A Spatial Hearing Deficit in Early-Blind Humans

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An important issue in neuroscience is the effect of visual loss on the remaining senses. Two opposing views have been advanced. On the one hand, visual loss may lead to compensatory plasticity and sharpening of the remaining senses. On the other hand, early blindness may also prevent remaining sensory modalities from a full development.

In the case of sound localization, it has been reported recently that, under certain conditions, early-blind humans can localize sounds better than sighted controls. However, these studies were confined to a single sound source in the horizontal plane. This study compares sound localization of early-blind and sighted subjects in both the horizontal and vertical domain, whereas background noise was added to test more complex hearing conditions.

The data show that for high signal-to-noise (S/N) ratios, localization by blind and sighted subjects is similar for both azimuth and elevation. At decreasing S/N ratios, the accuracy of the elevation response components deteriorated earlier than the accuracy of the azimuth component in both subject groups. However, although azimuth performance was identical for the two groups, elevation accuracy deteriorated much earlier in the blind subject group. These results indicate that auditory hypercompensation in early-blind humans does not extend to the frontal target domain, where the potential benefit of vision is maximal. Moreover, the results demonstrate for the first time that in this domain the human auditory system may require vision to optimally calibrate the elevation-related spectral pinna cues. Sensitivity to azimuth-encoding binaural difference cues, however, may be adequately calibrated in the absence of vision.

Key words: auditory system; sound localization; auditory scene analysis; signal-to-noise; human; compensatory plasticity; visual feedback; early blindness; calibration of spatial maps

Because of the mechanical properties of the inner ear, the auditory input is represented tonotopically at the level of the sensory receptor, rather than spatially. As a result, spatial hearing relies on the use of binaural and monaural acoustic cues. Interaural differences in arrival time and sound level are both used to extract the horizontal coordinate of the sound with respect to the head (azimuth) (Blauert, 1997). Complex spectral shape cues, caused by diffraction and reflection of acoustic waves at the pinna aperture (Shaw, 1966), enable the system to determine the sound position in the median plane (elevation) and to disambiguate frontal from rear locations (Musicant and Butler, 1984; Wightman and Kistler, 1989; Blauert, 1997). These spectral shape cues are known as the head-related transfer functions (HRTFs) (Wightman and Kistler, 1989). It has been well documented that the different acoustic cues are processed by separate neural pathways (for review, see Irvine, 1986). This property of the auditory system is also illustrated by behavioral studies. For example, pure tone stimuli are localized accurately in azimuth but not in elevation (Middlebrooks, 1992; Goossens and Van Opstal, 1999). Changing the spectral shape cues with molds abolishes elevation localization but has no effect on azimuth (Oldfield and Parker, 1984; Hofman et al., 1998). Moreover, azimuth localization is more robust against background noise than the detection of sound elevation (Good and Gilkey, 1996).

The complex and idiosyncratic way in which the acoustic cues relate to sound elevation in combination with the plasticity of this relationship (Javer and Schwarz, 1995; Hofman et al., 1998) strongly suggests that the system needs an independent feedback signal to learn and/or refine this relationship. On the basis of a large body of evidence from barn owls (Knudsen and Knudsen, 1985; Knudsen et al., 1991), ferrets (King et al., 1988), guinea pigs (Withington-Wray et al., 1990), cats (Wallace and Stein, 2000), and a number of other mammalian species (Heffner and Heffner, 1992), it is thought that visual feedback plays an important role in auditory spatial learning. Blind-reared owls have a degraded representation of auditory space in their midbrain optic tectum and localize sounds less precisely than normal owls. Also, in guinea pigs, ferrets, and cats, the early loss of vision prevents the normal development of an orderly acoustic spatial map in the superior colliculus (Withington, 1992; King and Carlile, 1993), a

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structure known to be crucial for rapid orienting to visual and auditory targets (Sparks and Mays, 1990).

On the other hand, it has also been reported that early blindness may lead instead to compensatory plasticity in remaining sensory systems. In the case of acoustic behavior, this has been shown for cats, in which early loss of vision improved certain aspects of sound localization (Rauschecker and Kniepert, 1994). Early blindness in cats may also lead to sharpened spatial tuning of auditory cortical neurons (Korte and Rauschecker, 1993; Rauschecker, 1999). Recently, improved spatial hearing has also been reported for visually deprived ferrets (King and Parsons, 1999).

Thus, loss of vision may either enhance or deteriorate auditory localization. Yet, it is not clear to what extent these two opposing mechanisms are at work in the sound localization system of early-blind humans. Earlier studies, which concentrated on sound azimuth localization, demonstrated little difference between blind and sighted subjects (Wanet and Veraart, 1985). More recent studies, however, have reported that under particular conditions the blind may actually possess superior localization abilities (Ashmead et al., 1998; Lessard et al., 1998; Röder et al., 1999).

A typical, but important, aspect of these studies is that subjects could rely, in principle, on either binaural difference cues or monaural intensity judgements to determine sound azimuth. Because these cues relate to azimuth in a straightforward way, it is conceivable that blind subjects may have calibrated these cues on the basis of acoustico-motor feedback alone. This is less obvious for the idiosyncratic and complex way in which the spectral cues vary with sound-source location, and especially elevation, where binaural difference cues are generally thought to be lacking. Moreover, these high-dimensional cues may change considerably during growth in a way that can hardly be accounted for by genetics alone.

Therefore, a test that is more likely to reveal the effects of early blindness should incorporate the use of spectral shape cues as well, preferably in more complex acoustic environments. In an earlier study we found that early-blind subjects reach comparable accuracy to sounds presented in the frontal two-dimensional (2D) hemifield (our unpublished observation). The present paper investigates sound localization of the blind in this target domain when the target is embedded in an auditory background scene. Naive sighted subjects served as controls.

Part of the results reported in this study have been presented previously in abstract form (Zwiers et al., 1999).

MATERIALS AND METHODS

Subjects. Six blind subjects (B1–B6; five male, one female; 23–42 years of age) participated in the experiments. All subjects were considered early blind because visual acuity in their better eye was below 1/300 within the first year after birth. Apart from their blindness, motor performance and hearing abilities were normal in all subjects.

Seven normal-sighted control subjects (S1–S7; all male; 22–31 years of age), who were inexperienced in sound localization experiments, were recruited from within the department and kept naive as to the purpose of the experiment.

All subjects were given a short practice opportunity to get acquainted with the localization paradigms.

Apparatus. Subjects were seated in a completely dark and sound-attenuated room (3 × 3 × 3 m) in which the ambient background noise level was ~30 dB SPL, A-weighted (dBA). Reflections above 500 Hz were effectively absorbed by acoustic foam. The auditory target (described below) was presented by a broadband speaker that had a flat characteristic (<5 dB) between 2 and 15 kHz. The background stimulus was delivered by an array of nine small speakers distributed evenly on a ring centered in front of the subject (speaker distance, 85 cm; eccentric-

ity relative to straight ahead, 45°). All stimuli were synthesized at 50 kHz, tapered with smooth onset and offset ramps, and generated by a digital-analog conversion (National Instruments, DT2821).

The target speaker was mounted on a two-link robot, which consisted of a base with two nested L-shaped arms driven by two computer-controlled stepping engines (Hofman and Van Opstal, 1998). This setup enabled rapid and accurate positioning of the speaker at a fixed distance of 0.90 m at any location on the frontal hemisphere centered at the subject's head. Potential localization cues emanating from the stepping motors were excluded by introducing a random movement before the start of each trial (Frens and Van Opstal, 1995).

Target and response coordinates were expressed as azimuth and elevation angles in a double-pole coordinate system with the origin coinciding with the center of the head (Hofman and Van Opstal, 1998).

The 2D orientation of the head in space was measured with a search coil, mounted on a light weight (150 gm) helmet, and positioned in the center of two oscillatory and perpendicular magnetic fields (Robinson, 1963). Horizontal and vertical components of head position were recorded at 500 Hz per channel. The subject was seated in the center of the room, with the head positioned in the center of the sphere defined by the robot. The target positions ranged from −35 to 35° in both azimuth and elevation.

Paradigm. The robustness of 2D sound localization was tested with a series of 150 trials in which an auditory scene was presented that consisted of ambient broadband background noise together with a salient auditory target. A signal-noise trial began with the presentation of a 1 sec duration white-noise background emanating from the speaker array. At 250 msec after trial onset, a 500 msec burst of broadband quasi-noise was presented by the robot's speaker, which served as the auditory target. The intensity of the background noise was kept fixed at a level of 58.5 dBA, whereas the intensity of the target was varied randomly among 37.5, 40.5, 46.5, 52.5, and 58.5 dBA. The quasi-noise target had the same amplitude spectrum as the Gaussian white-noise background (0.2–20 kHz bandwidth) but differed in its temporal structure; it had a fixed periodicity of 20 msec (making it sound like a 50 Hz hum). The location of the target was randomly selected from 25 stimulus boxes to ensure a high degree of uncertainty regarding possible target positions (Hofman and Van Opstal, 1998). In 25 interleaved control trials, the background noise was off to test localization performance on the quasi-noise stimulus alone. In all trials, the task of the subject was to point with the nose as quickly but above all as accurately as possible toward the perceived position of the target sound.

RESULTS

2D sound localization in simple auditory scenes

Figure 1 shows the endpoints of the head movement responses of one of our sighted (Fig. 1*a,b*) and blind subjects (Fig. 1*c,d*) toward the broadband quasi-noise target sound in the control condition (no background noise). Linear regression (Press et al., 1992) was separately performed on azimuth (Fig. 1*a,c*) and elevation response components (Fig. 1*b,d*). Both subjects faithfully respond to targets in all directions as indicated by the high correlation between target position and movement response for both components.

On average, the gain (G) and the residual error (δ) for the azimuth responses were significantly higher for the blind group than for the sighted (1.1 ± 0.4 vs 0.73 ± 0.1, $p = 0.01$, and 6.0 ± 3.1 vs 3.4 ± 1.7, $p = 0.04$, respectively; Kolmogorov–Smirnov test) (Press et al., 1992), indicating that these responses were more accurate as well as more variable. Accordingly, the auditory spatial resolution was indistinguishable between the two groups because the correlation coefficient (r) for azimuth was identical (0.97 ± 0.01 vs 0.98 ± 0.02, respectively; $p = 0.47$). A similar pattern of differences was found for the elevation response components, which did not, however, reach statistical significance ($p > 0.19$). As commonly found for sighted subjects (Wightman and Kistler, 1989), the overall performance for elevation was worse than for azimuth in both subject groups. These findings confirm and extend our earlier results obtained with Gaussian
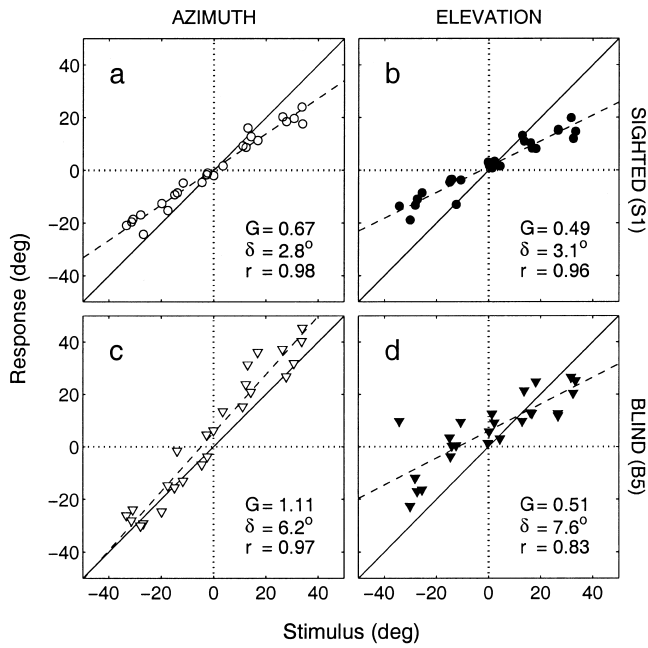
Figure 1. Sound localization in the control condition. The stimulus–response relations for azimuth (*open symbols*; *a, b*) and elevation components (*closed symbols*; *b, d*) of first head movements of sighted subject S1 (*circles*; *a, b*) and blind subject B5 (*triangles*; *c, d*) are analyzed separately. The data are fitted by a linear regression line with gain (*G*) and offset. The residual error (δ, in degrees) is the SD around the fitted line, and *r* is Pearson's linear correlation coefficient between stimulus and response position. For an ideal observer, all the data should be found on the *solid line y = x*.

white noise targets (our unpublished observations). Moreover, the quasi-noise control data were indistinguishable from a white-noise control session that was always conducted immediately after the signal-noise experiments (data not shown).

2D sound localization in complex auditory scenes

Apparently, when circumstances are near optimal, only minor performance differences between blind and sighted subjects are apparent. However, what if the sound localization system is put to a more challenging test by the addition of background noise? Figure 2 shows the responses of sighted subject S2 toward the target for the different S/N conditions (Fig. 2*a*), as well as the calculated regression parameters (Fig. 2*b*). Note that the azimuth component (*open symbols*) is more robust against the disturbing effect of background noise than the elevation component (*filled symbols*). With decreasing S/N ratio, the subject's gain and correlation for elevation rapidly decline, whereas azimuth performance maintains a high level for a longer time before the decrease sets in.

Figure 3 shows the data for blind subject B2. The results appear to be similar to those of the sighted subject in that azimuth performance is more robust against added background noise than elevation performance. Note, however, that for the blind subject this difference is particularly pronounced because elevation responses are already deteriorated for the highest S/N ratios. Yet this subject's azimuth behavior is very similar to that of the sighted subject.

The impression gained from Figures 2 and 3 is further substantiated in the other subjects. Figure 4*a* shows the values of the gain and correlation for all seven sighted subjects in the format of Figures 2*b* and 3*b*. Figure 4*b* displays these parameters for all six
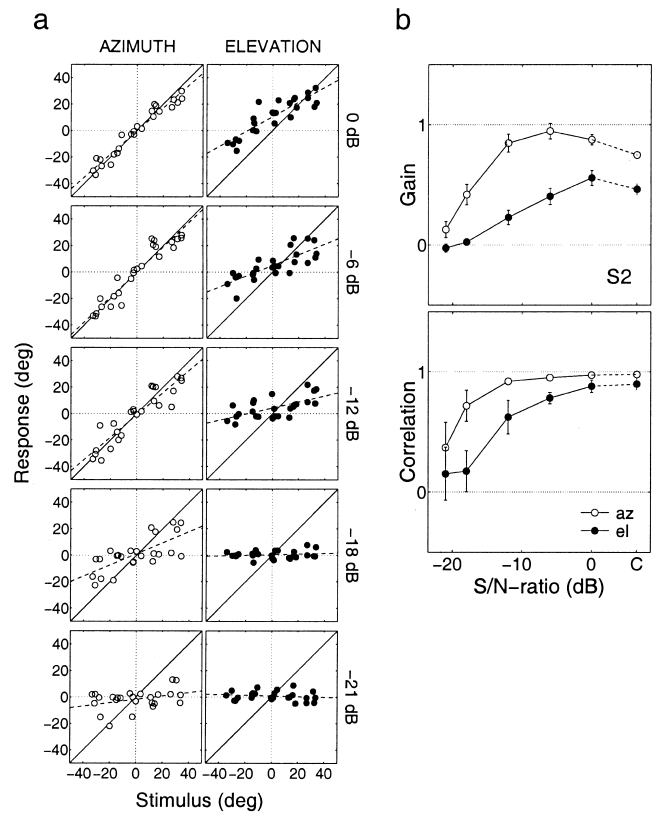

Figure 2. The effect of background noise on sound localization: sighted subject S2. *a,* The *left-hand* and *right-hand columns* show the stimulus–response relations from high (*top*) to low S/N ratios (*bottom*). Note that the accuracy of azimuth and elevation response components changes systematically with S/N ratio. *b,* To better illustrate this point, two representative regression parameters (gain and linear correlation coefficient) for azimuth ($\bigcirc$) and elevation ($\bullet$) are plotted as a function of S/N ratio. Note that values converge to the control condition (*C*) for the highest S/N ratio and to zero for the lowest S/N ratio for both response components. Note also that elevation performance starts to deteriorate at a higher S/N ratio than azimuth performance. Error bars are calculated with the bootstrap method (Press et al., 1992) and depict 1 SD of the mean.

blind subjects. Note the larger variation in azimuth gains for the blind subjects for all S/N ratios tested (similar to those in our unpublished observations). In Figure 4*c*, results from each group were averaged and gains were normalized to enable a direct and unbiased comparison between the two groups. To that end, the following normalized gain-error measure was adopted: $G_E = |G/G_C - 1|$, in which *G* is the measured gain for the particular S/N condition, and G_C is the gain obtained for the control condition (quasi-noise without background). Note that $G_E = 0$ when the measured value is indistinguishable from the control. It equals 1 when the measured gain is 0. The absolute value ensures that systematic overshoots and undershoots yield similar measures.

The results of Figure 4 show that azimuth localization is more robust against background noise than elevation detection. Indeed, for all blind and sighted subjects, the gain and correlation coefficient decline at higher S/N ratios for elevation than for the azimuth component. Similar response behavior has been reported recently for the localization of click trains in the presence of background noise (Good and Gilkey, 1996).

A direct comparison between sound localization performance of the blind and sighted subjects reveals some interesting differ-
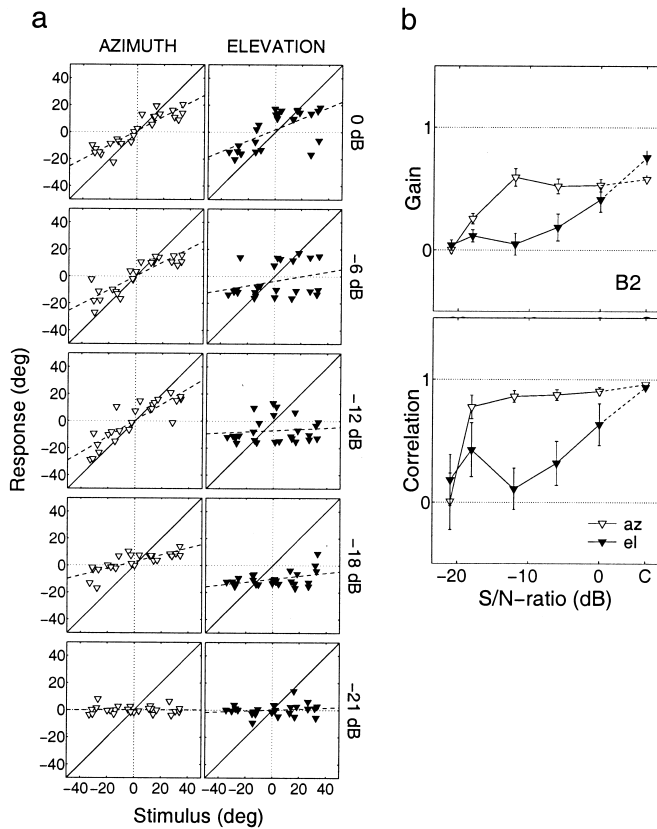
Figure 3. The effect of background noise on sound localization: blind subject B2. Data presented in the same format as Figure 2. Also, for this subject sound localization performance deteriorates systematically with declining S/N ratio. Note the large gap between the curves for azimuth ($\triangledown$) and elevation ($\blacktriangledown$), brought about by the rapid collapse of elevation performance.

ences. As can be seen most clearly in Figure 4*c*, azimuth performance of the blind is indistinguishable from the sighted because the two curves (*open symbols*) superimpose almost perfectly for all S/N ratios, for both the normalized gain error (G_E) and correlation. However, as indicated by the shaded area, the curves for the elevation gain and correlation (*closed symbols*) in the blind differ significantly from the elevation curves of the sighted. Thus, the system that relies on the complex and idiosyncratic spectral cues is disrupted much earlier in the early blind than in the sighted when the S/N ratio is lowered.

Note that for all subjects both the gain (*left-hand column*) and the correlation (*right-hand column*) vary systematically with S/N ratio. Also, both subject groups yield comparable results near the two extreme hearing conditions: high S/N ratios (0 dB) and very low S/N ratios (down to −21 dB). This is a strong indication that the measured effect is auditory in nature and cannot be attributed to other factors. In fact, the results for the highest S/N ratio are quantitatively similar to the control condition (see previous section) as well as to the results of other studies in the field (see introductory remarks). It was also verified in three sighted subjects (data not shown) that without background noise, localization of both sound azimuth and elevation was invariant for all used target intensities.

DISCUSSION

This study investigated the influence of the human visual system on the perception of sound position. Compared with earlier
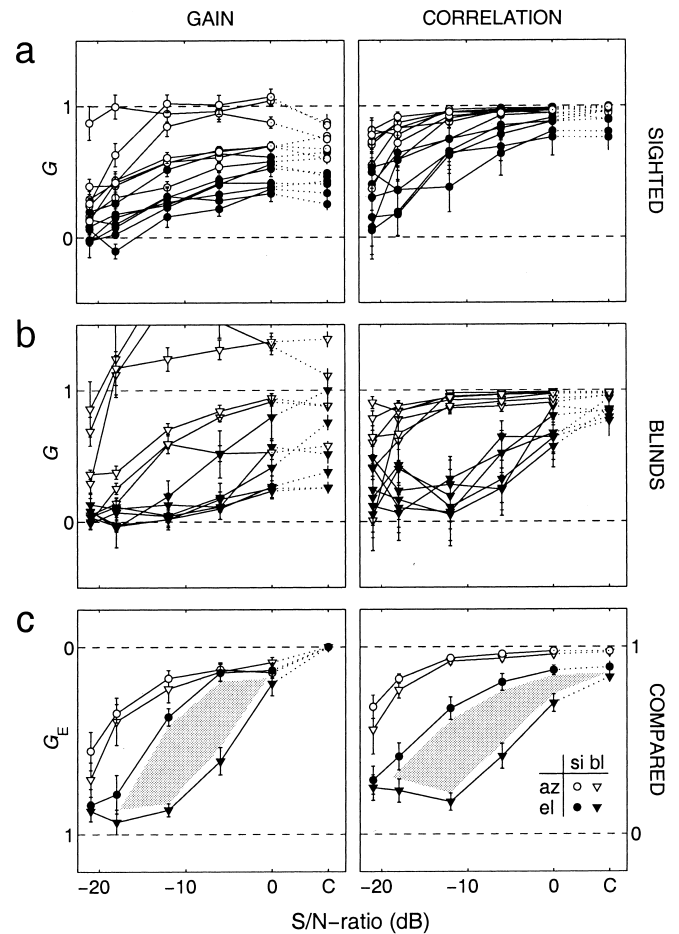

Figure 4. The effect of background noise on sound localization: all subjects. The gain (*left-hand column*) and correlation (*right-hand column*) for the stimulus–response regression on azimuth (*open symbols*) and elevation (*closed symbols*) are plotted as a function of S/N ratio. Symbols denote the same conventions as in Figures 2 and 3 (see *inset* in *bottom right panel*). The results of the sighted subjects (*circles*) are shown in *a*, of the blind subjects (*triangles*) in *b*, and of the group comparison in *c*. Note that the gain in *c* (*bottom row*) is normalized to correct for the high gains of some of our blind subjects (G_E; see Results). The *shaded area* illustrates the performance difference between blind and sighted subjects, cut off on each side at 1 SD from the group average. Note that at intermediate S/N ratios there is a highly significant difference (>4 SD) between the elevation components of both groups (*closed symbols*), but that the curves for azimuth performance (*open symbols*) superimpose almost perfectly for all S/N ratios. This feature is expressed in both the gain and the correlation coefficient as well as in the absolute localization error (data not shown).

studies, the range of targets was extended to two dimensions in the frontal hemifield, enabling investigation of the separate pathways for azimuth and elevation extraction. In addition, localization behavior was tested in a more complex acoustic environment, by adding background noise. The results show that although performance of the blind and sighted is nearly equal in a single-target localization task in two dimensions, the blind are less able to extract the elevation-related spectral cues in the more complex acoustic environment, a condition more reminiscent of the natural situation.

Our findings may not seem to support recent studies (Ashmead et al., 1998; Lessard et al., 1998; Röder et al., 1999) that reported equal or superior localization abilities of the blind under certain conditions. For example, the enhanced sensitivity to target dis-

placements in far-lateral space (Röder et al., 1999) would suggest that the blind are better at using spectral localization cues, because the binaural difference cues are less reliable at these locations. Note, however, that our subjects were tested in the frontal domain (within 50° from the midline) where visual feedback in sighted subjects may typically prevail in calibrating the sound localization cues. It is conceivable that although they are worse in the frontal region (as found in this study), the blind are superior in far lateral and rear regions, where vision is poor (or absent) and where sensory input from other systems (e.g., tactile and motor feedback, or both) may be required for both groups.

Another example of enhanced use of spectral localization cues in the early blind was put forward by Lessard et al. (1998), who found that some of their blind subjects outperformed the sighted in lateralizing stimuli under monaural listening conditions. However, monaural listening in combination with a target sound of fixed intensity allows for the use of perceived sound intensity as an alternative localization cue. Therefore, the results of Lessard and colleagues (1998) may also indicate that some blind subjects are better in using intensity cues rather than spectral shape cues.

Note also that these studies (Lessard et al., 1998; Röder et al., 1999) did not specifically test the use of spectral localization cues, because they did not extend the target range into the vertical domain. Furthermore, an important difference with the present study is that previous studies were not concerned with sound localization in a multisource environment.

Our results raise questions about the nature of the observed hearing deficit in the blind. How can it be that the blind have difficulties in extracting the spectral cues of a target sound embedded in a noisy background, whereas they perform normally when dealing with single targets? One possible explanation is that the hearing deficit in the blind is specific to signal-noise segregation and does not relate to the calibration (i.e., mapping) of localization cues. We believe this is not likely. First, the simultaneous extraction of azimuth cues is not affected in the blind (Fig. 4), indicating that all subjects detected the stimuli equally well. Moreover, the blind have been shown to do equally well, or better, in other central auditory skills, such as discriminating speech in noisy environments (Niemeyer and Starlinger, 1981).

Instead, we propose that the novel hearing deficit in the blind may relate to the neural representation of the elevation-related spectral filters (HRTFs). Indeed, an auditory system with a coarser, but properly calibrated, HRTF representation will be especially sensitive to disturbances, as in noisy environments, but will still function appropriately when localization cues are well discernable, as in quiet laboratory rooms. In such a view, "blurring" of the HRTF representation is brought about by a reduced quality of feedback information in the blind.

The present study shows for the first time that visual feedback might be essential for a full development of human sound localization in the 2D frontal hemifield, where the potential benefit of vision is maximal. The results do not support the hypothesis that the putative supervising role of vision can be fully taken over by other sensory modalities and, moreover, that sound localization acuity is actually suboptimal in the sighted.

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