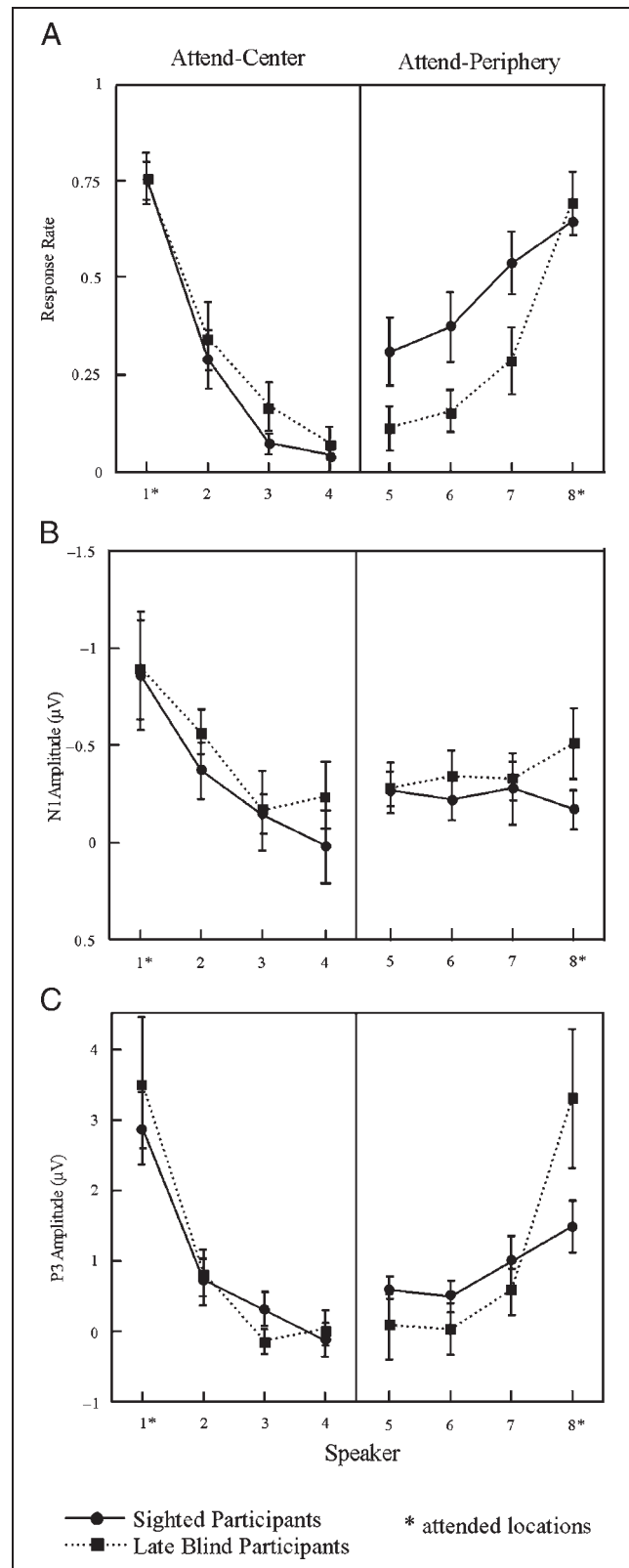
Behavioral Data

Response Rates

False alarms to deviants from the four speakers on the unattended side of the array were negligible for both groups (late blinds: $M = 1.97\%$, $SE = .60$; sighted: $M = 1.34\%$, $SE = .41$).

An overall analysis of variance (ANOVA) for rate of responding to deviants on the attended side was carried out with the between-subjects factor of Group (late blind, sighted) and repeated measurement factors of Condition (attend-center, attend-periphery) and Speaker (four speakers of the attended array). This analysis revealed that participants responded most frequently to deviants at the attended speaker (hits) and had fewer false alarms, the more distant the speaker was from the attended speaker itself [speaker: $F(3,48) = 63.80$, $p < .001$] (Figure 2A). This overall decline in response rates held for both conditions [attend-center: speaker: $F(3,48) = 70.26$, $p < .001$; attend-periphery: speaker: $F(3,48) = 29.13$, $p < .001$] as well as for both groups [late blind: speaker: $F(3,24) = 27.69$, $p < .001$; sighted: speaker: $F(3,24) = 42.12$, $p < .001$]. The slope of this gradient, however, differed depending on the attention condition [Condition \times Speaker: $F(3,48) = 7.63$, $p < .001$] and group of participants [Condition \times Speaker \times Group: $F(3,48) = 5.16$, $p < .004$]. Further analysis did not reveal any difference between the gradients of the two groups in the attend-center condition [Speaker \times Group: $F(3,48) = .33$, $p > .10$], whereas

Figure 2. (A) Response rates (mean \pm standard error). Responses to deviants at the attended Speakers 1 and 8 were correct responses, whereas responses to the remaining speakers were false alarms. The groups did not differ in their gradients when attending to Speaker 1 (attend-center condition), whereas late blind participants had a significantly steeper response gradient than sighted individuals when attending to Speaker 8 (attend-periphery condition). (B) Mean N1 amplitude (\pm standard error) to attended standards within 100–200 msec poststimulus. The groups did not differ in their spatial tuning of the N1; both groups had a significant attention gradient when attending to the central speaker, but not when attending to the peripheral speaker. (C) Mean P3 amplitudes (\pm standard error) to attended deviants within 300–500 msec poststimulus at IPz. In contrast to the other figures, increasing positivity is plotted upwards in this figure. Both groups had a sharply tuned P3 gradient in the attend-center condition, whereas only late blind participants showed a significant gradient in the attend-periphery condition.



in the attend-periphery condition, late blind participants had a steeper gradient than sighted participants [Speaker \times Group: $F(3,48) = 3.35, p < .04$]. In the attend-periphery condition, the sighted participants responded as often to Speaker 7 as to the attended Speaker 8 ($p > .10$). Late blind participants, however, were able to discriminate between those two speakers and responded significantly less frequently to Speaker 7 than to the attended Speaker 8 ($p < .01$).

Sighted participants were less accurate at localizing sounds in the periphery than in the center [sighted: Condition \times Speaker: $F(3,24) = 8.02, p < .001$]. Late blind participants, however, were as precise in the periphery as they were in the center condition [late blind: Condition \times Speaker: $F(3,24) = 1.26, p > .10$].

Reaction Times for Target Detection

The ANOVA of reaction times for target detection revealed a significant Condition \times Group interaction [$F(1,16) = 9.20, p < .008$]. Further analysis showed that sighted participants responded faster to targets at the central speaker ($M = 410$ msec, $SE = 16.1$) than at the peripheral speaker ($M = 453$ msec, $SE = 16.5$) [overall main effect of condition: $F(1,16) = 25.93, p < .001$; main effect of condition for sighted group: $F(1,8) = 27.88, p < .001$]. However, late blind participants' reaction

times did not differ between the two conditions [attend center: $M = 456$ msec, $SE = 17.7$; attend periphery: $M = 467$ msec, $SE = 17.6$; main effect of condition for late blind group: $F(1,8) = 2.60, p > .10$].

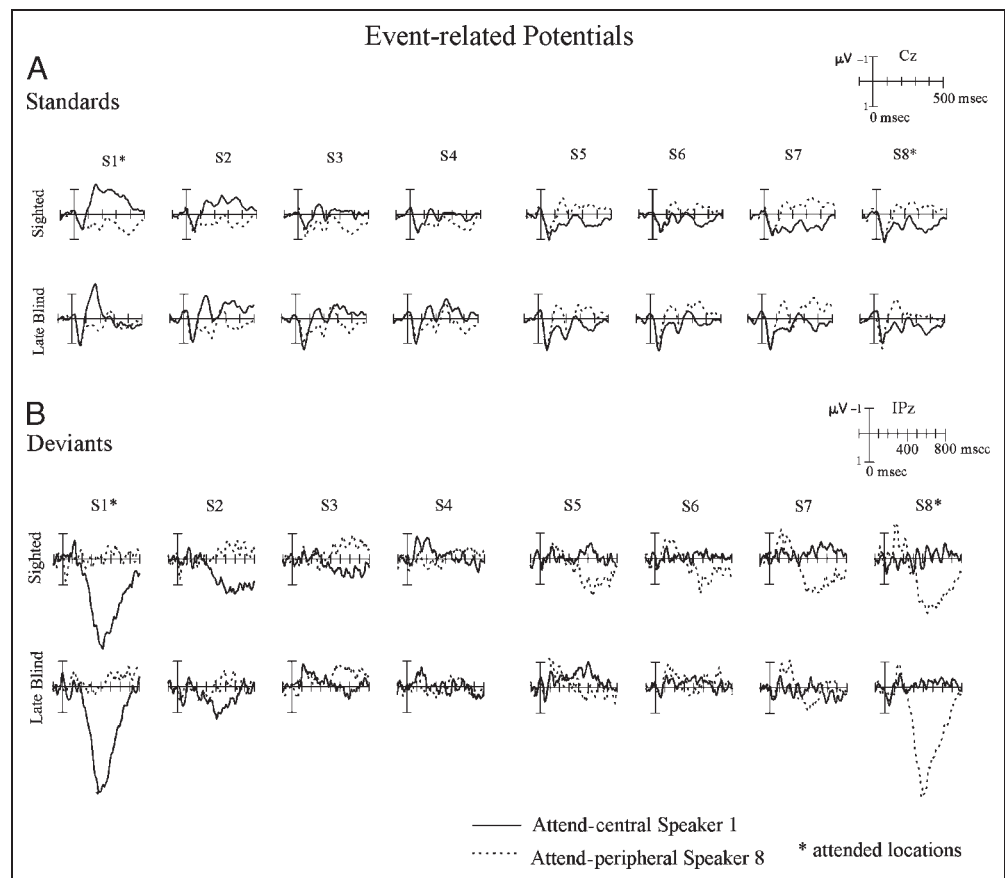
Electrophysiological Results

N1 (at Cz) to Standards on the Attended Side

The analysis of the N1 to standards from the attended speakers did not yield any overall amplitude differences between the late blind and sighted participants [group: $F(1,16) = 1.13, p > .10$; Group \times Speaker: $F(3,48) = 0.08, p > .10$] (Figures 2B and 3A). The amplitude of the N1 decreased with increasing distance from the attended speaker [speaker: $F(3,48) = 4.88, p < .02$]. This attention gradient was, however, only significant for the attend-center condition [Speaker \times Condition: $F(3,48) = 6.96, p < .002$; attend-center: speaker: $F(3,48) = 10.66, p < .002$] and not for the attend-periphery condition [attend-periphery: speaker: $F(3,48) = 0.07, p > .10$].

In the attend-center condition, sighted participants had a significant N1 attention gradient [sighted: speaker: $F(3,24) = 7.72, p < .01$], which was marginally significant for late blind participants [late blind: speaker: $F(3,24) = 3.97, p < .07$]; the two groups did not differ significantly, however, in their N1 gradients [attend-center: Group \times Speaker: $F(3,48) = 0.27, p > .10$].

Figure 3. Event-related potentials. (A) ERPs to standard stimuli. ERPs recorded from Cz in response to standard stimuli when attending to Speaker 1 (attend-center, solid line) and when attending to Speaker 8 (attend-periphery, dotted line). (B) ERPs to deviant stimuli. ERPs recorded from IPz in response to infrequent deviant stimuli when attending to Speaker 1 (attend-center, solid line) and when attending to Speaker 8 (attend-periphery, dotted line).



In the attend-periphery condition, neither group showed a significant N1 gradient [attend-periphery, late blind: speaker: $F(3,24) = 0.35, p > .10$; attend-periphery, sighted: speaker: $F(3,24) = 0.16, p > .10$], and the gradients of the two groups did not differ from one another [attend-periphery: Group \times Speaker: $F(3,48) = 0.48, p > .10$].

Distribution of the N1 Attention Effect

Both groups had a fronto-centrally distributed N1 attention effect when attending the central speaker as well as when attending the peripheral speaker [main effect of anterior–posterior: $F(4,64) = 35.25, p < .0001$; Anterior–Posterior \times Group: $F(4,64) = 2.02, p > .10$] (Figure 4A). When attending to the peripheral (right) speaker, the N1 attention effect was left-lateralized for both groups [attend-periphery: hemisphere: $F(1,16) = 5.78, p < .03$; Hemisphere \times Group: $F(1,16) = 0.03, p > .10$], whereas there was no lateralization when attending the central speaker [attend center: hemisphere: $F(1,16) = 1.01, p > .10$; Hemisphere \times Group: $F(1,16) = 0.39, p > .10$; overall: Condition \times Hemisphere: $F(1,16) = 7.02, p < .02$]. In neither condition did the N1 distributions differ significantly between the late blind and sighted groups.

P3 (at IPz) to Deviants

The amplitude of the P3 elicited by the infrequent deviant stimuli declined significantly with increasing distance from the attended speaker [speaker: $F(3,48) = 21.14, p < .0001$] (Figures 2C and 3B). Sighted participants showed a much sharper tuning of the P3 in the attend-center than in the attend-periphery condition [sighted: Condition \times Speaker: $F(3,24) = 6.70, p < .003$]. For late blind participants, however, the P3 gradients obtained in the attend-periphery and attend-center conditions did not differ [late blind: Condition \times Speaker: $F(3,24) = 0.22, p > .10$].

In the attend-center condition, the P3 gradients were sharply tuned for both groups [attend-center, late blind: speaker: $F(3,24) = 10.34, p < .007$; attend-center, sighted: speaker: $F(3,24) = 19.21, p < .0001$; attend-center: Group \times Speaker: $F(3,48) = 0.52, p > .10$]. For both groups, the P3 amplitude to deviants at the attended speaker (Speaker 1) was larger than at the remaining three speakers of the center (sighted: 1 vs. 2, 3, 4: $p < .01$; late blind: 1 vs. 2: $p < .05$, 1 vs. 3, 4: $p < .01$).

In the attend-periphery condition, however, late blind participants had a more sharply tuned attention gradient for the P3 [attend-periphery, late blind: speaker: $F(3,24) = 7.67, p < .02$] than sighted participants [attend-periphery, sighted: speaker: $F(3,24) = 3.21, p < .06$; attend-periphery: Speaker \times Group: $F(3,48) = 3.38, p < .06$]. For late blind participants, deviants at the attended speaker (Speaker 8) elicited a significantly larger P3 than deviants at the remaining three speakers

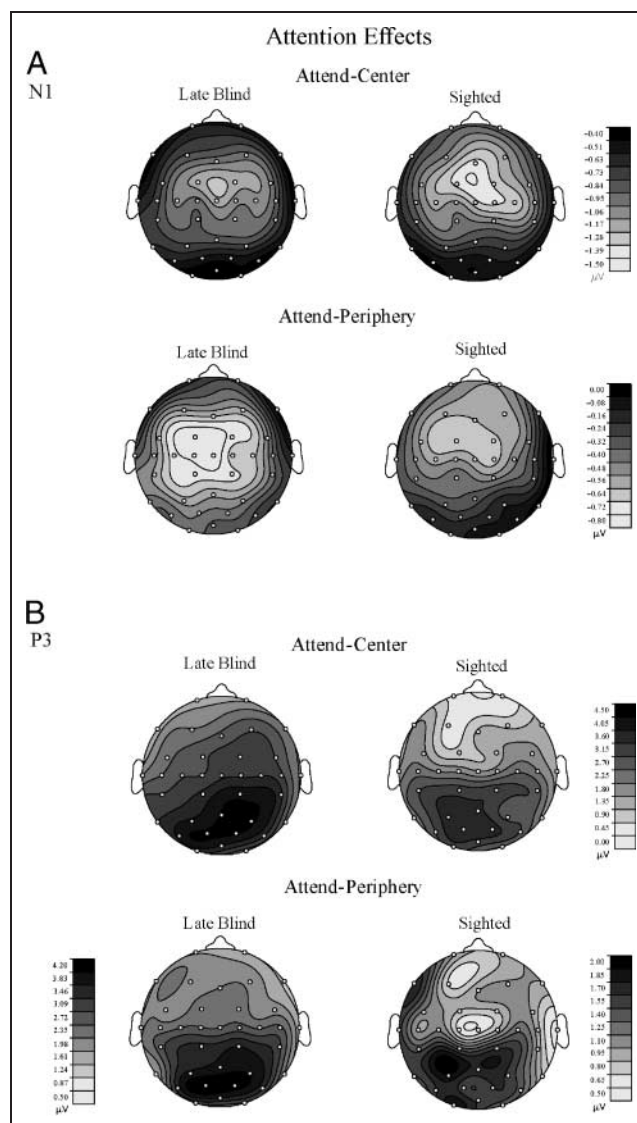


Figure 4. Topographic voltage maps of the attention effects. (A) The N1 attention effect. N1 amplitudes (100–200 msec poststimulus) in response to standards from the unattended Speaker 1 were subtracted from ERPs to standards at Speaker 1 when it was attended (attend-center) and correspondingly for Speaker 8 in the attend-periphery condition. Both groups showed a fronto-centrally distributed N1 attention effect when attending to center. When attending to periphery, the effect was left-lateralized in late blind as well as in sighted participants. (B) The P3 attention effect. P3 amplitudes (300–500 msec poststimulus) in response to deviants from the unattended Speaker 1 were subtracted from ERPs to deviants at Speaker 1 when it was attended (attend-center) and correspondingly for Speaker 8 in the attend-periphery condition. The posteriorly distributed P3 attention effect was right-lateralized for late blind participants when attending to center, whereas it was not lateralized when attending to periphery. By contrast, sighted participants showed a left lateralization of the posteriorly distributed effect in both conditions.

in the periphery ($p < .05$). Also for the late blind participants, there was a steep drop from Speaker 8 to Speaker 7; the P3 amplitudes to deviants from Speakers 5, 6, and 7 were not even significantly different from

zero. By contrast, for sighted participants, deviants from the attended Speaker 8, as well as from Speakers 5 and 7, elicited significant P3 deflections ($p < .01$, for Speaker 6: $p < .10$).

Distribution of the P3 Attention Effect

The two groups differed in lateralization of the posteriorly distributed P3 attention effect to deviants at the attended speaker [Condition \times Hemisphere (left vs. right) \times Anterior–Posterior (four levels) \times Group: $F(3,48) = 3.03$, $p < .04$] (Figure 4B). Late blind participants showed a right lateralization in the attend-center condition, whereas the distribution was not lateralized in the attend-periphery condition [Condition \times Hemisphere \times Anterior–Posterior: $F(3,24) = 3.67$, $p < .04$]. For sighted participants, in contrast, the P3 attention effect was more pronounced over the left hemisphere in both conditions [Hemisphere \times Anterior–Posterior: $F(3,24) = 3.96$, $p < .04$].

DISCUSSION

The present study examined behavioral and ERP indices of the tuning of auditory spatial attention in late blind and matched sighted human adults. The task required detection of deviant target sounds from one speaker in a free-field array of eight speakers that were all randomly emitting comparable sounds. The behavioral results showed that the two groups localized sounds in the center of the auditory field equally well. By contrast, late blind participants were more precise than sighted participants at localizing sounds in the peripheral auditory field. Furthermore, whereas sighted participants performed less accurately in the peripheral than in the central field, late blind individuals were equally precise in both fields.

The focusing of attention was assessed by recording ERPs to the sounds from attended and adjacent speakers and calculating gradients of ERP amplitude around the attended location. The amplitude gradients of the N1 of the auditory ERP to attended standard stimuli did not differ between sighted and late blind participants for either the central or peripheral stimuli. For both groups, the N1 amplitude gradient was steeper for the attend-center than for the attend-periphery condition. With attention to the center, the amplitude of the P3 elicited by deviant sounds also displayed similarly steep gradients in both groups. However, the spatial gradient of the P3 elicited by peripheral sounds was steeper in late blind individuals than in the sighted controls. Indeed, in the late blind individuals, deviants from peripheral speakers elicited as steep a P3 gradient as deviants from central speakers.

It has been shown previously that congenitally blind individuals have improved auditory localization abilities compared to sighted individuals in the horizontal plane

(Röder, Teder-Sälejärvi, et al., 1999; Rice, 1970). The present results, together with previous findings by Abel et al. (2002), suggest that early visual experience followed by visual deprivation does not impede similar improvement of localization abilities. Furthermore, the comparison of the behavioral data with those from Röder, Teder-Sälejärvi, et al. (1999) shows that both congenitally blind and late blind individuals can focus attention on peripheral sounds more precisely than sighted controls. For centrally located sounds, however, the two blind groups did not show an advantage over control participants.

Röder, Teder-Sälejärvi, et al. (1999) demonstrated that for peripheral (but not central) stimuli, the N1 to standards indexing early attention processes was more sharply tuned in congenitally blind individuals than in sighted controls. Using the same paradigm in this study, we did not find a similarly sharp tuning of the N1 to peripheral sounds in late blind individuals. In fact, late blind participants did not differ from sighted participants in their early (N1) attention gradients; both sighted and late blind groups showed a sloping gradient for the central but not for the peripheral field. In addition, Röder, Teder-Sälejärvi, et al. found that for congenitally blind participants, the attention effect on the N1 had a more posterior distribution when participants attended peripheral speakers. In the present study, the attention effect had the same fronto-central distribution for late blind and sighted participants. These results indicate that the superior behavioral performance of the late blind participants, unlike the congenitally blind individuals, is probably not mediated by reorganization and adaptive improvement of early attention processes.

In contrast, the P3 attention gradients mirrored the behavioral data for the sighted as well as the late blind group. Both groups showed similarly steep gradients of P3 amplitude and response rate for detection of deviants from central speakers. Both response rate and P3 amplitude were highest for deviants from the attended central speaker (Speaker 1) and dropped off sharply for deviants from the adjacent speaker (Speaker 2). When attending to deviants from peripheral speakers, however, only late blind individuals showed steep gradients of response rate and P3 amplitude. Their response rate and P3 amplitude were significantly higher at the attended speaker (Speaker 8) than at the immediately adjacent speaker (Speaker 7), indicating a sharp tuning of attention. Furthermore, for late blind participants only, the gradients of response rate and P3 amplitude were equally steep in the attend-periphery and attend-center conditions.

A major goal of this study was to compare late blind and congenitally blind individuals in their auditory localization capabilities and the underlying neural mechanisms. Individuals who were blind from birth performed as well as late blind individuals in the same task, but had

a more sharply tuned gradient of early spatial attention (indexed by the N1), which was in turn closely related to their behavioral gradients (Röder, Teder-Sälejärvi, et al., 1999). By contrast, the present results indicate that the late blind individuals' behavior was rather mediated by late selection processes, indexed by the P3 at 300–500 msec, which reflects further analysis of stimulus properties, target discrimination, and decision making (Hillyard & Picton, 1987). The behavioral performance of both the late blind and sighted individuals was closely correlated with their P3 attention gradients, with late blind individuals displaying higher accuracy in the periphery than sighted individuals. These results show that the adult brain is still capable of reorganizing as a result of altered experience, but the neural mechanisms available for cross-modal compensation differ in the developing and adult brain. Evidently, there seems to be a limited time period (“sensitive period”) in human development when early attentional filtering processes can be altered by experience. By contrast, late attentional processes as reflected by the P3 appear to be modifiable throughout life. Within the present paradigm, these two different mechanisms lead to similarly accurate behavior. However, other aspects of auditory processing might possibly receive a relatively greater benefit for early versus late tuning of attention.

Studies employing animal models have demonstrated the role of early visual experience for calibrating sound localization (e.g., in barn owls, Knudsen, Esterly, & du Lac, 1991). It may be asked whether visually and nonvisually calibrated space differs and, if so, how (for a review, see Thinus-Blanc & Gaunet, 1997). Röder, Rösler, and Spence (2004) demonstrated that when judging the temporal order of tactile stimuli presented to the left and right hands, the performance of sighted and late blind participants was significantly impaired by crossing their hands over the midline, whereas congenitally blind individuals were completely unaffected by this manipulation. This suggests that sighted and late blind individuals utilize external, visually induced reference systems not available to congenitally blind adults.

Using the same auditory attention paradigm as the present study, Münte, Kohlmetz, Nager, and Altenmüller (2001) found that conductors, pianists, and nonmusicians showed sharply tuned N1 attention gradients to central sounds, whereas for sounds in the periphery, only the conductors displayed a sloping N1 gradient. However, in contrast to the results for congenitally blind individuals (Röder, Teder-Sälejärvi, et al., 1999), the scalp distribution of the N1 attention effect for conductors did not differ from that of other musicians. This distributional similarity of the two groups may be linked to the present finding that the N1 distributions of sighted and late blind adults did not differ. These results reinforce the hypothesis that improved sound localization is mediated by different reorganization mechanisms in developing and adult brains.

In summary, both congenitally blind and late blind individuals were found to be more precise than sighted people at localizing and focusing attention on sounds in the periphery. However, whereas this effect appeared to be mediated by enhanced early attentional filtering in congenitally blind individuals, late blind people were found to be superior at deploying late attentional processes of target discrimination and recognition. Further research is required to fully characterize the time periods in human development when different types of experience produce alterations in early and late mechanisms of attention.

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