Plasticity in human sound localization induced by compressed spatial vision

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Auditory and visual target locations are encoded differently in the brain, but must be co-calibrated to maintain cross-sensory concordance. Mechanisms that adjust spatial calibration across modalities have been described (for example, prism adaptation in owls), though rudimentarily in humans. We quantified the adaptation of human sound localization in response to spatially compressed vision $(0.5 \times \text{lenses for } 2-3 \text{ days})$. This induced a corresponding compression of auditory localization that was most pronounced for azimuth (minimal for elevation) and was restricted to the visual field of the lenses. Sound localization was also affected outside the field of visual-auditory interaction (shifted centrally, not compressed). These results suggest that spatially modified vision induces adaptive changes in adult human sound localization, including novel mechanisms that account for spatial compression. Findings are consistent with a model in which the central processing of sound location is encoded by recruitment rather than by a place code.

The auditory and visual systems encode target location in fundamentally different ways. Nevertheless, the two modalities must provide a common representation of space to properly identify and localize targets that emit both an image and a sound. Similarly, vestibular inputs depict head motion and orientation through yet another modality which must be concordant with motion signals from the other senses. Little is known in humans about the precision and calibration of auditory spatial processing relative to other sensory modalities.

When multisensory information is integrated in the brain, vision often dominates the localization percept. For example, in ventriloquism the hand puppet appears to talk rather than the artist. Presumably, the richness and spatial accuracy of visual information, given the direct mapping of the outside world onto its sensory receptor (the retina), underlies its dominance in resolving sensory conflicts. Beyond multimodal perception, vision is even thought to shape the spatial representation in the auditory modality itself, as shown in barn owls¹, cats^{2,3}, ferrets⁴ and humans^{5–7}. Insight into cross-sensory coordination has been acquired from studies on the adaptation of sound localization to lateral shifts of visual space induced by prisms. Particularly in the barn owl, detailed information has been gathered about how prism adaptation results in a corresponding shift in both the behavior and neurophysiology of sound localization, despite the erroneous representation induced in auditory space with respect to the environment^{1,8}.

Prism adaptation has also been studied in humans⁹, although it is not clear whether the observed spatial plasticity can be attributed to changes in the sound localization system. A visual shift can be compensated at a variety of spatial processing stages. For example, in visually guided finger pointing, the locus of adaptation could reside along a chain of nested coordinate transformations that include the retinal map itself (target-to-eye), eye-to-head, head-to-body and body-to-arm mapping, as well as directly within a second sensory modality providing spatial input (sound-re-head).

In this study, we examined a new form of visually-induced adaptation in human sound localization. Several features distinguish our approach. First, we used binocular 0.5× lenses to modify visual space. Unlike prisms, which induce a bias (homogeneous lateral shift) of the entire visual-spatial map, 0.5× lenses compress the spatial visual field by half, inducing a reduction in visual spatial gain. Plastic mechanisms that could adapt to this novel type of spatial mismatch have not been studied. Second, the use of 0.5× glasses avoids the confounding issue of nested coordinate mappings (as applicable in prism adaptation⁹), as visual compression cannot be readily compensated by a simple adjustment in head-to-body mapping or in subsequent spatial processing stages. Third, the exposure period for lens adaptation lasted for up to three days, well above the few hours of exposure typical in human prism studies9. Moreover, adaptation was induced by active interaction of subjects in their natural multisensory environment rather than passive visual training under laboratory conditions^{10,11}.

Finally, we tested for the potential locus of cross-sensory spatial plasticity. In particular, we focused on the retinal input, the signal related to eye-in-head, and the auditory representation of space (sound-re-head). Two spatial localization tasks were used, one in which the eyes were free to move and guide a laser pointer toward the perceived sound position ('target-fixation'

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Fig. 1. Pre-adaptation sound localization responses from one representative subject. Linear regressions (dashed line) were performed on the azimuth (**a**, **c**) and elevation (**b**, **d**) components of the stimulus–response relation (each point corresponds to a single trial). *G* is the overall gain (slope of the regression line), δ is the residual error after regression, and *r* is Pearson's correlation. Subjects performed well in both the target-fixation (**a**, **b**) and central-fixation (**c**, **d**) paradigms. Note lower variance and higher gain for azimuth than for elevation (also note different scales).

task) and another in which subjects fixated a central visual spot and used their peripheral retina to guide the pointer to the target ('central-fixation' task). In all cases, the head remained fixed in space. Combined with the neural representation of soundre-head, the central fixation task relies on a retinal mapping of the peripheral pointer (eye position is constant while the pointer moves on the retina), while the target fixation task depends on a signal related to eye-in-head (the eyes move to align the target and pointer with the fovea). Further, plasticity in the auditory representation of space was studied by extending the target range to two dimensions (2D). In this way, we found different adaptations in the separate processing pathways for sound azimuth (binaural time and intensity differences) and elevation (pinna-related spectral cues)¹². Note that adaptive changes occurring in either of these auditory subsystems are independent of visual-motor mappings and should therefore (equally) show up in both localization paradigms.

RESULTS

Sound localization before adaptation was precise and consistent for both types of pointing tasks, as judged from the nearoptimal values of spatial gain (slope of the stimulus–response relation) and the high correlation coefficients across the target range tested (exemplified in Fig. 1 for one subject). In line with previous studies, performance was slightly better for azimuth than for elevation^{13,14}.

Sound localization was assessed before, during (daily for up to 3 days) and after adaptation to $0.5 \times$ lenses (Methods). An initial comparison of regression coefficients over the entire target range (as in Fig. 1) indicated only a subtle effect of visual compression on sound localization (spatial gain), and more so in azimuth than in elevation (Fig. 2a–d). Because the lenses restricted the visual field to a ~20° radius (Fig. 2f), visual–auditory interactions dur-



Fig. 2. Grand-average spatial gain adaptation. Average spatial gains across subjects (**a**–**d**) are shown before (pre), during (days 1,2,3) and after recovery from (post) adaptation to $0.5\times$ lenses, calculated from regression analysis as in **Fig. 1**. Gains are normalized to the pre-adaptation results. Error bars depict one s.d. of the mean; * indicates statistically significant (P < 0.05) deviations from baseline. Results for azimuth (**a**, **c**) and elevation (**b**, **d**) as well as for target (**a**, **b**) and central (**c**, **d**) fixation paradigms are shown. Decreases in gain are more common for azimuth than for elevation, but remain subtle in this form of analysis. (**e**) In contrast, average AVOR gains (not normalized) show robust gain adaptation (down to 0.6 over 3 d) and recovery to normal (post). (**f**) Target distribution used in all experiments. The shaded area outlines the visual field viewed through the 0.5× lenses.

ing adaptation were similarly limited. This, in turn, probably limits the region of spatial gain adaptation, which can be easily masked in a broad regression analysis. We therefore focused our regression analysis to the region of potential cross-sensory interaction (gray zone in Fig. 2f). In this way, the adaptive effects of $0.5\times$ lenses on spatial gain became more clear, while other parameters, such as the residual error after regression, response bias (that is, regression offset) and correlation coefficient, were not affected by lens adaptation (data not shown).

An alternative cross-sensory calibration phenomenon in response to 0.5× lenses is the well-described¹⁵ adaptive plasticity that occurs in the angular vestibulo-ocular reflex (AVOR). We studied AVOR plasticity in all subjects to serve as a control for the effectiveness of our adaptive paradigm. The results indeed show a robust effect of 0.5× lenses on reducing AVOR gain during horizontal head rotation (Fig. 2e). As response properties (gain and phase) remained roughly flat across the tested frequency range, results were pooled across subjects and stimulus frequencies.

Recall that the rationale for focusing our analysis of sound localization on the restricted visual field of the lenses was the supposition that adaptation to altered visual input is driven by cross-sensory experience and will therefore reflect its spatial limitations. To evaluate the extent to which this is true, we estimat-



Fig. 3. Local changes in auditory spatial gain (combining azimuth and elevation). (**a**, **c**) The change in gain (relative to its pre-adaptation value) as a function of 2D target location on the last day of lens adaptation. The dark-blue vertical strip in the central field primarily reflects a central decrease in azimuth response gain. (**b**, **d**) The recovery of local gain after removal of the $0.5 \times$ lenses (relative to adapted values). Note that the recovery plots show broad changes, indicated by the near uniform yellow color of the plots. Also note the similarity between the results of the target-fixation (**a**, **b**) and central-fixation paradigms (**c**, **d**).

ed the local spatial gain of sound localization (slope of the stimulus-response relation) across the entire target domain. This approach emphasizes central changes that are most likely to be induced by lens adaptation, while avoiding the over-weighting of peripheral data points inherent in regression. As a first step, linear regressions were performed on azimuth responses within azimuth bins (20° width, pooled across elevation), calculated in 1° steps across the azimuth range to yield local spatial azimuth gains. Similarly, local spatial gains in elevation were computed within elevation bins (15° height, pooled across azimuth) at 1° steps across the range of elevation. For each 2D bin location, the corresponding azimuth and elevation gains were then multiplied together to yield a combined measure of local spatial gain. Finally, the change in local gain for each bin was calculated by taking the difference between values obtained before and after lens adaptation.

The resulting analysis (Fig. 3), averaged across subjects, depicts a central-most region in which spatial gain dropped considerably (down to -0.5, blue 'cold-spot' in Fig. 3a and c) after $0.5 \times$ lens adaptation. This region roughly resembles the visual field provided by the lenses (Fig. 2f), except for the expanded effect in elevation. Note that the results for the two tasks (target and central fixation) are quite similar. Interestingly, a similar analysis of the recovery from lens adaptation indicates a broad rebound of local gain (Fig. 3b and d) without a central 'hot spot'. This may reflect the fact that the available visual field during recovery was likewise broad, given the absence of the lenses.

These findings (Fig. 3) confirm that lens adaptation was maximal within the visual field provided by the $0.5 \times$ lenses. To pinpoint the potential locus of adaptation, however, it is important to further quantify the adaptive behavior and test for differences between the target and central fixation tasks, and between azimuth and elevation. To this end, we adopted a parametric model in which the adaptive changes observed in local spatial gain (Fig. 3a and c, for example) are described by a Gaussian function:

$$\Delta G(x) = a \cdot \exp(-(x/b)^2) \tag{1}$$

where *x* is target position, and *a* (the maximum value of the gain change) and *b* (its spatial extent) are free parameters. Note that the local gain equals the partial derivative of the relation between target and response location. Thus, integration of the local gain change (ΔG in equation 1) yields the local change in response location (ΔR):

$$\Delta R(x) = \frac{1}{2}\sqrt{\pi} \cdot a \cdot b \cdot \operatorname{erf}(-x/b) + c \tag{2}$$

where 'erf' is the error function and c is a constant. The advantage of equation (2) is that it can be fitted directly to the entire pooled set of raw data (point-by-point changes in response location), without first having to estimate local response properties (like local gain).

Several observations can be made from this analysis (Figs. 4 and 5): (i) a clear modulation is apparent in azimuth (P < 0.05, student's *t*-test) but not in elevation, (ii) the largest gain change (negative slope in the curves for azimuth) is found in the center of the field and approaches the lens magnification factor (ideal a = -0.5), (iii) the width of the adapted area is within that of the lens' available visual field (parameter *b*), but is larger for the target-fixation task than for the central-fixation task (P < 0.05, student's *t*-test), and (iv) the largest change in response location, ΔR , reaches its greatest deviation at the edges of the adapted field and carries unaltered (that is, with normal spatial gain) into the periphery. The implications of these findings are discussed below.

DISCUSSION

Our results show that spatially scaled vision induces systematic and adaptive changes in sound localization that restore the spatial calibration between the two modalities. Specifically, a reduction of visual spatial gain induced by 0.5× lenses was largely matched by a comparable reduction of spatial gain in sound localization. The effect was robust but primarily limited to azimuth. Spatial gain adaptation was governed by, and effectively limited to, the region of visual space provided by the lenses. We therefore conclude that it requires active cross-modal experience for its acquisition.

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Fig. 4. Adaptive changes in sound localization for the same subject illustrated in **Fig. 1**. Normal (pre-adaptation) responses were subtracted from adapted values for each target location to yield the adaptive changes in response across the array of target locations. Response changes in azimuth and elevation are shown for both the target-fixation (**a**, **b**) and central-fixation (**c**, **d**) paradigms. The white trace represents the running average through the data, whereas the dark gray area depicts one s.d. from this average.

Locus of adaptive processing

Evidence indicates that the adaptation of sound localization induced by a compression of visual space reflects modifications primarily within central auditory spatial processing. First, spatial adaptation was demonstrable whether subjects used eye movements (target fixation task) or peripheral vision (central fixation task) to guide the laser pointer in localizing auditory targets. This suggests that the major site of adaptation does not reside within the visual or oculomotor systems. Although the results were qualitatively similar, a small but significant difference was obtained between the two paradigms. The broadening of the adapted region in the target fixation task (compare Fig. 5a and c) may reflect additional changes in the signal conveying eye position in the head (as in prism adaptation⁹), some subtle form of plasticity in visual capture (like ventriloquism) unique to the central fixation paradigm, or both. Yet, neither mechanism can readily explain the overall adaptation in sound localization responses, particularly with regard to the local changes as a function of eccentricity and their limitation to azimuth.

This leads to a second key finding: clear differences were observed between results in azimuth and elevation. It is well documented that sound azimuth and elevation are processed by independent neural pathways that depend on different spatial cues, at least initially in the brainstem¹⁶. These differences impose ramifications in behavior^{14,17–19}. For example, narrow-band sounds are accurately localized in azimuth but not in elevation^{13,20}. Altering spectral cues with external-ear molds abolishes elevation localization but has no effect on azimuth^{21,22}. Moreover, localization of sound azimuth is more robust against background noise than elevation²³, and the two domains are differentially affected in the blind⁷. This distinction between azimuth and ele-



Fig. 5. Adaptive changes in sound localization for all subjects (format as in Fig. 4). Data points represent the individual sound azimuth (a, c) and elevation (b, d) response components at the last day of adaptation minus their corresponding pre-adaptation values. Equation (2) was fitted to the data (solid black curve) to quantify the lens-induced adaptation. Parameter values that could not be determined reliably are denoted 'n.s.'. The model describes the data well, as expressed by high correlation coefficients (r = 0.68 in a) and the close resemblance between model (black) and running average (white) curves. The scatter in the data (the gray area depicts one s.d. around the running average) is relatively small (\sim 5°), even though the noise level was increased by pooling raw data across subjects and by taking response differences. Note that the largest changes in azimuth response location are found at the edges and outside the visual field of the lenses, and that the transition in the central region is somewhat broader (and with greater variance) for the target-fixation task (a, b) than for the central-fixation task (c, d). Also note that elevation response changes are negligible.

vation corresponds with our finding that adaptive behavior also differs between these intrinsic auditory dimensions. In contrast, no such difference is reported after visually induced adaptation in the saccadic system²⁴.

Despite the apparent lack of adaptation in elevation localization (in contrast to azimuth), the possibility remains that additional time may be required to adapt elevation-related spectral cues to modified vision. Indeed, the three-day exposure period in the current experiment is short compared with the month needed for substantial prismatic adaptation in the barn owl⁸, or the 20 days needed for humans to learn new spectral cues²².

Taken together, our findings strongly suggest that the observed plasticity in spatial localization behavior mainly resides within the central auditory system. Thus, as in barn owls^{1,8}, spatially modified visual–auditory experience induces changes in human sound localization. However, unlike in barn owls^{25,26}, guinea pigs and ferrets²⁷, the plasticity reported in this paper is not limited to early development. In addition, these experiments indicate a new form of auditory plasticity: that of spatial gain and not bias. Note that either form of auditory spatial adaptation entails a clear deviation from (and therefore an erroneous representation of) the actual location of sound in space, and instead conforms audition to the modified spatial representation provided by vision.



Fig. 6. Effect of target elevation on the adaptation of sound azimuth localization. Changes in response location as a function of target azimuth for three elevation bands $[+7^{\circ} \text{ to } +22^{\circ} (\text{top}), -8^{\circ} \text{ to } +7^{\circ} (\text{center}), \text{ and } -23^{\circ} \text{ to } -8^{\circ} (\text{bottom})]$ show similar results for all three bands (all fit parameters of equation (2) differed significantly from zero, but not from each other, when tested with a *t*-test). The format is the same as in **Figs. 4** and **5**.

Local adaptation and its relation to neural coding

Two fundamental features characterize the plasticity of sound localization described in this study (Fig. 7a, c, e and g). First, the central compression of auditory space in azimuth extends to all elevations studied (Figs. 3 and 6). Second, the adaptive reduction of auditory spatial gain is limited to the visual field of the $0.5\times$ lenses, which in turn limits the visual–auditory interaction that presumably drives the acquisition of plasticity. In other words, the actual localization of auditory targets shifts centrally to match the visual spatial compression of the lenses. Interestingly, the maximum shift occurs at the edges of the adapted field (as expected), but then continues unaltered into the periphery despite the absence of visual–auditory interactions in that region of space. Note that the change in sound localization behavior in the periphery is not one of spatial gain but of accuracy.

An alternative adaptation scheme might have held localization accuracy unaltered in the periphery (Fig. 7b, d, f and h). However, that would have required a more complex behavior of spatial gain, for the central decrease in gain would then require an opposing peripheral increase to restore overall spatial accuracy at large azimuth eccentricities. Note that in this scheme, different regions of sensorimotor space adapt independently (pointby-point), which requires a spatial coding mechanism with independent elements (a topographic map). Such a coding mechanism is found in the midbrain of the barn owl²⁸ and mammals^{4,29}. Recent prism adaptation results³⁰ have indicated that the tuning of inter-aural time differences (ITD) in the barn owl's superior colliculus appears to adapt in a point-by-point manner. The adaptation results of our study, however, point to a differ-



Fig. 7. Two schemes of sound localization adaptation. Plots at the left (a, c, e) depict local changes in azimuth performance when adaptation is limited to a central gain reduction (a). The same effect is plotted as a change in response location (c) and as a stimulus-response relation (e) of an ideal subject before (dashed line) and after (solid line) adaptation. Arrows in (**c** and **e**) denote the same response change (ΔR). The largest changes in response location (not gain) occur at the edges of the adaptation region and extend outside the visual field of the lenses. This is more directly shown in g, where adapted changes in response location are illustrated in 2D. Note how the changes in response location (arrows) extend outside the visual field of the lenses (shaded area). Plots at the right (b, d, f, h) show an alternative scheme in which central negative gain changes are countered eccentrically by opposing changes (shown as narrow maxima in b). In this adaptation scheme, changes in response location outside the visual field of the lenses return to zero (d, f, h). The actual data closely resemble the scheme on the left.

ent neural coding scheme, as changes in the central part of the response field clearly affect responses at peripheral locations (Fig. 7a, c, e and g). A mechanism that accounts for this effect is a system in which sound localization cues are first integrated across their entire range before being mapped into a spatial representation. In such a model, sound location is encoded by the entire population of cells (neural recruitment).

An example of this latter coding scheme has been proposed³¹ (at least as a first processing stage) for the mapping of interaural intensity differences (IIDs) onto azimuth. In this simple scheme (Fig. 8), binaural neurons (so-called IE and EI type neurons) respond in a sigmoid fashion to IIDs. Each neuron in the population has a different working region (IID threshold) that spans only a small fraction of the azimuth range. The outputs of all neurons are weighted and summed at a subsequent neural stage to yield a viable representation of space (Fig. 8a, solid line). The observed adaptation to $0.5 \times$ lenses can then be explained by assuming a decrease in the weights of only those neurons with their working range in the visual field of the lenses (central set

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of dashed neurons in Fig. 8a). Simulations of this model show that local gain adaptation indeed results in a response change across azimuth that resembles our experimental findings (Fig. 8a, dashed line). As our experiments yielded no change in elevation, it is not clear whether spectral cues would be represented in a similar way. Interaural timing differences (ITDs) are initially encoded by a topographic arrangement of interaural delay lines in both the mammalian³² and the avian³³ auditory brainstem. It would therefore be of interest to test which adaptation scheme (Fig. 7) applies to the localization of low-frequency sounds, a process known to depend only on ITDs.

METHODS

Subjects. Nine normal human subjects (seven male, two female; ages 20–32) participated in the experiments. Subjects were recruited within the University of Rochester community. All subjects but one were inexperienced in sound localization experiments. All were given a short practice period for acclimation to the laboratory and experimental tasks. Subjects were free of pathology related to the senses or nervous system, and all showed normal performance on a routine clinical audiogram. The study was performed in accordance with the 1964 Declaration of Helsinki, and all subjects gave informed consent to participate.

Sound localization system. Subjects were seated in a dark, soundattenuated room lined with acoustic foam (Sonex; Illbruck, Minneapolis, Minnesota). The head was held fixed throughout all experiments by a custom bite-bar and positioned such that Reid's baseline was horizontally aligned. The target assembly consisted of an 8 cm, 2way coaxial speaker (Blaupunkt, Broadview, Illinois) that was mounted on a dual-axis servo-controlled robotic arm. This setup enabled rapid and accurate positioning of the speaker in azimuth $(\pm 120^\circ)$ and elevation $(\pm 50^\circ)$ at a fixed distance from the subject's head (cylindrical radius of 2 m). Potential localization cues emanating from the stepping motors and mechanics were eliminated by generating a random movement and masking noise during speaker positioning. An acoustically transparent black curtain in front of the speaker screened any potential view of the speaker and robotic system. **Fig. 8.** Recruitment model of azimuth-encoding IID cells. (a) Individual neurons (inset) have different IID thresholds. Perceived azimuth is determined by the summed population response (Σ), in which all neurons are equally weighted (solid curve). The responses adapt to the compressed image by reducing the weights of the neurons that have their working range in the exposed area (dashed cell responses). Note that the summed population response after adaptation (dashed curve) differs from the pre-adaptation response across the entire azimuth range. (b) Both the change in local response gain (dashed curve) and in response magnitude change (solid curve) correspond well to the observed behavior.

The well-localizable auditory stimuli consisted of ongoing pulsating Gaussian white noise (0.1–20 kHz; period 150 ms; intensity 75 dB SPL). To indicate the perceived sound location, subjects manually controlled a freely rotating two-axis laser pointer that projected a red dot on the black curtain just in front of the speaker. Pointer orientation was registered by precision encoders on each axis. Target and response coordinates are expressed as azimuth and elevation angles in a double-pole coordinate system¹² with the origin at the center of the head.

Vestibulo-ocular reflex system. The horizontal angular vestibulo-oculo reflex (AVOR) was measured in darkness during passive whole-body sinusoidal rotation about the yaw axis at frequencies of 0.25, 0.5 and 1.0 Hz (peak velocity, 40 °/s). A multi-axis motion control system was used for this purpose, as described elsewhere³⁴. During rotation, subjects were instructed to maintain fixation in the dark on a remembered earth-fixed visual target presented briefly beforehand. Eye movements were measured by an infrared CCD camera technique (ElMar, Toronto, Canada) and further analyzed³⁴ off-line to yield response phase and gain for each trial.

Sound localization protocol. A sound localization experiment consisted of two series of 87 trials. In one series (the 'target-fixation' paradigm), the subject was instructed to align the red dot from the laser pointer with the perceived sound location as accurately as possible, while foveating the target. In the other series ('central fixation' paradigm), a second laserprojected dot was projected centrally on the screen, and subjects were instructed to maintain continuous fixation on this spot while using the visual periphery to guide the laser pointer to the auditory target. The trial and sound ended when the subject approved his/her pointer setting by pushing a button. Target locations were randomly selected to create a distribution of 87 targets, ranging from $\pm 50^{\circ}$ in azimuth and from $\pm 22^{\circ}$ in elevation (Fig. 2f). The same randomized sequence was used for each subject. Note that in all conditions, subjects were tested open-loop, as no feedback was given regarding response accuracy, and subjects were seated in darkness with their heads fixed.

Adaptive paradigm: compression of spatial vision. The visual field was spatially compressed by means of binocular Galilean lenses (Nikon; Kanagawa, Japan) of magnification $0.5\times$. The lenses were mounted on a spectacle frame fitted to each subject, including any spherical refractive correction required. The field of view through the lenses generally covered a ~20° radius, shifted downward by ~5° in our experimental coordinate scheme. The visual field outside the lenses was masked.

The 0.5× lenses were worn continuously for either two (n = 5) or three days (n = 4), with the exception of sleeping hours. Adaptation to the modified visual input was monitored by conducting experiments before (baseline, recorded at least twice), during (daily for 2–3 days) and after (re-adaptation) wearing the lenses. While wearing the lenses, subjects were encouraged to proceed with active natural behavior with the help of a chaperone. In addition, during daily 2-h conditioning sessions to further enhance cross-sensory interaction, subjects returned to the laboratory to view a series of randomly presented audiovisual targets presented over a wide range of positions.

A sound localization and AVOR trial set was performed after the first 8 h of adaptation, and then on subsequent days. The lenses were always removed during testing (recall that experiments were carried out in total darkness and with the head fixed). At the end of the adaptation period, the lenses were removed, and subjects were retested after at least one day.

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Competing interests statement

The authors declare that they have no competing financial interests.

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