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RESEARCH ARTICLE

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Two-dimensional sound-localization behavior of early-blind humans

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Abstract To investigate whether the visual system is crucial for adequate calibration of acoustic localization cues, sound-localization performance of early blind humans was compared with that of sighted controls. Because a potential benefit of vision is mainly expected for targets within the two-dimensional (2D) frontal hemifield, localization was tested within this target range, while using sounds of various durations and spectral content. Subjects were instructed to point, in separate experimental sessions, either with their left arm, or with their nose, in the direction of the perceived target position as accurately as possible. The experiments required the use of all available sound-localization cues such as interaural differences in phase and intensity, as well as the complex spectral shape cues provided by the pinnae. In addition, for long-duration stimuli, subjects could have had access to head motion-induced acoustic feedback. Moreover, the two pointing methods allowed us to assess different response strategies for the two groups. In an additional series, subjects were instructed to respond as quickly as possible. The results show that, in general, 2D sound-localization performance of blind subjects was indistinguishable from that of sighted subjects, both for broad-band noise and for pure tones. In the fast head-pointing task, the latency distributions of both groups were equal. These findings suggest that visual feedback is not required to calibrate the available localization cues – including the idiosyncratic and complex spectral shape cues for elevation. Instead, the localization abilities of blind people show that the putative supervising role of vision may be supported, or taken over, by other non-visual feedback systems. The results do not provide support for the hypothesis that blind people can hypercompensate for the loss of vision in the frontal hemifield by developing superior sound-localization abilities. Despite the general correspondence in localization behavior, some specific differences related to pointing strategies as well as to those between blind and sighted subjects were apparent. Most importantly, the reconstructed origin (bias) of arm pointing was located near the shoulder for the blind subjects, whereas it was shifted and located near the cyclopean eye for the sighted subjects. The results indicate that both early blind and sighted humans adequately transform the head-centered acoustic target coordinates into the required reference frame of either motor system, but that the adopted response strategy may be specific to the subject group and pointer method.

Keywords Sound localization · Blindness · Compensatory plasticity · Latency · Arm pointing · Head pointing · Spatial behavior · Human

Introduction

This paper investigates localization behavior of early blind human subjects responding to sounds presented in the frontal two-dimensional (2D) hemifield and compares this to the performance of normal-sighted, naive control subjects.

The ability to make an accurate orienting movement toward a peripheral target in an environment in which many stimuli may compete for attention requires the extraction and selection of the spatial relations between the different stimuli. For example, in complex multimodal scenes, the auditory system may guide the visual system to foveate potentially interesting targets (Perrott et al. 1987; Stein and Meredith 1993). This is not a trivial task, as the different sensory modalities are represented in different frames of reference and are encoded in different neural formats. In its initial stages, visual input is encoded retinotopically and, as vision is locked to the

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eye, it is represented in an eye-centered (oculocentric) reference frame. On the other hand, acoustic input is referenced to the head (craniocentric), but as a result of the cochlear mechanics auditory sensory input is organized tonotopically, rather than spatially.

As a consequence, sound localization relies on the neural processing of implicit acoustic cues. It has been well documented that these cues are processed by independent binaural and monaural neural pathways (Oldfield and Parker 1986; Wightman and Kistler 1989, 1997; Middlebrooks 1992; Frens and Van Opstal 1995; Hofman and Van Opstal 1998). Interaural differences in phase (IPDs) and sound level (ILDs) are both employed by the human auditory system to extract the horizontal coordinate of the sound with respect to the head (sound-source azimuth). Complex spectral shape cues, which arise from the diffraction of acoustic waves at the pinna cavities (López Poveda and Meddis 1996), enable the system to determine the position of the sound source in the median plane (sound elevation) and to disambiguate frontal from rear locations. These spectral shape cues are known as the head-related transfer functions (HRTFs; Musicant and Butler 1984; Wightman and Kistler 1989; Middlebrooks 1992; see Blauert 1997 for review).

In addition to these static cues, active head movements and changes in static head orientation induce systematic changes in the input that could act as a source of acoustic feedback (Noble 1981; Perrott et al. 1987; Perret and Noble 1997) and influence the sound-localization response (Goossens and Van Opstal 1999).

Calibration of acoustic cues

To localize a sound, the auditory system depends on knowledge about the relationship between the acoustic cues and the spatial position of the sound source. The complex and idiosyncratic way in which the acoustic cues relate to sound elevation in combination with the plasticity of this relationship (owl: Knudsen and Knudsen 1985; human: Javer and Schwarz 1995; Hofman et al. 1998) suggests that the system needs feedback to learn and refine this relationship. It has been suggested, for owls (Knudsen et al. 1991; Brainard and Knudsen 1993), ferrets (King et al. 1988), guinea pigs (Withington-Wray et al. 1990), and a number of other mammalian species (Heffner and Heffner 1992), that the visual system plays an important role in this learning process.

On the other hand, it has also been advocated that the loss of a sensory modality may often lead to compensatory plasticity in remaining modalities, such that the remaining senses get sharpened. In the case of acoustic behavior, this has been shown for cats and ferrets, in which early loss of vision appeared to improve, rather than to deteriorate, sound-localization behavior (Rauschecker and Kniepert 1994; King and Parsons 1999) and – in cats – to sharpen the spatial tuning of auditory cortical neurons (Korte and Rauschecker 1993; also Rauschecker 1995, 1999). More recently, early blindness in cats (Yaka et al. 1999), as well as in humans (Kujala et al. 1995; Kujala et al. 2000; Weeks et al. 2000), has been reported to invoke acoustic activity in the deprived visual cortical areas, suggesting that the auditory system in blind subjects may attain an expanded neural representation. Similar cortical reorganization has been demonstrated in the language areas of deaf subjects using sign language (Neville et al. 1998).

Research topic

It is not obvious to what extent early blindness in humans is accompanied by a deterioration in sound-localization accuracy (such as in owls), or to what extent compensatory mechanisms might have sharpened auditory spatial acuity (such as in cats and ferrets).

Earlier studies, which concentrated on sound azimuth localization, demonstrated little difference between blind and sighted subjects, although under echoic conditions localization by the blind appeared to be inferior to that of sighted subjects (Fisher 1964; Jones 1975). In addition, Wanet and Veraart (1985) have reported that blind and sighted subjects reach similar accuracy in indicating sound direction, although the blind subjects in the study of Haber et al. (1993) performed less accurately.

More recent studies, however, have shown that, under certain conditions, blind humans may actually possess superior sound-localization abilities. For example, the experiments of Lessard et al. (1998) indicate that under monaural conditions some of their blind subjects display an enhanced localization ability in the horizontal plane. In addition, the results of Ashmead et al. (1998) suggest that blind children can better discriminate changes in sound elevation and sound distance. Recently, Röder et al. (1999) have shown an increased sensitivity, both psychophysically and electrophysiologically (EEG), to position changes at far-lateral azimuth locations, where the binaural difference cues are less reliable. These studies would suggest that the blind may also be superior in employing the pinna-induced spectral cues.

Note, however, that in the majority of studies subjects could in principle have relied on the use of either binaural difference cues or monaural intensity judgements for localization in the horizontal plane. Both cues are related to sound azimuth in a rather straightforward and monotonic way. Moreover, the relative *discrimination* of sounds may be based on different processes to those underlying the absolute *localization* of sounds. It is therefore not clear to what extent subjects actually relied on either of these different acoustic cues in generating their responses.

Thus, a more challenging test for the sound-localization system of blind humans should incorporate the explicit use of the spectral shape cues as well. These cues are highly idiosyncratic and vary with sound-source elevation in a complex way. Moreover, these cues may change considerably during growth, in a way that can hardly be accounted for by genetic (pre-)programming.

The present paper investigates sound-localization behavior of blind subjects in the frontal 2D space to a variety of acoustic stimuli. We reasoned that, especially within that target range, a potential contribution of vision to the tuning of sound-localization behavior should become apparent.

To that end, congenital blind subjects were asked to point as accurately as possible, either with their nose or with their left arm, to broad-band sounds that were presented at randomly selected locations within the 2D frontal hemifield. The use of these different pointers allows the investigation of adopted pointing strategies and the required coordinate transformations underlying these different sensorimotor behaviors. We also tested whether the latency of sound-localization responses might be indicative for compensatory plasticity in these subjects, by instructing them to make goal-directed head movements as quickly as possible. Finally, we conducted localization experiments in which broad-band sounds of different durations, and pure tone pips of different frequencies, were randomly interleaved. In this experiment it was investigated to what extent acoustic feedback, as well as the different acoustic cues, are used in determining the sound-localization responses. In all experiments, naive sighted subjects served as controls. Some of the results reported in this study has been presented in abstract form (Zwiers et al. 1999).

Methods

Subjects

Six early blind subjects (B1–6; five men, one woman; 23–42 years of age) participated in the experiments. Subjects were considered blind, as their visual acuity was below 1/300 within the 1st year after birth (see Table 1). A visual acuity below 1/300 means that subjects were not able to detect hand movements at a distance of 1 m from their better eye. Subjects were recruited with help from the regional institute for the blind. Apart from their blindness, motor performance and hearing were normal in all subjects. The characteristics of the subjects are provided in Table 1.

Eleven normal-sighted control subjects (Sa–k; all male; ages 23–41 years) that were all inexperienced in sound-localization experiments were recruited from within and outside the department and were kept naive as to the purpose of the experiment. All subjects were given a short practice opportunity (up to 10 min) to get acquainted with the setup and localization paradigms. None of the subjects reported any hearing or motor problems.

The study was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All subjects gave their informed consent prior to their inclusion in the study.

Stimulus presentation

Subjects were seated in a completely dark and sound-attenuated room (3×3×3 m) in which the ambient background noise level was approximately 30 dB (A-weighted, dBA). Reflections above 500 Hz were effectively absorbed by acoustic foam that was mounted on the walls, floor, ceiling, and every large object present. Auditory stimuli were produced by a broadband lightweight speaker (Philips AD-44725), which had a characteristic that was flat within 12 dB between 2 and 15 kHz (not corrected for). The auditory stimuli were generated digitally at a 50-kHz sampling rate (National Instruments DA board, DT2821) and tapered with a sine-squared on- and offset ramp of 5 ms duration. The sound intensity was measured at the position of the subject's head with a calibrated sound amplifier and microphone (Brüel and Kjær; BK2610/BK4144), and kept at a fixed level of 60 dBA SPL.

The speaker was mounted on a two-link robot, which consisted of a base with two nested L-shaped arms (see Frens and Van Opstal 1995; Hofman and Van Opstal 1998, for details) that were driven by separate stepping engines (Berger Lahr VRDM5), both controlled by a PC 80486. This setup enabled rapid (within 2 s) and accurate (within 0.5°) positioning of the speaker at a fixed distance of 0.90 m at any location on a virtual sphere. It has been verified in earlier studies (Frens and Van Opstal 1995) that the sounds produced by the stepping motors did not provide any consistent localization cues to the subject. Prior to the actual positioning command, the speaker was always moved into a random direction, at least 20° away from the previous location. In this way, speaker displacement cues that could be related to movement duration of the stepping motors were completely eliminated.

Target and response coordinates are expressed as azimuth (α) and elevation (ε) angles, determined by a double-pole coordinate system in which the origin coincides with the center of the head. In this reference frame, target azimuth, α_T, is defined as the angle between the target and the midsagittal plane. Target elevation, ε_T, is the angle between the target and the horizontal plane through the ears with the head in a straight-ahead orientation (Knudsen and Konishi 1979).

Response paradigms

Mismatches between the actual target positions and the subject's responses can be due to an erroneous perception of sound location, but also by a particular motor strategy or errors in the motor response itself. This might be relevant when testing the blind, as they have been reported to be often motorically delayed at infancy (Adelson and Freiberg 1974). A possible solution to this ambiguity is to use more than one response method. To that end, two different methods were employed: head-pointing, and pointing with the left (stretched) arm (Haber et al. 1993). An earlier pilot study indicated no difference in pointing behavior for the left or right arm.

Head-pointing method

The 2D orientation of the head in space was measured with the magnetic induction technique (Robinson 1963). The usefulness of

Table 1 Characterization of the six early-blind subjects that participated in this study. All subjects had a visus below 1/300 within their 1st year after birth. At this level, subjects have never been able to detect the movement of a hand at 1 m distance. Blind subject B6 was treated for a pituitary adenoma at the age of 5 years. All subjects had normal hearing

Subject			Vision in the better eye (right eye/left eye)	Cause of early blindness
Number	Age (years)	Sex		
Bs-1	29	M	Only light perception (+/+)	Retinopathy of prematurity
Bs-2	34	M	Only light perception (+/+)	Congenital microphthalmos and coloboma
Bs-3	42	M	No light perception (–/–)	Enucleation of both eyes (tumor)
Bs-4	23	M	Only light perception (–/+)	Retinopathy of prematurity
Bs-5	28	F	Only light perception (–/+)	Retinopathy of prematurity
Bs-6	36	M	Only light perception (+/–)	Pituitary adenoma at age 5 years

this method has been described in previous papers from our group (Frens and Van Opstal 1995; Hofman and Van Opstal 1998; Goossens and Van Opstal 1999). In short, two orthogonal pairs of coils, attached to the room's edges, generated two oscillating magnetic fields (30 kHz horizontally, and 40 kHz vertically) that were nearly homogeneous and orthogonal in the area of measurement. The magnetic fields induced two oscillating voltages in a small (diameter 2 cm) induction coil that was rigidly attached via a lightweight helmet (150 g) to the center-top position of the subject's head. The magnitude of these voltages is directly related to the 2D orientation of the head re field coils. The signals were demodulated by two lock-in amplifiers (PAR-128A), tuned to either field frequency, low-pass filtered (cut-off 150 Hz), sampled at a rate of 500 Hz per channel (DAS16), and finally stored on hard disk for further analysis.

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 range that was tested with this response method was $\alpha_T \in [-70, 70]^\circ$ for target azimuths, and $\varepsilon_T \in [-40, 65]^\circ$ for target elevations, respectively.

Arm-pointing method

The 3D-positions of the subject's left arm were measured with an infrared (IR) tracking system (Watsmart, Northern Digital). Two IR-sensitive cameras, mounted in the upper left corners of the room, were used to digitally sample, at a rate of 100 Hz, the exact positions (within 0.4 cm) of three IR LED markers: one on top of the left shoulder, one near the left elbow, and one on the tip of the left index finger. These positions were chosen such that when the arm was stretched, they would form a straight line defining the direction of the arm pointer.

Because of the limited field of view of the IR cameras, the subject was positioned about 45 cm rightward and 45 cm backward relative to the center of the robot's target sphere. As a consequence, the stimulus range was slightly reduced, to azimuths $\alpha_T \in [-55, 25]^\circ$, and elevations $\varepsilon_T \in [-30, 40]^\circ$.

As will be explained, the arm-pointing data are expressed in azimuth/elevation angles relative to the left shoulder, rather than to the center of the head, thereby shifting the target ranges to $\alpha_S \in [-50, 30]^\circ$ and $\varepsilon_S \in [-30, 40]^\circ$, respectively. The small intensity changes (within 5 dB) that were related to the corresponding small variations in stimulus distance were not corrected for. Figure 1 provides a schematic illustration of the experimental conditions.

Experimental paradigms

The following aspects of sound localization were studied in separate experiments: (1) the accuracy of 2D sound localization for long-duration broad-band noise, (2) the latency of sound-localization responses, and (3) the use of acoustic feedback and the influence of the sound spectrum.

All six blind subjects and three of the sighted subjects (c, e, and f) participated in all three experiments. Four sighted subjects (a, b, d, and g) participated in experiments I and II only, whereas the four remaining sighted subjects (h–k) performed only in experiment III. Note that in this way all three experiments were tested with seven sighted control subjects.

During the experiments, no feedback was given to the subject about performance. At the beginning of the session, a few practice trials were given to let the subject get acquainted with the experimental procedures.

Experiment I

The accuracy of sound localization was tested by presenting a 500-ms-duration broad-band (0.2–20 kHz) noise stimulus to randomly selected positions in the 2D frontal hemisphere (see sections Head-pointing method and Arm-pointing method for stimulus position ranges, and Results for actual target distributions). Two sets of 110 responses were measured: in the first set, the subject had to respond with the stretched left arm; in the second set, the head served as the pointer to indicate perceived sound location.

The subject initiated a trial by pushing a button whenever he/she felt ready and was pointing straight ahead (i.e., in the central fixation direction, $[\alpha_R, \varepsilon_R]=[0, 0]$). Subsequently, after 250 ms, a white-noise sound burst at a fixed intensity of 60 dBA was presented. The task of the subject was to quickly point towards the perceived position of the target as *accurately* as possible. Two seconds after stimulus onset, and well after response offset, a short beep indicated the ending of the trial, after which the robot would reposition the speaker before the start of a new trial.

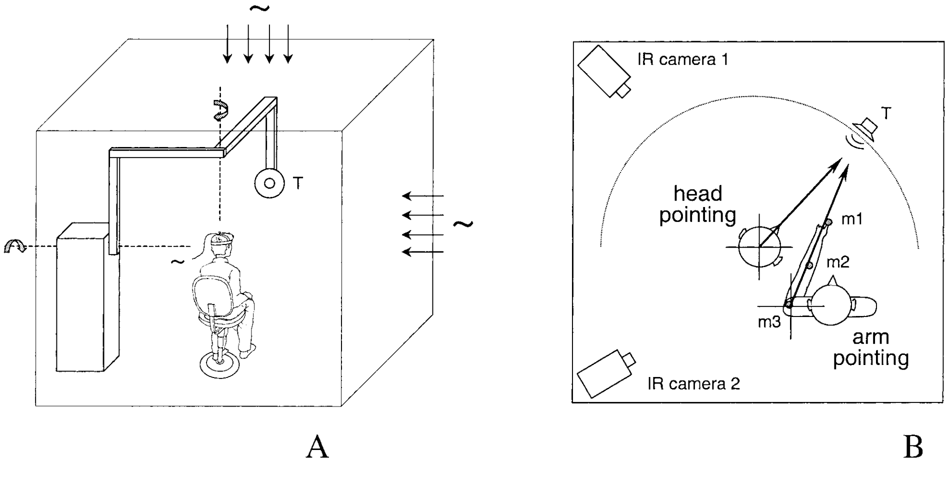

Fig. 1A, B Experimental situation in the two experiments. During head-pointing, the subject is seated in the center of the laboratory room (subject seen from behind in **A**). The auditory target (*T*) is randomly positioned on the subject's frontal hemisphere by a two-link robot arm. The subject's head movement responses were measured by the magnetic induction method, for which a small measurement coil was attached to the subject's head and four coils of 3×3 m along the room's edges generated two orthogonal oscillating magnetic fields (*arrows at the upper and right side of the cube*). In the arm-pointing task, the subject is positioned 45 cm rightward and backward re center (**B**). The arm movement responses are tracked by recording the 3D position of three markers on the subject's left arm (*m1, m2, m3*) with two infrared cameras

Experiment II

The latency of sound-localization responses was tested with the same stimuli as in experiment I. However, the subject was now explicitly urged to point to the target as *quickly* as possible. To avoid effects of fatigue, only the head-pointing method was used in these experiments.

Experiment III

As the head movement typically overlaps with the presentation epoch of the stimulus, the relatively long stimulus duration of experiments I and II allows in principle for the use of ongoing acoustic feedback (see Introduction). Such a strategy could for example be beneficial for the localization of sound elevation of pure tones. To test for the possible use of head-movement induced acoustic feedback, in experiment III subjects responded to both short-duration (150 ms, 50 trials) and long-duration (500 ms, 50 trials) noise bursts. In addition, long-duration (500 ms) tone pips of either 750 Hz or 5,000 Hz (25 trials each) were randomly interleaved with the other two stimulus types, in order to verify whether the responses in elevation relied exclusively on spectral shape analysis and to separately test on the use of interaural time and intensity cues. Target positions were drawn at random from 25 stimulus boxes, spanning a range of azimuths and elevations $\in [-30, 30]^\circ$. The subjects were instructed to point with their head as accurately as possible toward the perceived target position.

Data analysis

Calibration of head position in space

The measured induction voltages from the head coil were precalibrated on the basis of head fixations made to 72 visual targets (green LEDs) distributed over the frontal hemisphere (Goossens and Van Opstal 1997; Hofman and Van Opstal 1998). This precalibration, with which the sensitivity of the coil (in millivolts per degree) could be determined, was carried out by one of the authors (M.Z.), before the start of the experiments. The head fixations were performed by aligning a 40-cm-long visual pointer that was rigidly attached to the helmet with the LEDs. The end point of the rod was aligned with the viewing eye. By aligning the tip of the rod with the visual targets, the target coordinates could be subsequently mapped onto the coil signals.

This was achieved by training two three-layer neural networks, by the back-propagation algorithm, on the collected fixation data, separately for the horizontal and vertical head position components (see Goossens and Van Opstal 1997 for details). The neural networks could account for the static nonlinearity, inherent in the magnetic induction method, as well as for minor crosstalk between the coil signals of the horizontal and vertical magnetic fields.

The networks were applied to the raw data of the actual experiments for off-line calibration, to map the measured induction voltages onto the corresponding 2D orientations of the head, $[\alpha_R, \varepsilon_R]$ (in degrees) in space. The absolute accuracy of the calibration was within 3% over the entire response range (Goossens and Van Opstal 1997, 1999).

Calibration of hand position in space

The calibration of the Watsmart system was done prior to the experiment by a standardized procedure (prescribed by the manufacturer) consisting of multiple recordings, at various positions in the area of measurement, of a dedicated calibration frame equipped with 72 IR markers. This data set served to calculate the parameters that linearly transform the camera readings into LED positions in 3D cartesian space (coordinates expressed in millimeters). To independently check for the accuracy of the calibration algorithms provided by the manufacturer, two LEDs, that were mounted on a rod at a fixed distance of 40 cm from each other, were moved by hand across the measurement space. Off-line calibration of the LED position data indicated a mean reconstructed distance between the two LEDs of 39.8±0.3 cm.

Choice of origin

In our paradigm, subjects were asked to point toward the perceived target position, either with their stretched left arm or with the tip of their nose. Note that the pointing direction is determined by both the choice of pointing method and the pointing origin.

In nose-pointing, it is not obvious what the pointing origin is. The helmet was placed such that the plane of the coil was approximately parallel to the frontal plane of the head and centered through the ears. The pointing origin was thus defined by setting the offset coil signals to zero when the subject assumed a comfortable straight-ahead pointing direction.

In arm-pointing, it has been shown that, when using their index finger as a pointer, sighted humans often use their cyclopean eye, rather than their shoulder, as the pointing origin (McIntyre et al. 1997). It is unclear, however, whether this is also true for blind subjects, as the functional coupling of the arm pointer and vision is absent. Therefore, to ensure an unbiased comparison between the arm-pointing responses of blind and sighted subjects, we expressed the pointing direction of the arm for both groups in azimuth/elevation angles relative to the left shoulder, rather than relative to the cyclopean eye. The influence of shifting the pointer origin relative to the cyclopean eye was estimated, by simulation, to underestimate the response gain and the residual error by 8% and 10% at most (respectively), whereas the correlation values of the stimulus-response relations remained unaffected. The main effect (99%), however, resulted in an equivalent change in the bias of the optimal regression line.

Parameter extraction

Start and end positions of the head movements were selected off-line by means of custom-made saccade detection software (Hofman and Van Opstal 1998). The markings of the on- and offset of the movements were set on the basis of fixed velocity and acceleration/deceleration criteria and could be interactively updated by the experimenter. Start and end positions of the arm were determined over brief segments of data in which the signals were stable. To ensure unbiased selection criteria, no stimulus information was provided to the experimenter. An illustration of this procedure is shown in Fig. 2.

Statistics

The optimal linear fit of the stimulus-response relation was found by minimizing the sum-squared deviation of the following equation:

$$\alpha_R = a + b \cdot \alpha_T \quad \text{and} \quad \varepsilon_R = c + d \cdot \varepsilon_T \qquad (1)$$

for the azimuth and elevation components, respectively. In Eq. 1, *a* and *c* (in degrees) are the response bias (offset of the fitted line), and *b* and *d* are the dimensionless gains (slopes) of the stimulus-response relations. Confidence levels for Pearson's correlation coefficients were obtained through the bootstrap method (Press et al. 1992). The results of statistical tests were considered significant when its chance level was less than 5%.

For head-pointing, the target coordinates, $[\alpha_T, \varepsilon_T]$, were expressed in angles re head. As indicated previously, for the arm-pointing data the target coordinates were given relative to the shoulder: $[\alpha_S, \varepsilon_S]$. Trials in which the target eccentricity was outside $[-50, 50]^\circ$ were discarded from the analysis, as for some subjects these responses exceeded the recording range of the head.

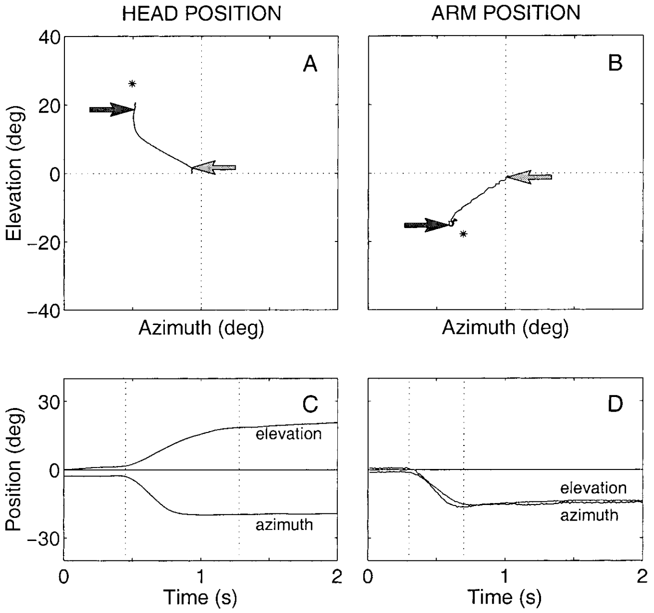

Fig. 2A–D Trajectories of arm (**A**) and head (**B**) movements, and the beginning (*light arrow*) and endpoints (*dark arrow*) that were selected on the basis of the velocity profiles of the arm (**C**) and head (**D**) movements, respectively (*dashed lines*). Information about the position of the auditory target (the *asterisk* in **A**, **B**) was not available to the experimenter during the selection process

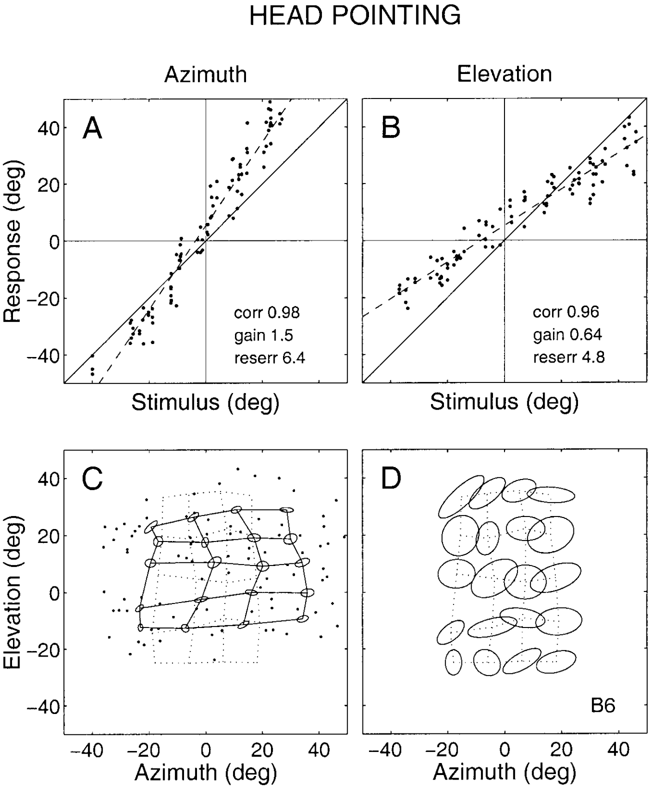

Fig. 3A–D Head-pointing localization data from blind subject B6 in experiment I. Responses were made toward broad-band noise bursts (duration 500 ms). **A** Azimuth components. Note the high gain and correlation of the responses. **B** Elevation components. Note that the response gain is lower than for azimuth. **C** Response grid for the same data shown in **A**, **B**. *Solid lines* connect averaged responses to neighboring stimulus locations (see Methods). *Dotted lines* connect averaged stimulus locations for the same responses. Perfect localization would have both grids superimposed. *Small ellipses* indicate the standard error of the local response distributions for each point of the response grid (see Methods). **D** Ellipses indicate the standard deviation of the local response distributions, superimposed on the corresponding target grid. Note local variability in both size and orientation of the ellipses

The gain, bias, residual error (standard deviation relative to the fitted line), mean absolute error (the mean sum-squared deviation from the line), and linear correlation coefficient that were extracted from the fit procedure display different aspects of sound-localization behavior. The gain and bias relate to the spatial accuracy of localization behavior, whereas the residual error and the correlation coefficient relate to the variability and spatial resolution of the system, respectively. The absolute localization error depends on both the accuracy and the variability of the responses.

Note that, in the presence of a given amount of scatter, the correlation between stimulus and response position also depends on the gain of the relation. This means that for a given residual error (quantified by the mean scatter around the regression line) the correlation increases with an increase in gain. Note also that, when the residual error and the gain are fixed, the correlation increases with the measurement range.

A possible drawback of the regression method described here is that local field effects are averaged out. On the other hand, the limited number of trials makes it impossible to apply statistics when studying localization behavior in spatial detail. A possible way out is to trade some of the spatial resolution for numerical power and bin local groups of points together. To this end, a grid of four horizontal by five vertical bins was defined. The bins had a 50% overlap and were evenly distributed over the stimulus range.

In each bin, the mean stimulus and response positions were calculated. Linear interpolations were made between neighboring positions so as to form a stimulus and response grid (see, e.g., Fig. 3C). In this way, a quick impression of the localization accuracy as a function of spatial direction can be acquired. Note that for the ideal observer the two grids coincide.

To obtain a similar 2D map of the localization variability, the variance in the pointing error was calculated as a function of polar angle (principal component analysis). For each bin, this variance was visualized by a polar plot which was positioned at the corresponding mean stimulus position. The elliptic shape of the polar plot, i.e., the orientation and length of the main axes, was determined by the direction and size of maximal and minimal variance (see, e.g., Fig. 3D). Note that the orientation of the ellipses is upright if azimuth and elevation components of the responses are statistically independent.

Results

Experiment I: head and arm pointing to 500-ms broad-band noise

Head pointing

To enable a quantitative comparison of the response behavior of both subject groups, linear regression lines were determined for the azimuth and elevation components of the head movements as function of the respective target coordinates (see Methods). A typical example of this analysis is shown in Fig. 3 for blind subject B6. The top panels (Fig. 3A, B) show the individual data points of the head displacement vectors, together with

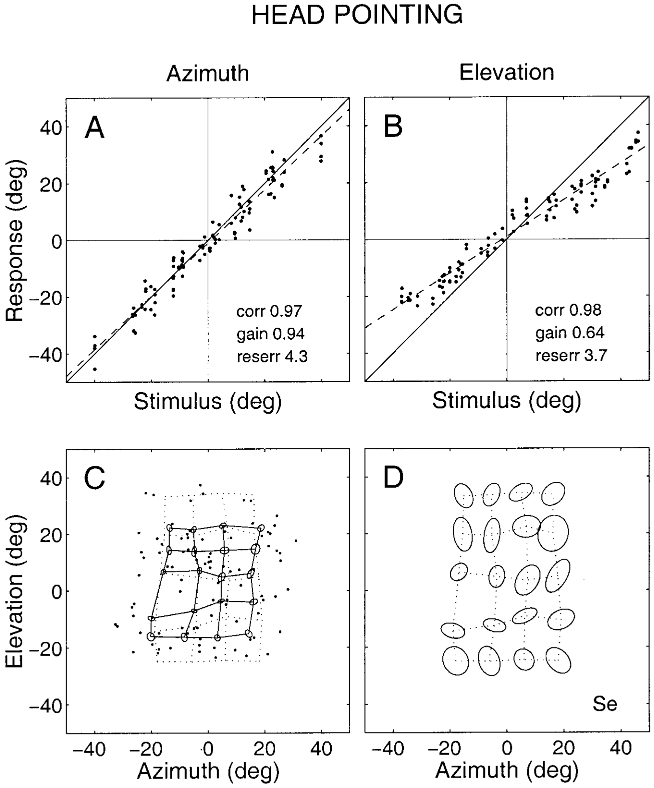

Fig. 4A–D Head-pointing localization data from sighted subject Se. Same format as Fig. 3. Note that for this subject the azimuth gain **(A)** and response variability (residual error) is lower than for the blind subject of Fig. 3 ($P<0.05$). This is also expressed by the smaller response grid **(C)** and smaller variance ellipses **(D)**

the optimal regression lines. Note the high correlations for both response components and the relatively modest scatter around the fitted lines. Although the gains of both response components clearly differ from one (1.5 for azimuth, 0.61 for elevation), the responses of the subject are well related to the target coordinates.

This is also illustrated in the lower panels (Fig. 3C, D), in which the local accuracy and variability of the subject's responses have been calculated (see Methods). By comparing the response grid (Fig. 3C, solid lines) to the target grid (dashed lines), it can be seen that the subject's responses adequately capture the actual distribution of the targets throughout the stimulus range. The overall deformation of the response grid illustrates the underestimation of target elevation and the overestimation of target azimuth that was also observed in the regression analysis. Yet, minor local field defects for perceived sound elevation emerge for the upper and lower left-hand regions. Also, the perceived sound azimuth varies slightly (but systematically) with elevation in the center regions.

The shapes of the ellipses in the variability map in Fig. 3D show that the subject's responses are consistent throughout the stimulus range. In line with the emergence of the local accuracy deficits, some minor irregularities can be seen here as well.

A typical example of data from one of our sighted subjects (Se) is provided in Fig. 4, in which the responses are shown in the same format as in Fig. 3. As the regression results (Fig. 3A, B) and the response grid (Fig. 3C) both show, also this subject's responses are closely related to the actual stimulus positions. Note that the azimuth gain, i.e., the horizontal stretch of the response grid, as well as the variability (expressed by the residual error) is smaller than for blind subject B6 ($P<0.05$).

Inspection of the head-pointing data of all subjects further substantiates the findings in the two subjects exemplified already. The local field defects were minor and idiosyncratic in all subjects, whereas the azimuth gains and variability typically differed between subject groups. This is shown qualitatively in Fig. 5, which displays the local response and variance grid for three other blind (left) and sighted (right) subjects.

The quantitative results of the regression analysis for all subjects are shown in Fig. 6. As shown in Fig. 6A, the azimuth component of the responses of the blind subjects was typically overestimated (gain 1.26±0.06), whereas this component was underestimated in the sighted subjects (gain 0.92±0.06). This difference in gain is statistically significant when tested with a two-sided *t*-test with unequal variances ($P=0.002$). Yet, to test whether the response *accuracy* for either group of subjects is different, gain overshoots (typical for the blind) and gain undershoots (typical for the sighted) should be weighted similarly. To that end, we adopted the following "gain-error" measure, G_E, to express the deviation of the measured gain, G_{Meas}, from the expected value of 1.0:

$$G_E = 1 - |1 - G_{Meas}| \tag{2}$$

Note that G_E equals G_{Meas} when the gain is less than 1. For the blind group, the gain-error for azimuth yields $G_E=0.74\pm0.06$, which is not significantly different from the value obtained for the sighted subjects (0.87±0.04). So, on average, both groups responded equally (in)accurately in azimuth, although their head-movement response gains differed markedly.

The center panels of Fig. 6 show that the blind responded with a higher variability for azimuth (residual error 9.5±1.1°, against 5.7±0.7° for the sighted; $P=0.02$) but not for elevation (7.3±1.0°, against 5.1±0.5° for the sighted; $P>0.05$).

The bottom panels of Fig. 6 show that the correlation between target and response position was high for both the blind and sighted subjects, demonstrating good spatial resolution of their auditory systems. The difference in the correlation coefficients for elevation between the blind (0.92±0.01) and the sighted group (0.95±0.01) was not statistically significant. The difference in azimuth correlation between the two groups was even smaller and not significant either (0.96±0.01 vs 0.97±0.01, respectively). Note that, due to the fact that the correlation depends on response gain (see Methods), the higher residu-

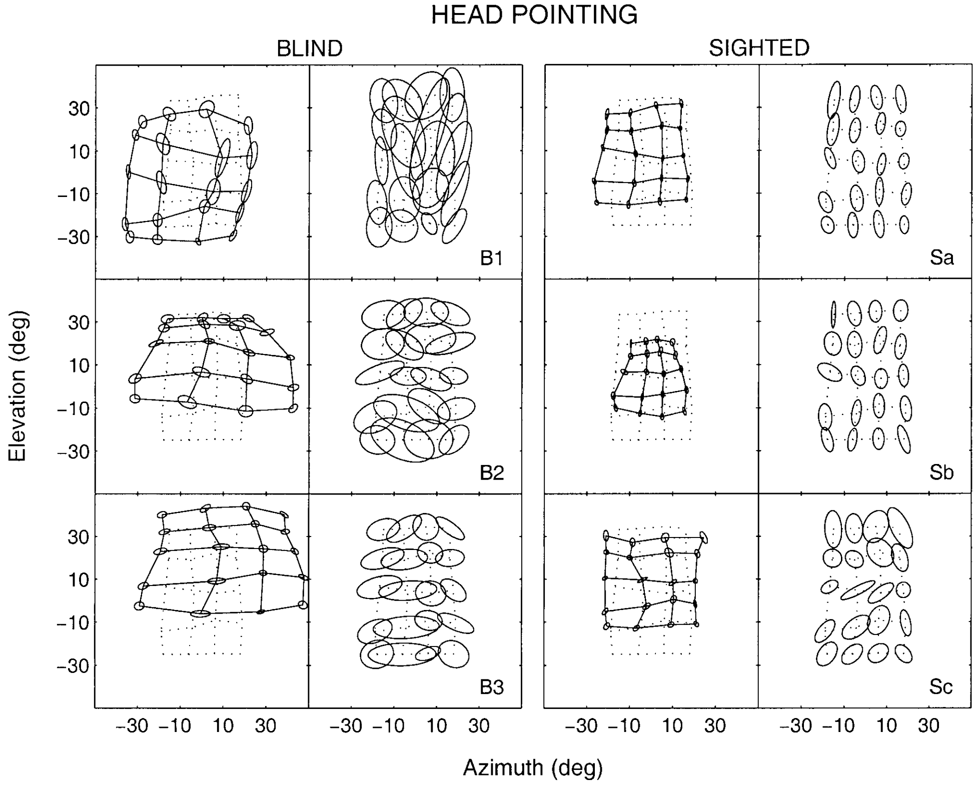

Fig. 5 Examples of the localization data for the head movements of six more subjects. Response grids (*left-hand column*), and local response variability ellipses (*right-hand column*) for three blind subjects (*left*) and three sighted subjects (*right*). The blind subjects typically overshoot target azimuth, whereas the sighted subjects undershoot this component. Error distributions (*variance ellipses*) of the sighted are smaller than those for the blind

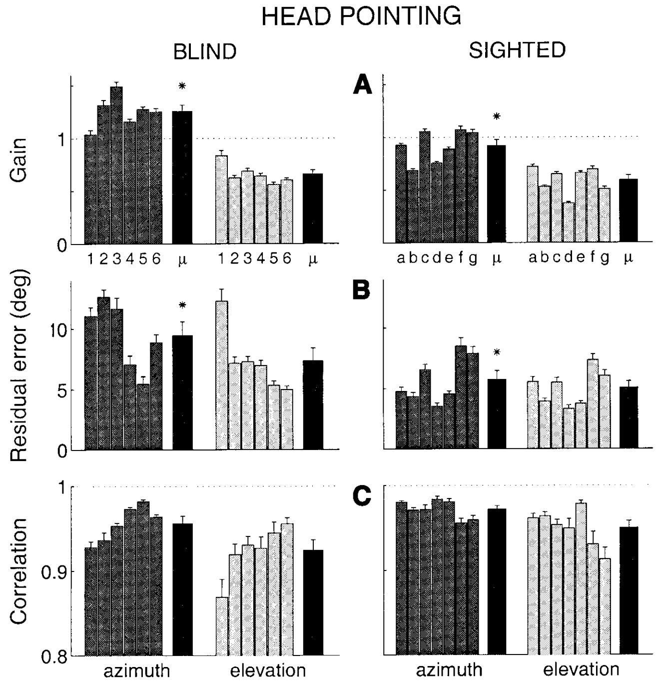

Fig. 6A–C Summary of the head-pointing regression results for all blind and sighted subjects. **A** Response gains. **B** Residual errors. **C** Linear correlation coefficients. *Dark-gray bars:* azimuth response components. *Light-gray bars:* elevation response components. Subjects are indexed by *1–6* (blind) and *a–g* (sighted). *Black bars:* mean (with standard deviation) across subjects. Note the high azimuth gain and azimuth residual error for the blind, which differ significantly (*$P<0.05$) from the sighted. The other differences are not statistically significant

al error for azimuth of the blind subject group is leveled out by the accompanying higher azimuth gains.

Arm pointing

The quantitative analysis performed on the arm-movement data yielded similar results as the head-movement data, with only minor differences. As an example, the results for one of our blind (B3) and sighted subjects (Sd) are shown in Fig. 7A (top row) in the same format as Fig. 3. Note that also the arm-pointing responses are well related to the actual target locations, and that the azimuth gain of the blind subject appears to be lower than in the case of head pointing.

As is illustrated by the data of three other blind and sighted subjects in Fig. 7B (three bottom rows), the minor local field defects seemed to be idiosyncratic and quite dissimilar to the local anomalies found in head pointing (Fig. 5). This indicates that these local anomalies may reflect properties of pointing, rather than of auditory localization. Closer inspection of the grids in Fig. 7B suggests, however, that the responses of the sighted subjects seem to be systematically shifted rightward. Such a shift is not obvious in the data from the three blind subjects.

Differences in pointing behavior between the two groups are further illustrated and summarized in Fig. 8, which shows the averaged variability data for all subjects within each target bin. The local response variances do not systematically change with target eccentricity for

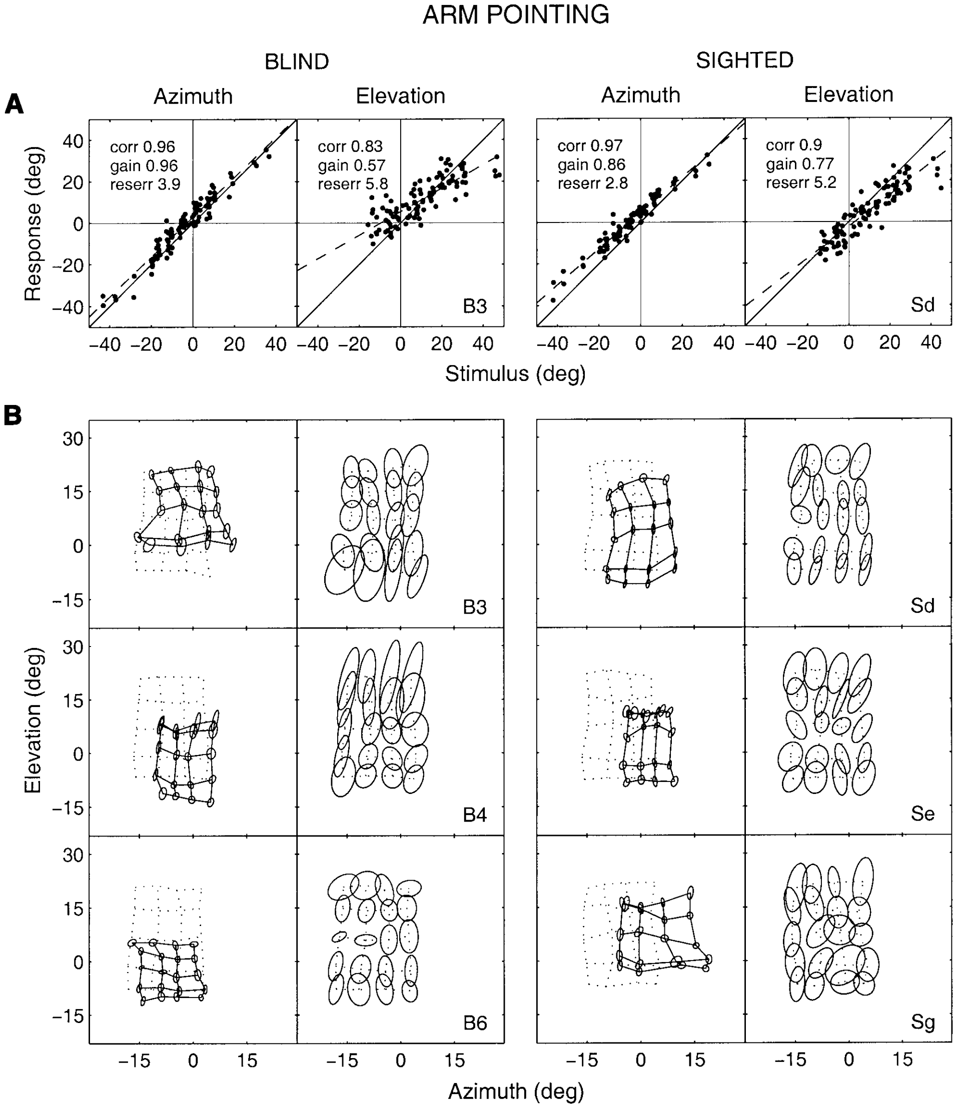

Fig. 7 **A** Arm-pointing data from blind subject B3 (*left*) and sighted subject Sd (*right*) in experiment I (broad-band noise, 500 ms). Like for head pointing, response correlations are high. **B** Summary of the localization data for the pointing arm movements of three individuals from both subject groups. Data are presented in the same format as Figs. 3, 4 and are referenced with respect to the subject's left shoulder (see Methods). Note that the sighted subjects tend to point from an origin that is shifted rightward. Such a shift is not observed in the response data of the blind subjects

either group or pointing method. An overall difference in response variability between the blind and sighted is clear for the head-pointing data (left-hand column), but is absent for the arm-pointing results (right-hand column).

The results of the regression analysis for the arm pointing responses for all subjects are summarized in Fig. 9. Again, the results of the blind and sighted are very similar as none of the regression parameters differed significantly between the two groups ($P>0.05$; *t*-test).

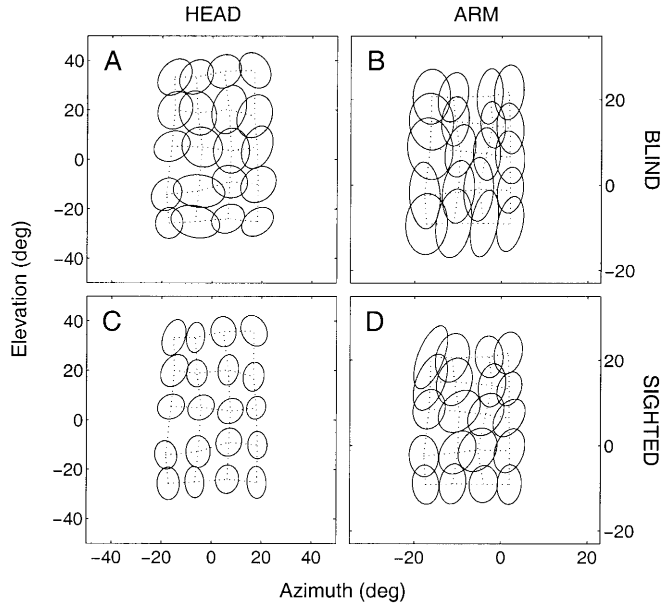

Fig. 8A–D Local response variability, superimposed on corresponding points of the target grid, for both head- (*left*) and arm pointing (*right*), averaged across subjects. Note the systematically lower variability in the head-movement responses of the sighted subjects (**C**), which was statistically significant. This difference disappeared, however, for the arm-pointing data. Note also, that there is no trend for neither the blind nor the sighted subjects to respond with a lower variability at more eccentric locations

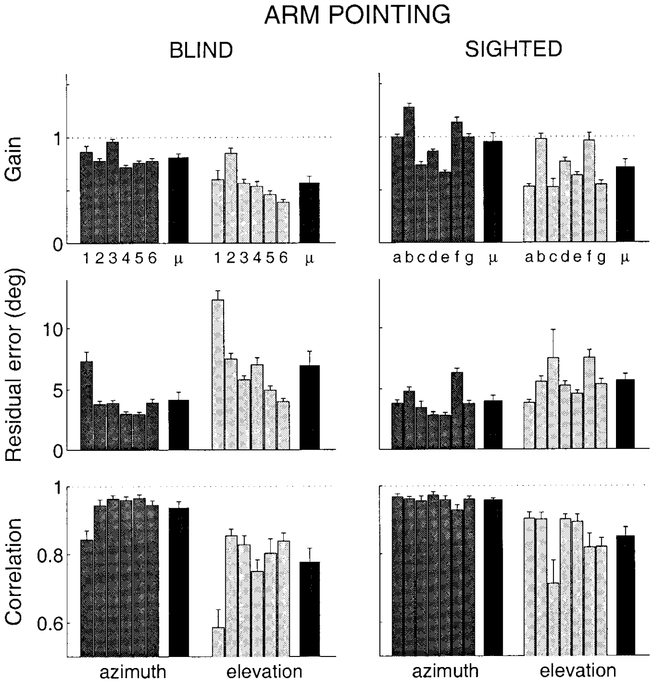

Fig. 9 Summary of the arm-pointing regression analysis of experiment I for all subjects. Same format as Fig. 6. In contrast to the head-pointing data, none of the regression parameters between the two groups differed significantly

Head versus arm

The previous paragraphs show that the outcome of the comparison between the sound-localization abilities of the blind and sighted depends on whether the subjects pointed with their head or their arm. A direct comparison between these two pointer methods might provide insight as to the extent to which this apparent discrepancy is related to specific motor variability and/or pointing strategy (see also Methods). For the sighted subjects, the performance difference when pointing with head or arm was insignificant, except for the residual error of the azimuth component of the responses, which was smaller when pointing with the arm (4.0±0.5° and 5.7±0.7°, respectively; P=0.02, paired t-test). Similarly, for the blind group, the residual error of the azimuth component of the responses was smaller for the arm than for the head (4.1±0.7° vs 9.5±1.1° respectively; P=0.003, paired t-test). Yet, in this group, the azimuth gain of the arm movement responses was smaller too (0.81±0.04 for the arm vs 1.26±0.06 for the head; P=0.0005, paired t-test).

The correlation coefficient for the elevation and azimuth components also differed significantly between the two pointing methods in both subject groups. This difference might be caused by the difference in apparent stimulus range (see Methods) and is therefore likely to be unrelated to perceptual and/or pointing features.

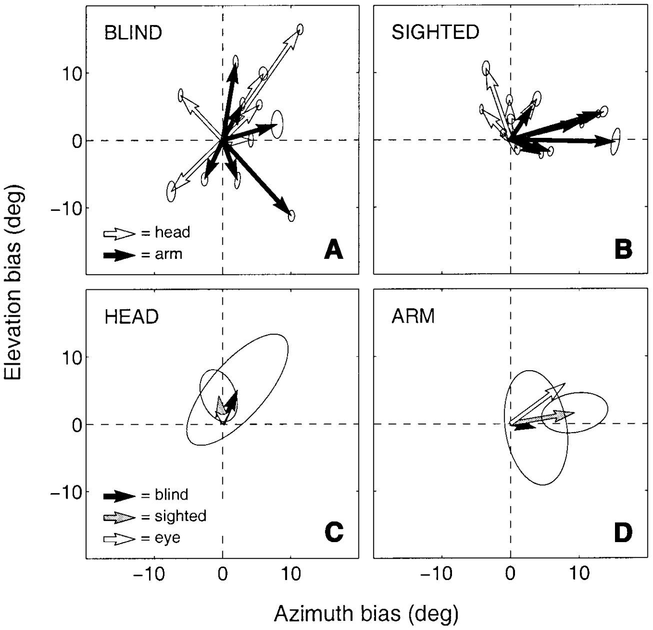

Fig. 10A–D Differences in response-bias vectors for head and arm suggest different pointer origins. **A** Bias vectors for each blind subject (*black arrow,* arm; *gray arrow,* head). **B** Bias vectors for each sighted subject. **C** Averaged bias vectors for the head-pointing responses of each subject group. **D** Averaged bias vectors for the arm-movement responses of each subject group (*white arrow,* estimated location of the cyclopean eye). Standard deviations are indicated by *ellipses*. In contrast to arm pointing by the blind, whose origin is close to their shoulder joint, sighted subjects tend to point from their cyclopean eye. For head pointing, there is no difference between the blind and sighted

Pointer origin

Another aspect of pointing strategy is the choice of the pointer origin by the subjects. In our analysis the data were calibrated by defining the comfortable straight-ahead direction as the pointing origin for the head, and the left shoulder joint as pointing origin for the left arm. If, on the other hand, subjects had programmed their movements from a different representation of the pointer origin, the data would have been characterized by a systematic shift in the regression bias.

Qualitatively, it could be noted in Fig. 7 that the bias of the sighted subjects tends to be shifted rightwards, a trend that seems absent in the examples of the blind subjects. This interesting feature is further quantified in Fig. 10, in which the bias vectors (defined by their azimuth and elevation components) are shown for all blind (Fig. 10A) and sighted subjects (Fig. 10B), separately for the head (light arrows) and arm pointers (dark arrows). Note how the biases for both the head and arm pointers are distributed around zero in the blind subjects. The bias vectors for the sighted subjects, however, appear to be distributed differently for arm and head pointing: The head-pointing bias vectors are distributed like in the blind subjects, whereas the arm-pointing biases have a systematic rightward component.

This can be seen more clearly in the bottom two panels, which show the averaged bias vectors for the head (Fig. 10C) and arm (Fig. 10D), separately for the blind (filled black arrow) and sighted subjects (grey arrow). As illustrated by the elliptic standard deviations around the mean, the head bias vectors do not differ significantly, neither between subject groups, nor from zero. The same applies to the arm-pointing bias in the blind. However, the mean arm-pointing bias in the sighted subjects does differ significantly both from zero and from the arm-pointing bias of the blind (*P*=0.04). Interestingly, the bias vector of the sighted subjects is close to the bias expected when subjects point from their cyclopean eye, rather than from their shoulder joint (origin of the coordinate system).

Experiment II: accurate vs fast

So far, only the spatial mapping of acoustic cues was studied, as subjects were specifically instructed to respond as accurately as possible to the perceived target location, without stressing response speed. Compensatory plasticity, however, could also become apparent in a reduction of response reaction times (Neville 1990). When the onset latencies of the head movements in experiment 1 are compared, it seems that the blind group typically responded faster than the sighted subjects (Fig. 11A; mean group latencies 228±29 ms for the blind, and 299±37 ms for the sighted subjects).

To verify whether this feature would persist, in experiment II subjects were specifically instructed to respond *as fast as possible* to the target location. Only the head-movement pointing method was employed in this task. Fig. 11B (“fast”) shows that the onset latencies in this experiment were indeed significantly reduced, when compared with the “accurate” task (Fig. 11A), both for the blind and the sighted subjects. However, the previous difference between the two groups disappeared in the “fast” task (171±10 ms vs 175±11 ms, respectively).

Note also, that the localization error did not significantly alter in the fast response task, neither for the azimuth components (Fig. 11C), nor for the elevation components (Fig. 11D). The same is true for the other regression results (data not shown). Thus, in the fast task, all subjects responded with comparable accuracy to the accurate task, but they were markedly faster.

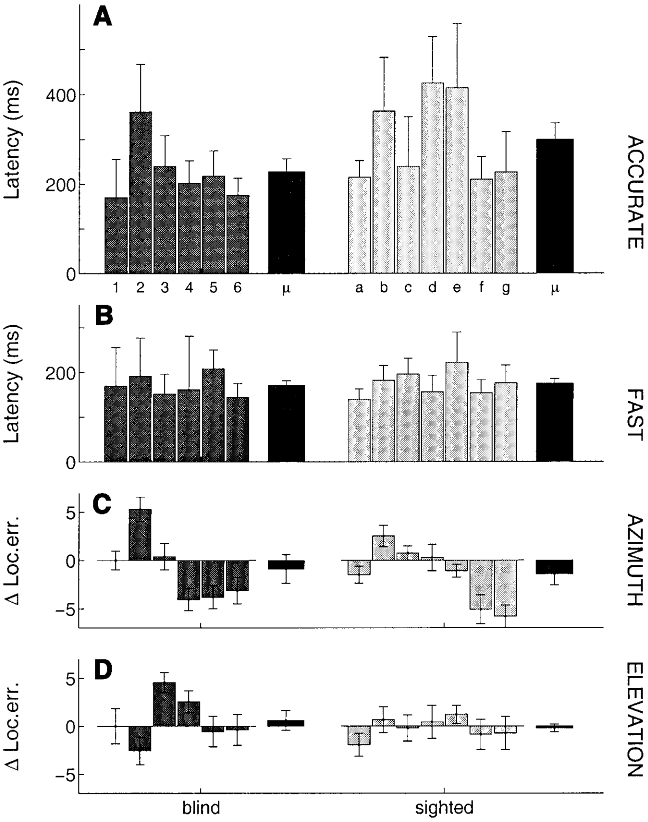

Fig. 11A–D Summary of the response latencies of the blind (*dark bars*) and sighted subjects (*light bars*) in the accurate (A) vs fast (B) head-response condition. Although the blind respond faster in the accurate task (A), this difference disappears when subjects are pressed for speed (B). The difference histograms in the *two bottom rows* show that the average absolute response error in the two conditions was the same for both azimuth (C) and elevation (D)

Experiment III: influence of duration and stimulus spectrum

An important question, left unanswered by the results from experiments I and II, is whether the blind have indeed only relied on spectral shape cues to generate their orienting responses in elevation. In both experiments, stimulus duration was always 500 ms, so that response latencies typically fell well within the stimulus presentation period (Fig. 11). Moreover, the stimuli had broad-band spectra. Hence, it is conceivable that subjects may also have used acoustic feedback cues during their head movements instead. In addition, orienting toward pure tones (which provide no reliable spectral localization cues) might benefit from head movements, as the acoustic filters of the pinna induce head-position related intensity variations for high sound frequencies (above 4 kHz), but not for low frequencies (below 2 kHz).

To further study this point, 13 subjects (six blind, seven sighted) participated in a third experiment, in which four different stimulus types were presented randomly interleaved at each of 25 randomly selected locations: the control stimulus (500 ms Gaussian white noise, GWN), a short-duration noise burst (150 ms GWN) that ended before head movement onset, and two long-duration (500 ms), pure tone pips (low frequency 750 Hz; high frequency 5,000 Hz).

Figure 12 shows the regression results of this experiment for the head-movement responses of a typical blind subject. The subjects’ responses correlate well for both azimuth (Fig. 12A, C, E, G) and elevation (Fig. 12B, D, F, H) to the two broad-band noise stimuli (Fig. 12A–D). Note the consistent response behavior to either broad-

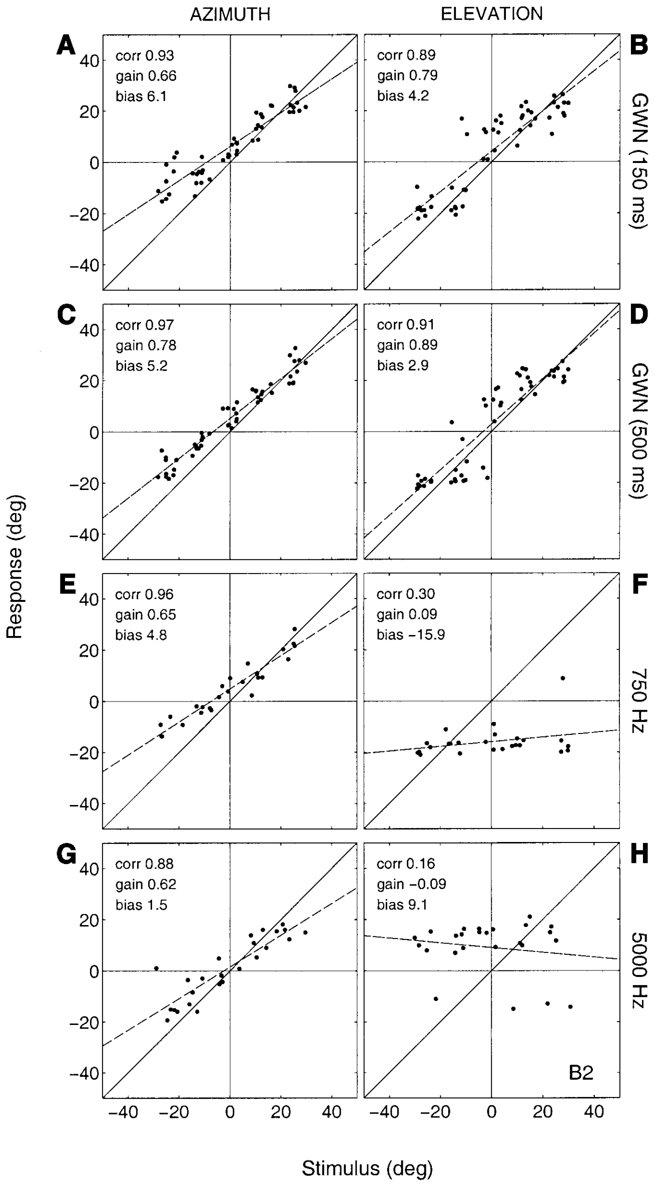

Fig. 12A–H Regression analysis for each stimulus type in experiment III. Data from blind subject B2. Azimuth response components for all four stimulus types are highly correlated with stimulus azimuth. Note that responses toward the 500-ms GWN stimulus (**C, D**) have slightly higher gains than those to the 150-ms noise burst (**A, B**), both in azimuth (**A**, **C**, **E**, **G**) and in elevation (**B, D**, **F, H**). Response elevations toward the pure tones are uncorrelated with stimulus elevation for both the low-frequency tone (750 Hz; E, F), and the high-frequency tone (5 kHz; G, H). Subject perceives the low-frequency tone at a fixed low elevation of about –14°; the high-frequency tone is perceived at a fixed elevation of about +8°, regardless the actual stimulus location

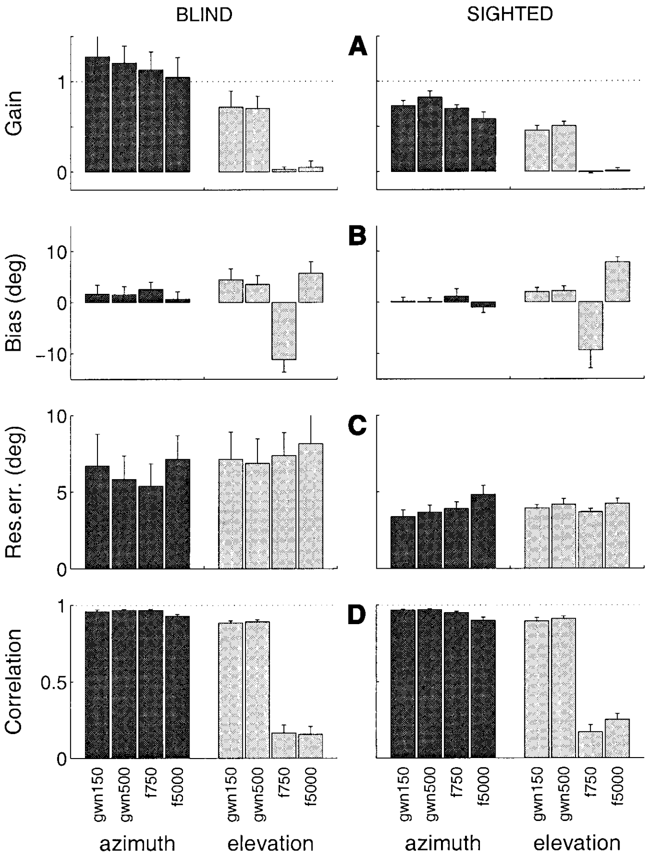

Fig. 13A–D Summary of the results of experiment III. Data have been averaged across subjects within each group (blind, *left;* sighted, *right*), and for each response component (azimuth, *dark bars*; elevation, *light bars*), for each stimulus condition separately (GWN500: long-duration noise burst; GWN150: short-duration noise burst; f750: pure tone of 750 Hz; f5000: pure tone of 5000 Hz). **A** Response gains; **B** response bias; **C** residual errors after regression; **D** linear correlation coefficients. Note how the low-frequency tone tended to be perceived at a low elevation (bias f750) and the high-frequency tone (bias f5000) at a higher elevation

band stimulus. Note also that the response gains were somewhat lower in this experiment than in the previous two experiments, but that the response gain is slightly higher for the longer-duration noise burst when compared with the short-duration stimulus.

The results for the pure tones (Fig. 12E–H) show that the subject responded with a high correlation to changes in target azimuth only, but that this correlation vanished for the response elevation component.

The results of experiment III averaged for all subjects from both groups are summarized in Fig. 13. For each stimulus type, the mean regression parameters for the two response components, azimuth and elevation, are given separately. As stimuli were randomly interleaved in the experimental session, it is possible to directly compare the results for each stimulus type.

The response variability (quantified by the residual error, in degrees) for the short- and long-duration noise burst stimuli was significantly higher for the blind group ($P<0.05$), for both response components (see Fig. 13C). In line with the previous experiments, the differences in response gain and in the correlation coefficients did not reach significance when tested between the two subject groups.

When the results between the short-duration and long-duration noise responses are compared, however, it appears that in the majority of cases the performance for the latter stimuli is slightly better (e.g., see Fig. 12). This aspect is especially pronounced for the gains of both response components. Indeed, if the "gain-error" is adopted to quantify these results (Eq. 2), the differences are statistically significant for both subject groups ($P<0.001$ for azimuth as well as for elevation, paired *t*-test on all subjects; data not shown).

If acoustic feedback underlies this improvement, the following conditions should be met: (a) response latencies for the long-duration stimuli should fall well within the stimulation period; (b) directional errors, occurring during the initial phase of the movement trajectories, should be more reduced toward the end of the movement when responding to long-duration stimuli.

Although all subjects responded well after the offset of the short-duration stimulus, roughly half of the subjects (three blind and three sighted) had increased their response latencies by about 200 ms for the long-duration stimuli. As the responses of these "slow" subjects did not meet the first criterion, their improvement in response accuracy could not have been caused by acoustic feedback.

We also analyzed several aspects of the movement trajectories to both noise bursts: errors in the initial movement direction (defined as the initial first degree of the movement trajectory), errors in the final movement direction (computed at movement offset), and errors in movement amplitude (computed as the absolute distance between target and response at movement offset).

The initial movement directions were statistically indistinguishable between long- and short-duration stimuli for all subjects. On average, all subjects made smaller amplitude errors for the long-duration stimuli ($P=0.03$, paired *t*-test). The error in the final movement direction was significantly reduced in the six "fast" responders ($P=0.05$; paired *t*-test), but not in the seven "slow" subjects (data not shown). Whether these results provide evidence for the use of acoustic feedback in this group is discussed in the next section.

Discussion

This paper investigated whether the human visual system is crucial for the development of accurate sound localization in the frontal 2D hemifield. To that end, the behavior of blind subjects under a variety of tasks and stimulus conditions was quantitatively compared with that of an age-matched group of normal-sighted, naive subjects.

Although sound-localization performance of the blind has been studied in the past, most studies confined the experiments to the horizontal plane or to a limited number of possible target locations. The present study combines, for the first time, a variety of sound-localization aspects within the same group of subjects: (1) target locations were randomly distributed in the frontal 2D space, thus simultaneously testing azimuth and elevation localization performance, while maintaining a large amount of uncertainty as to the possible locations of targets; (2) different response methods and tasks were applied with the same subjects ("head" vs "arm", and "accurate" vs "fast"); (3) localization performance was measured for different stimulus types, that were randomly interleaved, allowing for a direct test of the use of different sound-localization cues.

As targets were distributed randomly over the 2D frontal hemifield, pointing responses were analyzed separately for their azimuth and elevation components (Eq. 1). There is ample evidence in the literature that the perception of sound location, and the associated localization response, is independently processed for the azimuth and elevation channels (Blauert 1997, for review). This feature is underlined by the responses toward low-frequency and high-frequency tones which, for both groups, showed highly correlated localization behavior of the azimuth response component, but no significant correlation for elevation (Figs. 12, 13).

In line with earlier reports (Wanet and Veraart 1985; Ashmead 1998), our results show that azimuth performance of the blind to long-duration (500 ms), broadband noise stimuli is, on average, as accurate as that of normal-sighted subjects (Figs. 3, 4, 5, 6, 7, 8, 9). The mean performance of both groups was statistically indistinguishable, when looking at stimulus-response correlation, response gain, or response variability. Interestingly, this also held for the more challenging task of employing the complex and highly idiosyncratic spectral shape cues that relate to sound elevation (Figs. 6, 9). Moreover, the reaction-time distributions, obtained from the fast-response task, were identical for both groups, while localization performance was equally accurate for both tasks (Fig. 11).

Taken together, our data show that the visual system is not crucial for the development of an adequate 2D sound-localization system, as other systems are capable of calibrating the acoustic localization cues. The putative compensatory mechanisms in the blind do not give rise to auditory spatial hyperacuity in the frontal hemifield – where the potential benefit of vision is maximal. This will be further discussed.

Use of acoustic cues

By using different spectral stimulus types, the experiments allowed us to assess and compare the use of the different acoustic localization cues by both subject groups.

Binaural difference cues

The mean azimuth performance of the blind was indistinguishable from that of the sighted for all four stimulus types used in experiment III (Figs. 12, 13). The low-frequency, 750 Hz pure-tones provide subjects only with reliable ongoing phase differences as a localization cue for target azimuth, as intensity differences are negligible in the low-frequency range (Blauert 1997). The data in Fig. 13 show that azimuth localization was comparable for both subject groups, indicating that the time-difference cue was equally well represented. Both groups also appeared to perceive the low-frequency tones typically at a low elevation, regardless of the actual stimulus elevation.

High-frequency tones above 3 kHz no longer provide unambiguous phase-difference cues, but the interaural intensity differences are uniquely related to sound-source azimuth, albeit in a frequency-dependent manner. Again, the mean results were indistinguishable for the two groups, indicating that the blind have also learned to faithfully map these more complex cues. Like the sighted subjects, the blind typically perceived the target at an upward elevation, although the exact positions were somewhat idiosyncratic (data not shown, but see Fig. 13B).

Spectral shape cues

The elevation responses of blind and sighted subjects were comparable, in that the gains of both subject groups did not differ significantly, neither for the head-pointing task (Fig. 6), nor for the arm-pointing task (Fig. 9). As responses in elevation are entirely based on the pinna-related spectral shape cues, we conclude that the blind have successfully mapped these complex cues onto the elevation domain. This is not a trivial point, as these cues change in a complex way with changing pinna geometry. The mechanisms by which the blind might have acquired this mapping are still unclear.

Acoustic feedback

Although the intensity of a high-frequency tone varies systematically with target elevation due to the direction-dependent filtering properties of the pinnae (Goossens and Van Opstal 1999), subjects of neither group could utilize this potential cue for localizing target elevation during their rapid head movement toward the 5-kHz tone. This does not necessarily mean that head-movement feedback is not used at all, as the absolute intensity of a tone remains an ambiguous cue. The responses to the short- and long-duration noise bursts could provide more insight into this point. Indeed, it was found that the long-duration stimuli elicited slightly more accurate responses than the short-duration noise bursts.

As reported in the Results, however, half of the subjects from both groups had adopted a conservative response strategy in this paradigm by postponing their head-movement response to stimulus offset. The slight improvement in response accuracy for these “slow” responders, can therefore not be attributed to the use of head movement-induced feedback cues. Although we cannot exclude that the “fast” responders did employ such feedback cues, two alternative explanations might account for the slight improvement found in both groups:

1. Possibly, long-duration stimuli may induce larger (and therefore typically more accurate) head movements. Indeed, it has recently been shown, that the contribution of the head movement to a gaze-orienting task depends on stimulus modality (Goossens and Van Opstal 1997). Typically, head movements are larger for auditory-evoked gaze shifts than for visually elicited eye-head movements. Although this was not specifically tested in that study, it is possible that the head-movement amplitude may also depend on sound duration.
2. Alternatively, the auditory system may have benefited from the longer integration time available for the 500-ms noise burst. In a recent study, Hofman and Van Opstal (1998) showed that response gains for elevation increase as stimulus duration is increased from 3 to about 80 ms. No such effect was found on response azimuth. Although that study only concerned eye movement responses toward sounds, it cannot be excluded that similar effects might be apparent in head-movement responses, and up to much longer stimulus durations.

Nonacoustic factors

It may be noted that in experiment III the response gains were typically lower than those obtained in experiments I and II, especially for the blind subjects. This difference might be due to two stimulus context factors: first, in experiment III a more limited stimulus range for azimuth was applied than in experiment I ([–30, 30]° vs [–70, 70]°), which could have induced a range effect in the responses (Butler and Planert 1976; Kapoula and Robinson 1986). Second, the mixture of four different stimulus types, often poorly localizable, may have caused subjects to be less confident about their localization responses and therefore induced a more cautious strategy. Such a response mode was also apparent from the longer latencies obtained in this experiment, especially in the group of “slow” responders.

Comparison with other studies

Our data seem not to agree with recent studies that have suggested superior localization abilities in the blind. Most notably, the blind subjects tested by Röder et al. (1999) show an increased sensitivity for target displacements in far-lateral space, when compared with frontal targets in the horizontal plane. In the lateral region, the binaural difference cues are less reliable than monaural spectral shape cues, so their results may suggest that blind subjects are actually better at employing their spectral shape cues than normal-sighted subjects. The same has been suggested by Lessard et al. (1998) who concludes that some of their blind subjects were better than their sighted subjects in using spectral cues for lateralizing sounds.

These results may appear to be at odds with our conclusion that blind subjects do not perform better than sighted subjects in the elevation domain. Note, however, that our subjects were tested in the frontal target domain only (within 50° from the midline). In the frontal region, the binaural difference cues are quite reliable, and especially in this region sighted subjects might typically benefit from visual input as well. It is therefore conceivable that for this target range sighted subjects may have relied on their visual system to fine-tune their acoustic localization cues, whereas for far peripheral and rear locations, where vision is poor (or absent), the input from other systems (e.g., proprioceptive or vestibular feedback) come into play.

With regard to the interpretation of Lessard et al. (1998), two alternative hypotheses would not necessarily contradict our findings. Note that some of their blind subjects performed better than the sighted when lateralizing sounds in the frontal hemifield under monaural hearing conditions. However, it was not shown that the result of their forced choice left-right paradigm was robust for subtraction of the mean bias, caused by the perceptual shift toward the side of the free ear. It therefore remains unclear whether the sighted subjects too were able to *discriminate* the sounds from the left and right hemifield. Second and more importantly, as stimuli were always presented at the same sound level, absolute intensity, rather than monaural spectral shape cues, may have served as a localization cue. Thus, instead of being more sensitive to spectral cues, it is possible that the blind may have relied more strongly on absolute sound intensity cues in mapping sound azimuth.

Compensatory plasticity?

There are at least four different mechanisms that should be considered in explaining both our result that blind and sighted localize equally well in the frontal hemifield, as well as other studies suggesting superior performance at peripheral and rear locations (already discussed):

1. Vision is not used at all in training the human sound-localization system; instead, spatial hearing relies entirely on feedback from other sensory systems.
2. Vision is crucial for calibrating the auditory system in the frontal domain. Other sensory systems only aid in its calibration for far-lateral and rear target locations.
3. Vision does contribute in the sighted, but it is not the only system used for the frontal target domain. It is supported by other sensory feedback systems, which may take over in case of (early) blindness.
4. The localization cues are mainly (genetically) preprogrammed. Only some coarse feedback mechanism would be needed to provide adequate calibration (finetuning) of these cues.

On the basis of our results, and earlier studies in humans, the second mechanism can be rejected, as it would predict that the blind would not be able to localize sounds in the frontal hemifield at all. We also believe that the fourth mechanism is unlikely to establish an appropriate 2D sound-localization system. It is conceivable that the binaural difference cues are to a certain extent preprogrammed, as these cues are related to sound azimuth in a straightforward, monotonic way. However, it is not easy to envisage preprogramming of the highly individualized spectral shape cues, as these cues change in a complex, frequency-dependent way when the ear changes its size and shape during growth. Indeed, it has been shown recently that the calibration of these cues is an ongoing plastic process, even in adult humans (Hofman et al. 1998). Subjects wearing binaural molds relearn their localization capabilities in elevation during the course of a few weeks. It is difficult to imagine how this recalibration process would come about without some form of sensori(motor) feedback.

It is important to note, that in order to discriminate between hypotheses 1 (no compensatory plasticity) and 3 (compensatory plasticity), specific differences between the blind and sighted should have to be demonstrated for the visual-dominant frontal hemifield. Unfortunately, the relative contributions from the visual system and other sensorimotor systems to sound localization are at present unknown. It is therefore not possible to predict localization performance in the absence of vision for either hypothesis. Thus, only the demonstration of hypercompensation in the blind would provide valid evidence for compensatory plasticity mechanisms. Similarly, the demonstration of localization deficits in the frontal hemifield of the blind would show a role for vision in calibrating the human auditory system. Such deficits remain yet to be shown.

Although superior abilities have been assigned to the blind for peripheral and rear target locations (Lessard et al. 1998; Röder et al. 1999), some caution is warranted, as these studies measured relative target *discrimination* abilities in these regions, rather than absolute target *localization*. Different processes may underlie these spatial behaviors. Also recent findings that in early-blind humans occipital cortex is activated during an acoustic task (Kujala et al. 1995; Kujala et al. 2000; Weeks et al. 2000) is not necessarily proof of compensatory plasticity. For that to be the case, it should be demonstrated that these occipital activations are functionally related to the task, and that task performance would be impaired without these occipital (or other) activations. In the study by Weeks et al. (2000), localization performance of blind subjects is reported to be indistinguishable from that of sighted controls.

Reference frames

Our findings did not depend on the response task used: both the accuracy of the head-pointing method and the arm-pointing responses had similar characteristics for the two groups. This indicates that the transformation needed to map the head-centered acoustic input into the appropriate coordinates of either motor system was equally well developed in both blind and sighted subjects.

However, an interesting difference was obtained in the reconstructed pointer origin for the arm-pointing task: in line with earlier reports (McIntyre et al. 1987), the results showed that when sighted subjects point to the target with their index finger, the origin of pointing was much closer to their cyclopean eye than to their shoulder joint (Fig. 10). For the blind subjects, the pointing origin resulted to be at their shoulder joint. This marked difference suggests that the functional shift in the frame of reference for the arm is imposed by an intact visual system, and thus acquired by learning, rather than being a preprogrammed movement strategy.

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