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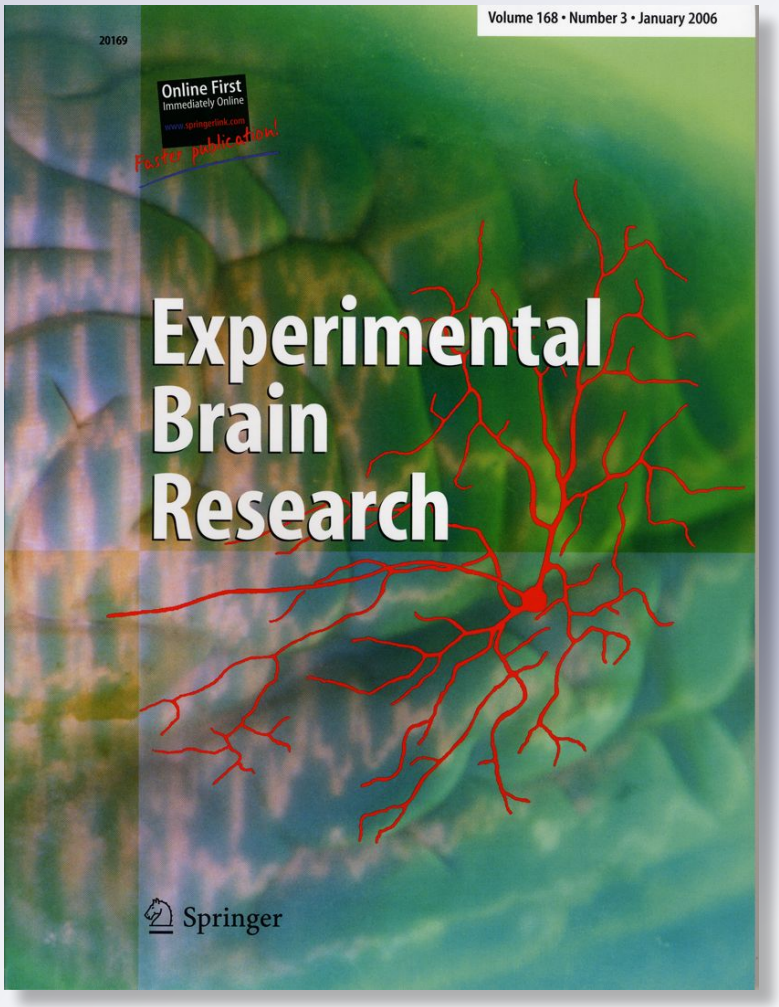

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RESEARCH ARTICLE

Sensory compensation in sound localization in people with one eye

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Abstract Some blind people are better at locating sounds than people with normal vision indicating cross-modal plasticity. People who have lost one eye have a unique form of visual deprivation that reduces visual afferent signals by half and can potentially also lead to cross-modal (as well as intra-modal) plasticity. To look for evidence of auditory-visual cross-modal compensation, we measured binaural and monaural sound localization in one-eyed people and compared them with normally sighted controls. One-eyed people showed significantly better binaural sound localization than controls in the central region of space (±78° from straight ahead), but they mislocalized sounds in the far periphery (on both the blind and intact side) by up to 15° towards the centre. One-eyed people showed significantly better monaural sound localization compared with controls. Controls' performance became asymmetric when they had one eye patched. Patching improved accuracy in the viewing field but decreased accuracy in the occluded field. These results are discussed in terms of cross-modal sensory compensation and the possible contribution of visual depth to interpreting sound localization cues.

Keywords Enucleation · Monocular viewing · Binocular viewing · Spatial sound processing · Cross-modal plasticity · Cross-modal sensory compensation

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Introduction

The loss of one sense can lead to changes in the way in which other senses are used. This is cross-modal plasticity. Cross-modal plasticity may arise from the recruitment of brain areas (usually assumed to be cortical brain areas) no longer used by the lost sense. Other sensory systems may take over these areas and provide increased computational power, and hence behavioural improvement, in the remaining, intact sensory systems. Alternatively, behavioural changes in other senses may arise from increased efficiency in processing or increased attentional resources allocated to the spared senses.

Auditory processing in the blind has been found to be better on some tasks such as speech perception (Niemeyer and Starlinger 1981), pitch discrimination (Gougoux et al. 2004) and verbal memory (Amedi et al. 2003). Early blind individuals are also able to localize auditory targets more accurately than sighted individuals under both binaural and monaural listening conditions (Ashmead et al. 1998; Despres et al. 2005; Lessard et al. 1998; Roder et al. 1999; Gougoux et al. 2004; Gougoux et al. 2005; but see Zwiers et al. 2001; Lewald et al. 2002), although not in the vertical plane (see Collignon et al. 2009b for a review). Others have shown that late blind, but not early blind individuals, have superior sound localization compared to blindfolded controls (Abel et al. 2002). Neuroimaging studies have confirmed recruitment of visual areas during the spatial processing of auditory stimuli in blind individuals (Gougoux et al. 2005; Leclerc et al. 2000; Weeks et al. 2000) with selective recruitment of right dorsal occipital cortex in the congenitally blind (see Collignon et al. 2011). Further, transcranial magnetic stimulation of the visual cortex adversely affects blind people's sound localization (Collignon et al. 2009a) and Braille reading ability (Kupers

et al. 2007). Together, these findings suggest a functional recruitment of the visual cortex by other sensory systems in the blind.

Visual loss in one-eyed people includes the obvious loss of visual field in the corresponding periphery, a reduction in the total number of available visual detectors and the loss of stereopsis. However, improvements in visual performance have also been noted. For example, one-eyed individuals have some more finely tuned visual spatial abilities than binocular controls (for a review see Steeves et al. 2008). The neural basis of such visual improvements may be connected to the partial deafferentation of some visual projection areas and the subsequent availability of those areas for recruitment in other tasks. Given that total blindness can result in improved auditory ability, implying recruitment of previously visual areas to subserve auditory tasks, we speculated that one-eyed individuals might also exhibit similar changes in their auditory abilities.

The loss of one eye does more than vacate cortical real estate. There are also changes in the location of the visual egocentre in which the egocentre permanently shifts towards the side of the remaining eye (Moidell et al. 1988) and, likely consequential to this, egocentric localization of distant targets becomes more accurate but also less precise than controls viewing monocularly (González et al. 1999). Further, the loss of binocular depth perception produces changes in the way in which visual tasks that typically depend on binocular depth perception are performed. For example, adults with only one eye make more lateral and vertical head movements when reaching and grasping to objects compared to controls viewing monocularly (Marotta et al. 1995). This may be a learned adaptive behavioural change to prolonged monocular experience since young children who have had one eye removed do not display these lateral head movements (González et al. 1989).

An often neglected fact about auditory localization is that obtaining the accurate direction of sound from interaural time and intensity differences requires knowledge of accurate distance information about the sound source. The head itself often obstructs a direct line from a sound source to one of the ears. The amount of obstruction depends on the sound source's eccentricity and its distance from the head. Hence, calibrating interaural arrival time and intensity differences for accurate sound localization require taking both eccentricity and distance into account. This calibration is likely to be dependent on auditory and visual feedback. Given that enucleated individuals show changes in their perception of (and interaction with) space and are obviously compromised in their use of binocular depth cues, it is possible that their ability to calibrate interaural timing and intensity differences with the spatial location of a peripheral sound may be affected.

Sound localization has never before been measured in monocularly enucleated humans. In the guinea pig, monocular enucleation prevents the normal development of the auditory space map in the superior colliculus (Withington et al. 1994). However, improvement in visual/somatosensory interactions (Van Brussel et al. 2011) as well as refinements in retinotopic organization (Faguet et al. 2009; Smith and Trachtenberg 2007) has been shown in the mouse visual cortex after monocular enucleation. These observations encouraged us to expect changes in human sound localization after enucleation.

People with one eye show intra-modal visual–visual sensory compensation and plasticity (reviewed in Steeves et al. 2008) but so far there has been no study to examine cross-modal sensory compensation. To look for the evidence of cross-modal sensory compensation, we measured auditory localization in people who had one eye surgically removed early in life but who retained normal vision in their remaining eye. We tested a group of monocularly enucleated individuals on sound localization in the horizontal plane under binaural and monaural listening conditions (both of which show improvement in the blind) and compared their performance to control observers viewing binocularly, monocularly and with eyes closed. We predicted that one-eyed individuals might exhibit better localization abilities than a control group based on possible recruitment of deafferented visual areas for auditory tasks.

Methods

Participants

Ten adult one-eyed participants (four women) who were registered at the Hospital for Sick Children in Toronto, Canada and who had had one eye enucleated (seven left, three right) due to retinoblastoma at a young age took part in this study. All participated in the binaural experiment and five of the ten one-eyed participants completed the monaural experiment. Age at enucleation ranged from 18 to 39 months (mean age = 23.8 months) and age at testing ranged from 19 to 54 years (mean age = 29.6 years). It is estimated that one-eyed participants lost visual function of the affected eye approximately 3–6 months before the date of enucleation. All had an ophthalmologically normal remaining eye with normal or corrected-to-normal acuity and reported no hearing deficits.

Fifteen binocularly normal observers (eight women) served as controls for the binaural experiments (mean age at testing 26 ± 5 years). Nine additional binocularly normal subjects (five women) served as controls for the monaural experiment (mean age at testing 26 ± 9 years). All had normal or corrected-to-normal vision and reported

no history of hearing impairment. Control participants' eye dominance was assessed by having them align their finger with a visual target on the wall 2.5 m away while viewing binocularly. For monocular testing, eye was covered with semi-opaque 3M medical tape to prevent form vision and minimize binocular rivalry. All observers gave informed consent. The experiment was conducted with approval of the Research Ethics Board of York University and complied with the 1964 Declaration of Helsinki.

Apparatus

The experiments were performed in a sound-attenuated room (2 × 2.24 × 2.14 m) lined with 3.8 cm thick sound-absorbing foam. Sixteen speakers (MAX Fidelity, model T26AFF5NEO; 5 cm in diameter) were mounted on a metal semicircular frame at eye height. The speakers were spaced equally at azimuthal angles from 90° left to 90° right in 12° increments (where 0° was straight ahead; see Fig. 1a). The array was hidden from view by a black, sound transparent cloth. A continuous numerical printed scale labelled from left to right was fixed to the frame just above the speaker array. The scale indicated increments of 1° with numbers on every other vertical line and resembled a ruler. In order to not restrict the range of responses, we extended the visual scale 25° past the end (90°) speakers (thus, 0 on the scale corresponded to −115° to the participant's left). A non-illuminated fixation point was present directly in front of the participant at the level of the speakers. Participants were seated 100 cm from the speakers facing the centre of the semicircle and the centre of the array corresponded to the centre of the subjects' interaural axis. The head was stabilized by a chin rest and forehead bar such that participants' ears were at the level of the speakers. Participants indicated their responses on a keypad (Targus model PAUK10C) located on a small table in front of the participant.

For the monaural experiment, participants wore a sound-attenuating headphone over one ear and had a wax earplug inserted into that ear. The other ear was unobstructed. Pilot data suggested that sounds on the side of the occluded ear were unlocalizable, therefore, only the speakers contralateral to the blocked ear were used (Fig. 1b). Pre-testing with both ears occluded confirmed that the test sounds could not be heard through this arrangement.

Sound stimuli

Sound stimuli for all experiments were double bursts of Gaussian white noise (51 dB; 30 ms ramped onset and offset, 10 ms rise and fall) separated by 30 ms (total duration 90 ms). This stimulus was chosen because it has been used previously in spatial sound processing research (see for example, Lessard et al. 1998). The stimulus was too brief for participants to orient to during presentation and was easier to localize than a pure tone (Abel and Tikuisis 2005; Middlebrooks and Green 1991). Sounds were created by a sound generating system (Tucker Davis Technologies, RP2) and directed to the appropriate speaker by a system of relays controlled by a PC running MATLAB.

Procedure

The procedure was identical for binaural and monaural experiments. Participants sat at the centre of the speaker array with their chin on the chin rest and their forehead pressed lightly against the forehead bar. They fixated a non-illuminated fixation point directly in front of them at 0° and they pressed a key on the keypad to start the session. A sound stimulus was then played through one of the speakers. Participants were asked to judge the location of the sound on the scale to the nearest 0.5°. They were free to move their head while making their response and were

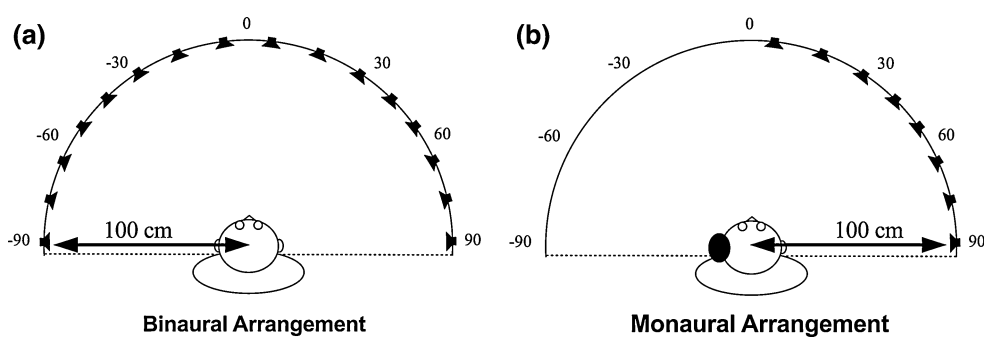

Fig. 1 Speaker arrangement. The speakers were obscured from view by sound transparent black cloth. A black and white scale with numbers every 2° and demarcations every 1° was positioned immediately above the speakers. **a** Binaural arrangement. Sixteen speakers were spaced equally from −90° to 90° and positioned at ear level at a distance of 100 cm from the centre of the observer's head. **b** Monaural arrangement. Eight speakers were spaced from 6° to 90° on the side contralateral to the occluded ear. References in the text to the centre refer to the straight ahead (0°), whilst the periphery refers to the side (towards ±90°)

asked to enter a number corresponding to the sound's perceived location on the scale into the keypad. Participants then returned their head to the chin rest and their gaze to the fixation point ready for the next trial and pressed the enter key to initiate the next trial.

The one-eyed participants performed the binaural experiment twice: once with the eyes open and once with the eyes closed.[1] Control participants performed the experiment three times: once with their eyes open, once with their eyes closed and once viewing monocularly with their non-dominant eye patched. Sounds were presented in psuedo-random order, such that each location was tested ten times for a total of 160 trials per run in a randomized design blocked according to viewing condition. Each run took approximately 15 min to complete. No feedback was given.

The one-eyed participants performed the monaural experiment four times: once with the ear on same side as the remaining eye occluded and once with the ear opposite to the remaining eye occluded. Both conditions were run with the eyes opened and closed. Control participants performed the experiment four times: once with binocular viewing, once monocularly viewing on the same side as the occluded ear, once viewing monocularly on the opposite side to the occluded ear and once with eyes closed. For each speaker position (Fig. 1b), sounds were presented ten times in random order for a total of 80 trials per run in a randomized design blocked according to viewing condition. Each run took approximately 7 min to complete. No feedback was given. Before testing, each participant performed five practice trials with the experimenter present to ensure that they understood the procedures.

Data analysis

The directional bias, defined as the average signed error (perceived location minus actual speaker position), was calculated for each speaker position. This is a typical measure of spatial sound localization ability (Hartmann 1983). Data were expressed relative to the participant's 'viewing' (negative speaker locations in our convention) or 'blind' (positive locations in our convention) side. Thus, a positive error indicates a shift towards the blind side and a negative error indicates a shift towards the intact side. For the monaural data, positive errors were defined as towards the centre and negative errors away from the centre.

Prior to the analysis, we performed correlations to measure relationships between performance and age at enucleation and age at testing. None were significant for this group of one-eyed participants, which may be due to the small sample size ($n = 10$) when performing a correlation, as well as the somewhat restricted range of age at enucleation (18–39 months of age).

Repeated measures analyses of variance (ANOVAs) with participant group as a between-subject factor and post hoc t-tests were used to compare performance across speaker locations. Where multiple t-tests and pairwise comparisons were used, the P values were corrected with the False Discovery Rate method. Violations of the sphericity assumption during ANOVA procedures were corrected by adjusting the degrees of freedom according to the Greenhouse–Geisser correction.

Results

Binaural hearing

Figure 2 shows the mean signed errors (perceived minus actual position) plotted as a function of speaker eccentricity for the one-eyed observers and compared with binocularly viewing (Fig. 2a) and monocularly patched (Fig. 2b) control observers. The curves are remarkably different. Two separate 2 × 16 repeated measures ANOVAs comparing the one-eyed observers with the control groups viewing binocularly (Fig. 2a) and monocularly (Fig. 2b), across all speaker locations revealed significant interactions ($F_{(6.11,\ 140.43)} = 7.431$, $P < 0.001$ and $F_{(5.65,\ 184.37)} = 4.511$, $P < 0.001$, respectively). That is, the participant groups showed different signed errors depending on where the speaker was located. Post hoc t-tests were conducted to compare the one-eyed participant group and the binocular and monocular control groups at each speaker location. One-eyed participants demonstrated better localization than binocular viewing controls for the majority of the speaker locations (corrected P values <0.05) and comparable performance at four speaker locations (−78°, −6°, +32° and +78°). One-eyed participants demonstrated similar performance to monocular viewing controls on the 'intact' side of space from −78° to −6° and significantly better performance than controls for speakers on the 'blind' side from +6° to +78°.

For the extreme peripheral speaker location (90°), one-eyed participants displayed consistently much larger directional biases towards the centre on both their 'intact' and 'blind' sides compared with either binocularly or monocularly viewing controls (P values <0.01).

Given the unusually large errors in the one-eyed participants' ability to localize the speakers at 90°, the repeated measures ANOVAs were run again with these two extreme points removed from the analyses. By doing so,

[1] In the eyes closed condition, participants looked at the fixation point, closed their eyes during the stimulus presentation (90 ms) while maintaining fixation and then opened the eyes.

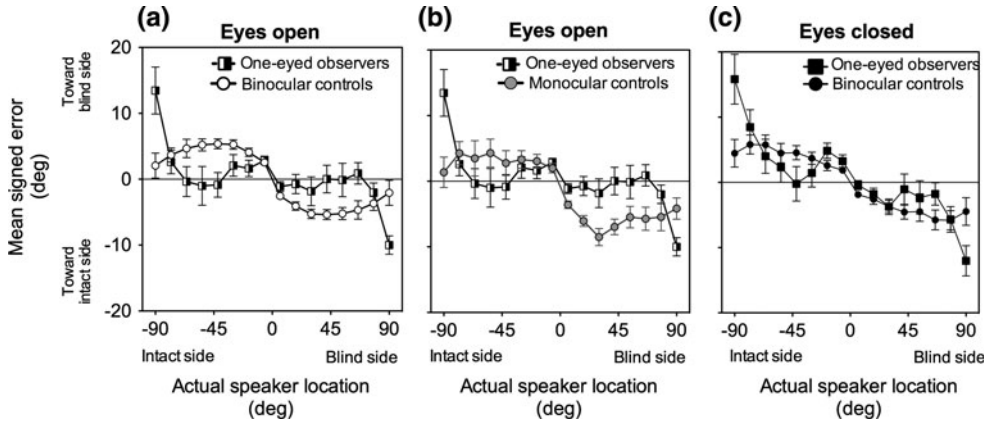

Fig. 2 Binaural localization. Mean signed errors (perceived minus actual location) for one-eyed observers (*square*) and controls (*circles*) plotted as a function of speaker position. **a** One-eyed observers (eyes open, *half-filled squares*) compared with binocularly viewing controls (*open circles*). **b** One-eyed observers (eyes open, *half-filled squares*) compared with monocularly viewing controls (*grey circles*) and **c** one-eyed observers (eyes closed, *filled squares*) compared with controls (eyes closed, *filled circles*). *Positive errors* indicate a directional bias towards their 'blind' side and *negative errors* indicate a directional bias towards the 'intact' side. Data from left and right speaker locations have been averaged for the binocularly viewing controls' data. All *error bars* denote SEM

the interactions did not maintain significance ($F_{(4.908,\ 112.89)} = 1.686$, $P = 0.145$ and $F_{(5.02,\ 115.36)} = 1.159$, $P = 0.334$, respectively), but the between-groups factors become significant ($F_{(1,\ 23)} = 12.507$, $P = 0.002$ and $F_{(1,\ 23)} = 8.981$, $P = 0.006$) confirming that our one-eyed group was more adept at localizing sounds compared with controls across the horizontal plane except for the most peripheral speaker locations tested.

Closing the eyes produced a significant change in the one-eyed observers' data ($F_{(1,\ 9)} = 11.733$, $P = 0.008$) but not the control group (ns; Fig. 2c). There was a significant interaction between the participant groups with the eyes closed and speaker location ($F_{(15,\ 345)} = 4.566$, $P < 0.001$) similar to the eyes-open comparisons. However, the interaction was carried by the clear differences in mean error for the two 90° points (these being the only points in which participant groups differed, revealed by *t*-tests *P*s < 0.05). When these data were removed from the analyses, there were no longer any differences between the one-eyed participants and controls.

Binaural hearing: intact versus blind side

To determine whether one-eyed and monocularly viewing control observers showed different patterns of performance when locating sounds presented ipsilaterally or contralaterally to the viewing eye, two 2 × 2 × 8 repeated measures ANOVAs were performed. One-eyed participants did not show a significant effect of side ($F_{(1,\ 9)} = 0.132$, $P = 0.724$), however, monocularly viewing controls showed a near significant effect of side ($F_{(1,\ 14)} = 4.420$, $P = 0.054$). Temporarily patching one eye of binocularly normal controls produced a systematic shift of perceived sound towards the centre on the side of space contralateral to the viewing eye (i.e. in the partially occluded field, see Fig. 2b). This asymmetry between the occluded and unoccluded side was not observed in the one-eyed participant group.

Monaural hearing

There were no differences that depend on whether the occluded ear was on the same or opposite side as the enucleated eye for the one-eyed observers (open or closed) or the same or opposite side of the patch for patched controls (one-eyed observers: open $F_{(1,\ 4)} = 0.684$, $P = 0.455$ and closed $F_{(1,\ 3)} = 4.01$, $P = 0.139$; patched controls: $F_{(1,\ 6)} = 0.977$, $P = 0.361$). Therefore, data for each participant from experimental blocks where the ear was occluded on the intact and prosthetic eye (or patched eye for controls) sides were averaged at eight speaker locations. Figure 3 shows the perceived position (Fig. 3a, b) and mean signed errors (Fig. 3c, d) of sounds presented monaurally on the side contralateral to the occluded ear for the one-eyed observers and controls. Two 2 × 8 repeated measures ANOVAs between the one-eyed group and the binocularly and monocularly viewing control groups revealed significant main effects of speaker location ($F_{(7,\ 77)} = 60.837$, $P < 0.001$ and $F_{(7,\ 77)} = 62.395$, $P < 0.001$, respectively). A slope of 1 in the mean signed error plots (Fig. 3c, d) corresponds to sounds heard as always coming from the same place, whilst a slope of zero (depicted as a horizontal dashed line in Fig. 3c, d) indicates no error. There was a near significant interaction between

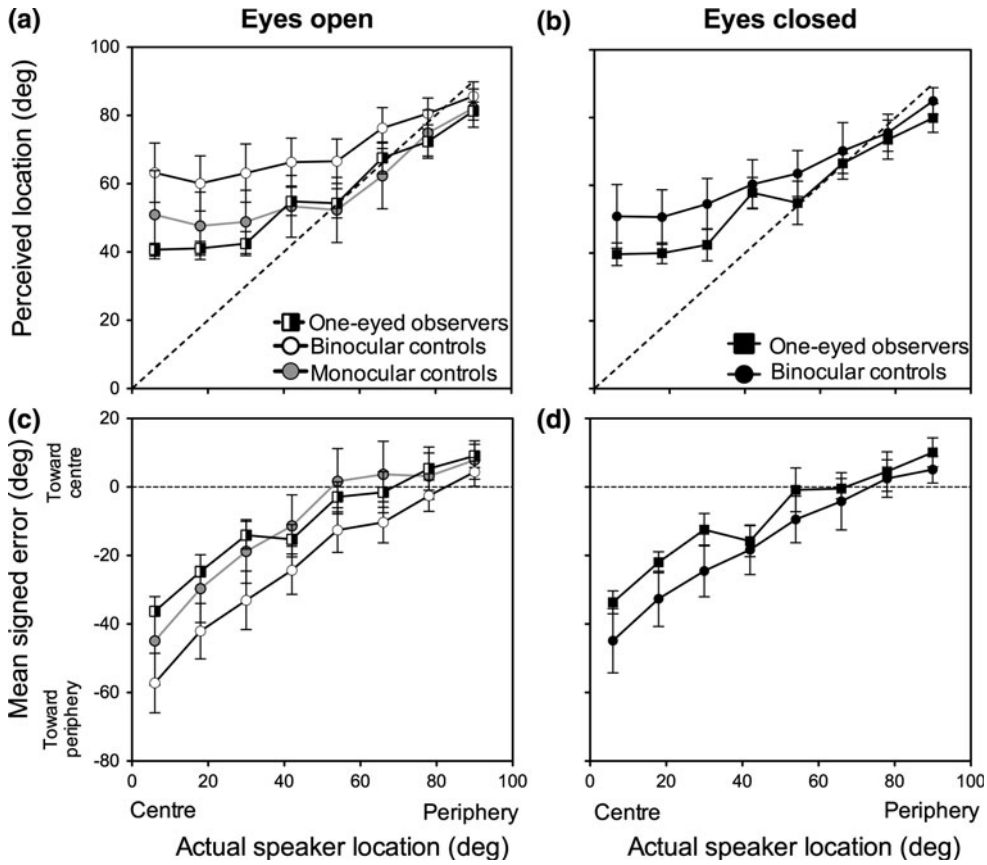

Fig. 3 Monaural localization. The mean perceived location of monaurally presented sounds as a function of speaker eccentricity **a** for one-eyed observers with eyes open (*half-filled squares*) compared with binocularly viewing (*filled circles*) and monocularly viewing (*grey circles*) controls, **b** for one-eyed observers with eyes closed (*filled squares*) compared with controls with their eyes closed (*filled circles*). A slope of 1, depicted by a *dashed line* in **a** and **b**, corresponds to perfect performance. **c**, **d** Mean signed errors for these groups (same symbols). *Positive errors* indicate a directional bias towards the centre (straight ahead) and *negative errors* indicate a directional bias towards the periphery (to the side). A slope of 1 (not shown) corresponds to sounds heard as always coming from the same place, whilst a slope of zero (depicted as a *horizontal dashed line*) indicates no error. *Error bars* denote SEM

one-eyed observers and control observers viewing binocularly as a function of speaker location (Fig. 3a; $F_{(7,\ 77)} = 2.064$, $P = 0.057$) indicating that the one-eyed participant group had significantly smaller errors at some locations. For some of the range ($\sim 6°$ to 42°), this reduction in error reflects that both groups heard the sound as coming from a constant direction independent of the speaker location, but that the one-eyed observers heard it as coming from a location nearer to the straight ahead (around 40° whereas, controls heard it as coming from around 60°).

When control participants were patched, their ability to localize sounds monaurally improved (Fig. 3a), which was confirmed by a significant main effect of viewing condition ($F_{(7,\ 77)} = 2.064$, $P = 0.017$). Patched controls, as opposed to binocularly viewing controls, performed as well as the one-eyed observers ($F_{(2.744,\ 30.185)} = 0.802$, $P = 0.493$). This appears to be largely due to patched controls localizing monaurally presented sounds more towards the centre.

Discussion

We report that loss of one eye produces an improvement in the accuracy of sound localization. One-eyed subjects were consistently more accurate than controls at locating sounds in all but the extreme peripheral locations (within 78° of straight ahead). The normal tendency to hear sounds as slightly displaced towards the centre was significantly less pronounced in the one-eyed participant group over a large part of space.

Patching one eye of control subjects produced a tendency for all sounds to be perceived as shifted towards the viewing field. This effect was on top of the regular perceived displacement towards the centre that was found during binocular viewing. That is, compared to the perceived locations when measured with both eyes open, the perceived location of sounds was shifted towards the centre for speakers on the occluded side and away from the centre for speakers on the viewing side. This effect thus added to the central drift tendency on the occluded side whilst partially cancelling it on the viewing side. Comparison of one-eyed participants' data with those from monocularly patched controls (e.g. Fig. 2b) needs to be interpreted in light of this asymmetry in the control group which was not found in one-eyed people.

Although sound localization was generally better in the one-eyed participant group compared with controls, one-eyed people exhibited much larger than normal errors when locating sounds in the extreme periphery. Sounds near the 90° position were mislocalized towards the centre to a considerably greater extent by one-eyed observers than they were for monocularly or binocularly viewing controls.

Monaurally, all subjects tended to hear sounds presented centrally as coming from a single direction, independent of speaker location. However, one-eyed observers tended to hear sounds as coming from a more central location resulting in less overall error on average. There was no difference in precision for localizing monaurally heard sounds between the control and one-eyed participant groups.

Evidence for cross-modal sensory compensation?

A main goal of this study was to see whether cross-modal sensory compensation occurred as a consequence of partial sensory deprivation by investigating the spatial sound processing abilities of individuals who had lost an eye early in life. Under binaural conditions, control participants demonstrated larger errors for sounds presented in the peripheral regions and smaller errors for sounds in the central region of space, with a tendency to displace the perceived positions of all sounds towards the centre. These observations are consistent with previous reports (Carlile et al. 1997; Hofman and Van Opstal 1998; Makous and Middlebrooks 1990; Middlebrooks and Green 1991; Oldfield and Parker 1984; Wightman and Kistler 1989). Our observation that one-eyed observers exhibited improved localization compared with controls may suggest cortical reorganization such as recruitment of deafferented cells in favour of auditory processing. Such a mechanism has been proposed to explain improved sound localization in early blind people (Lessard et al. 1998). One might predict that plasticity induced improvements in sensory processing via neural recruitment should specifically improve precision of performance.

The tendency to misperceive sounds towards the centre

The most obvious aspect of all the binaural localization data presented in this article is that all sounds were perceived, to a greater or lesser degree, to be originating closer to the centre than they really were. Why might this be? There is a tendency for many perceptual phenomena to collapse towards the centre in memory over time sometimes referred to as a contraction of the space map in the brain (Hubbard and Ruppel 2000; Kerzel 2002; Sheth and Shimojo 2001; Jaekl and Harris 2010). Since our subjective reports of sound position were made a few seconds after the sounds were presented, there was a memory component during which the perceived location could perhaps shift towards the centre. This explanation would then require that the tendency to drift to the centre was less or slower in one-eyed people and thus the consequent shift in perceived location towards the centre was less in this group resulting in greater accuracy.

An alternative explanation could be related to a tendency to revert to an egocentric reference frame, resulting in an 'attraction' to a body reference. This explanation has been advanced to explain why perceived orientation of external objects (and even gravity) is shifted towards the orientation of the body midline (Ceyte et al. 2009). In the present case, this tendency would provide a further rationale for the 'pull to the centre' as a tendency to see and hear everything as coming from the straight ahead 'body reference' direction.

Why does patching one eye shift sound location towards the viewing eye whereas one-eyed people show no such asymmetry?

When controls had one eye patched and viewed monocularly, sounds were mislocalized towards the viewing eye (Fig. 2b). This observation confirms Abel and Tikuisis (2005) and suggests a shift in the perceived location of sounds towards a shifted visual egocentre. The visual egocentre is a point within the head to which visual directions are related (Ono et al. 2002). In binocularly normal observers, this is between the eyes and displaced a few centimetres in the posterior direction. Monocular patching can evoke a shift in the egocentre (Porac and Coren 1986) and patching one eye in our control subjects introduced a tendency to shift the perceived location of all sounds in the direction of the viewing field (Fig. 2b). This is consistent with such a shift of the visual egocentre towards the side of the viewing eye. Monocular patching induces an ipsilateral spatial bias (Chen et al. 2009) and a preferential activation of attentional systems ipsilateral to the viewing eye (Roth et al. 2002), both of which are compatible with a similar shift in sound localization.

If patching our controls created a shift of perceived sounds towards their viewing field, why do one-eyed observers not show this same asymmetric bias all the time? Children under the age of 4 years show a shift in the visual egocentre towards their viewing eye after unilateral enucleation by about 75% of the distance between the true midline and the remaining eye (Dengis et al. 1993b). But perhaps one-eyed people adapt such that the location of the egocentre is restored to an anatomically symmetrical location. Indeed, the visual egocentre is found to be central in adults who have been monocularly patched for prolonged periods of time (Dengis et al. 1993a). Our findings provide more evidence for compensatory changes in sensory processing suggesting that loss of symmetrical visual input induces a change in the visual egocentre initially (Dengis et al. 1993b) but that the spatial processing system has recalibrated in our one-eyed observers to deal with their new monocular world.

Are one-eyed participants better at locating sounds monaurally?

One-eyed observers showed improved accuracy in locating monaurally presented sounds relative to controls, especially for more centrally presented sounds (Fig. 3c, d). In the periphery, performance was similar in the two groups. Our one-eyed people displayed a tendency to locate any sounds located within the central 40° to be at 40°. Controls, however, located all sounds within the central 60° to be at 60°. This indicates a greater 'centralizing' tendency for the one-eyed participants—the opposite of the case for binaural sounds, which were generally perceived to be located more peripherally than the estimates of the control group. Some early blind subjects (but not all) also show an improved ability to localize sounds monaurally (Lessard et al. 1998; Voss et al. 2011), which is consistent with the present finding of better monaural ability in the central region for our one-eyed participants.

Why do one-eyed people make large sound localization errors in the extreme periphery?

One of the robust differences between one-eyed participants and normal controls to come out of this study is the large errors made by one-eyed participants when binaurally localizing sounds in the far periphery (around 90° see Fig. 2). We have two suggestions to explain this observation.

Firstly, when we superimpose the binaural (from Fig. 2a, b) and monaural errors (from Fig. 3c, d) that one-eyed participants make (Fig. 4), it can be seen that the errors made in the periphery are similar under both listening conditions. These errors seem inherent to using monaural cues as the control subjects also exhibit similar errors in the far periphery with monaural listening. Thus, it could be that one-eyed participants are using monaural cues (specifically spectral cues) for localization in the periphery. This is consistent with the literature showing that some early blind individuals have superior use of spectral cues in auditory spatial processing (Doucet et al. 2005) and further, this ability has been shown to be

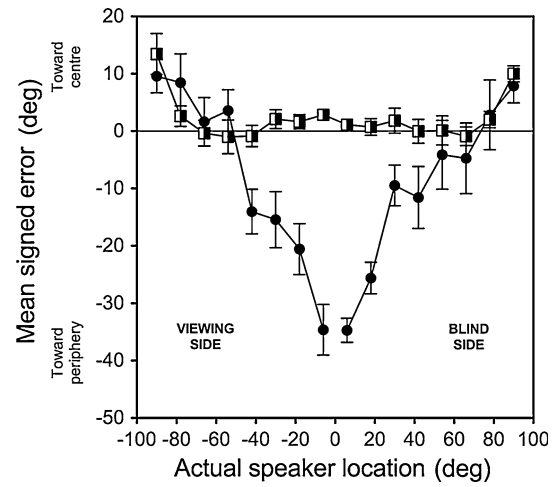

Fig. 4 Comparison of localization errors made by one-eyed observers with their eye open whilst listening either binaurally (*half-filled squares*) or monaurally (*filled circles*). Convention as for Fig. 3c, d, where a *positive error* denotes a shift to the centre. *Errors* are SEMs

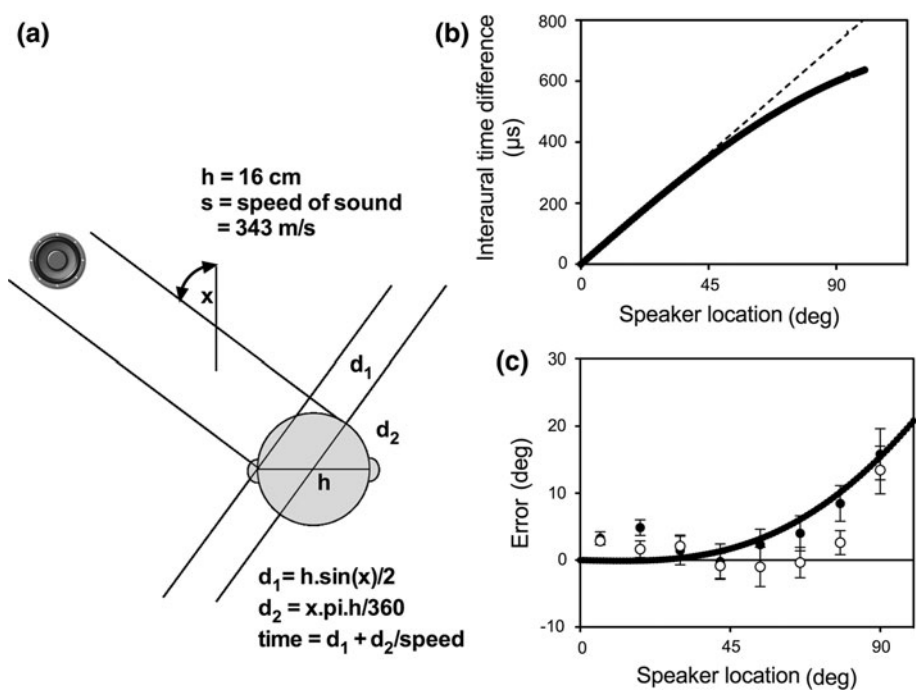

Fig. 5 The curvature of the head (**a**) causes the relationship between time-of-arrival difference and angular displacement of the sound to be non-linear as shown by the *solid black line* in (**b**). If subjects (incorrectly) assumed a linear relationship (*dashed line*) then errors of the type observed in our one-eyed participants could result. For example, a 600 µs difference would be interpreted as corresponding to a sound at 75° rather than at 90°: a 15° error (**c**). Superimposed on this theoretical *curve* are one-eyed observers' data with eye open (*open circles*) and eyes closed (*filled circles*). *Errors* are SEMs

subserved by recruited regions in occipital cortex (Voss et al. 2011).

A second possible explanation comes from the fact that the interaural time-of-arrival differences and intensity differences have a non-linear relationship with the eccentricity of a sound stimulus. This is shown in Fig. 5a, b. If observers were to incorrectly assume a linear relationship, then they would attribute the time-of-arrival differences produced by a sound in the periphery as arising from a sound closer to the centre. For example, a sound at 90° is associated with a time-of-arrival difference of 600 ms (for sounds at infinity and an observer with a 16-cm-diameter head). A linear extrapolation from the relationship in the central part of the field (dashed line in Fig. 5b) would predict that delay to be associated with a sound at only 75°. The pattern of errors that would result for all speaker locations is shown as a solid black line in Fig. 5c—very similar to the pattern of errors that we observed on our one-eyed observers, especially when measured with eyes closed (data superimposed).

Both of these explanations could be connected to the loss of the strong binocular depth cue resulting from the surgical removal of one eye. Monaural spectral cues can provide distance information (Kim et al. 2008), which might encourage our participants to rely more on monaural information in the periphery. Accurate interpretation of time-of-arrival differences needs distance information particularly if the angular displacement of a target is to be calculated from this cue. While participants with one eye do not show functional impairments in depth perception (reviewed in Steeves et al. 2008), they nonetheless have only monocular depth cues at their disposal which may make judgment of depth a more difficult process than for binocularly intact controls.

Conclusion

A person who has lost one eye early in life shows cross-modal sensory compensation and becomes more accurate than normal controls at locating sounds, similar to people with early blindness. The improvement in localization occurs not only in the blind field but, surprisingly, also in the intact field. Adaptive changes in auditory processing thus seem to occur across the entire visual field and not just in the part of the visual field that is blind. The improvement in auditory spatial abilities may be correlated with the loss of one half of visual afference, which eliminates stereopsis.

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