Ubiquitous enhancement of spatial hearing in congenitally blind people

Running title: Superior auditory localization in the blind

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ABSTRACT

Vision is thought to scaffold the development of spatial abilities in the other senses. How does spatial hearing therefore develop in people lacking visual experience? We comprehensively addressed this question by investigating auditory localization abilities in congenitally blind and sighted individuals using a psychophysical minimum audible angle task exempt of sensori-motor confounds. Participants were asked to compare the relative position of two sound sources located in central and peripheral, horizontal and vertical, frontal and rear spaces. We observed unequivocal enhancement of spatial hearing abilities in congenitally blind people, irrespective of the field of space that is assessed. Our results are conclusive in demonstrating that visual experience is not a mandatory prerequisite for developing optimal spatial hearing abilities and that, in striking contrast, the lack of vision leads to ubiquitous enhancement of auditory spatial skills.

Keywords: blindness, auditory localization, spatial hearing, Minimum audible angle.

INTRODUCTION

Vision conveys spatial information in the most reliable fashion when compared to the other senses. For instance, auditory or tactile information are typically remapped toward visual positions if inputs from separate senses are spatially misaligned (Botvinick & Cohen, 1998; Howard & Templeton, 1966); short-term prismatic adaptation to spatially conflicting visual and auditory stimuli biases subsequent auditory localization toward the source of misaligned visual inputs when the prisms are removed (Recanzone, 1998); and owls reared with prismatic deviation show permanent biases in auditory localization (Knudsen, 2002). Actually, one of the primary roles of spatial hearing might be to orient our vision toward the sound source for foveation and then use our motor system to visually guide appropriate action plans based on a precise location of the target using visual coordinates (Arnott & Alain, 2011; Gruters et al., 2018). All together, these studies suggest that vision is important in teaching the auditory system how to translate auditory localization cues into representations of space (Knudsen, 2002).

Does the prominent role of vision for space perception prevent people who are lacking visual experience from developing normal spatial hearing skills? Some studies supported the idea that congenitally blind people (CB) perform worse than sighted controls (SC) when involved in a horizontal auditory space bisection task (Gori, Sandini, Martinoli, & Burr, 2014) or when they have to localize sounds arranged along the vertical mid-sagittal plane (Lewald, 2002; Zwiers, Van Opstal, & Cruysberg, 2001). Similarly, works in visually deprived animals have shown less precise sound localization skills in dark-reared animals and abnormalities in the topography and precision in the spatial tuning of their superior colliculus (Knudsen, Esterly, & Du Lac, 1991). In striking contrast, other studies showed that CB have a higher localization acuity in the horizontal plane, in particular for peripheral sounds (King & Parsons, 1999; Josef P. Rauschecker & Kniepert, 1994; Röder et al., 1999; Voss, Lassonde, & Gougoux, 2004) or during monaural auditory localization (Lessard, Paré, Lepore, & Lassonde, 1998), presumably due to a more beneficial use of spectral auditory cues (Doucet et al., 2005).

These controversial results highlight that the role of visual experience in calibrating the development of spatial hearing remains poorly understood (Collignon, Voss, Lassonde, & Lepore, 2009; Gori et al., 2014). Addressing this question is however crucial to understand how vision scaffolds the development of spatial abilities in the remaining senses (Collignon et al., 2009). The present study therefore aimed to revisit this debate by comprehensively investigating whether and how the lack of visual experience affects spatial hearing abilities. Unlike previous studies, auditory localization skills were investigated using a purely perceptual psychophysical minimum audible angle task (Mills, 1958) exempt of sensori-motor confounds. Moreover, sound localization abilities were assessed in both central and peripheral, horizontal and vertical, frontal and rear portions of space. This allowed us to obtain, for the first time, a fine-grained psychophysical mapping of the global surrounding space of congenitally blind and sighted listeners. Of specific interest, inclusion of the condition where auditory sources are located in the rear space offers the unique opportunity to assess auditory localization skills under a condition where neither the blind nor sighted people can rely on direct sensory feedbacks to calibrate spatial hearing abilities.

MATERIALS AND METHODS

Participants

Seventeen congenitally blind (CB, 8 females, mean age ± SD = 32.6 ± 7.5 years) and 17 age and gender matched sighted (SC, 8 females, mean age ± SD = 31.4 ± 6.2 years) participants took part in the study. All blind participants lost their sight at birth or before three years of age.

Sighted participants had normal or corrected-to-normal vision. All participants reported normal hearing and no physical, neurological, or mental problems. Our sample size was determined by the availability of a maximum number of CB participants during the period of testing of this experiment (approximately 7 months). All CB participants were recruited only if fulfilling well-controlled criteria for inclusion: congenital visual impairment, never experienced more than rudimentary sensitivity for brightness (no patterned vision), blindness induced by peripheral deficits (eyes or optic tracks), no neurological or psychological comorbidity, no other sensory problems than visual deficits (see Table S1 in the Supplemental Material for further details).

To the limit of our knowledge, previous studies that investigated auditory perceptual skills in blind individuals involved smaller sample sizes (n between 5 to 15 participants). Furthermore, data were collected from a large number of conditions covering variety of auditory locations in each participant. In the present study, the experimental design relies on within subject analysis, e.g. each psychometric curve was first extracted at the single subject level, and goodness-of-fit of the psychophysical curves were evaluated through a bootstrapping procedure (N = 500). We did not conduct a formal, a priori power analysis.

Participants were blindfolded and instructed to keep their eyes closed throughout the experiments. All procedures were approved by the research ethics boards of the Centre for Mind/Brain Sciences (CIMeC) and the University of Trento and conducted in accordance with the

Declaration of Helsinki. All participants gave their informed consent prior to the study and were financially compensated for their time.

Apparatus and Stimuli

The experiment was performed in a semi-anechoic room. Sounds were delivered through 61 loudspeakers mounted on two semi-circular horizontal and vertical planes with a radius of 1.1m (see Figure 1). Participants were seated in the center of the apparatus with their head on a chin-rest, such that the speakers on the horizontal plane were at their ear level and those on the vertical plane were aligned with their mid-sagittal plane. Each arm of the apparatus consists of 31 loudspeakers in steps of 4° (the central speaker was shared between the two arms).

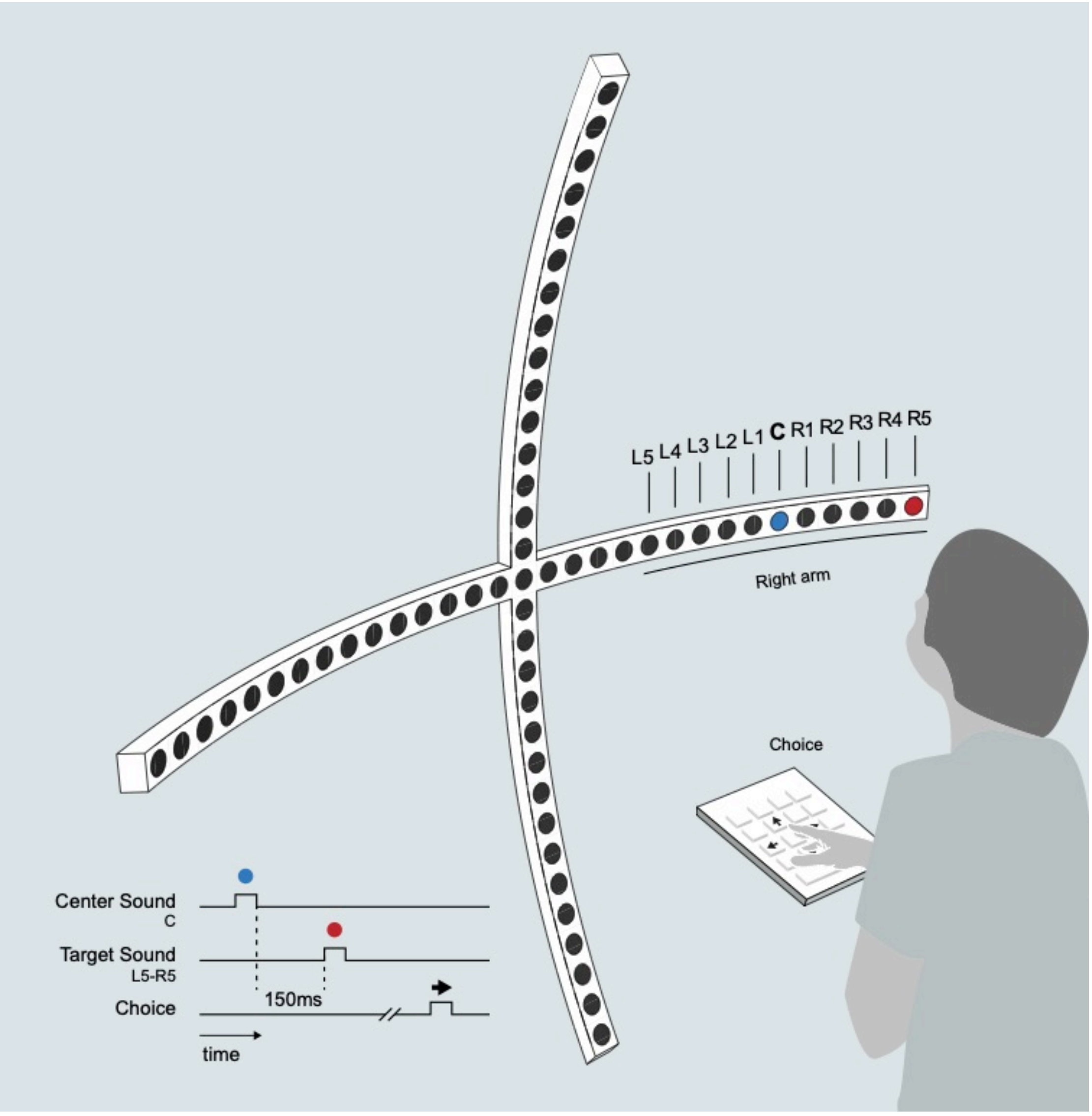

Fig. 1. Illustration of the sound apparatus and experimental design.

Auditory stimuli were 100 ms pink noise bursts (centre frequency -f_0- of 960 Hz; rise/fall time 6 ms), presented at 65 dB-A sound pressure level, as measured from the participant's head position with a free-field measuring microphone (Koolertron audiometer). Throughout the session, constant pink noise was presented at 41.8 dB-A from two loudspeakers positioned behind the acoustical apparatus for two purposes. First, such background noise creates an ecologically valid noisy environment that masks any localized sound that could emanate from any electrical apparatus located in the room. Second, the background noise may complexify auditory localization as compared to a purely silent environment and therefore may prevent ceiling effects that could have reduced the power of our design to reveal between-group differences (Voss et al., 2011, see review for further discussion Collignon et al., 2008; but see Christensen et al., 2019), which may partially explain disparities across studies. Participants responded via a keyboard placed at the right-hand side of the participant, in such a way to minimize lower sounds obstruction. The loudspeakers (4 Ohm impedance with 7W amplifier) were connected to a National Instrument PCI-PXI I/O module designed for precise control of audio-visual stimulus delivery with millisecond resolution. Stimuli delivery and response recording was controlled using Matlab (R2014b, MathWorks). All participants were blindfolded throughout the experiment. Sighted subjects were not allowed to see the apparatus before and during the experiment, in order to prevent any influence by visual information on the experimental setup.

In our study, we relied on a two alternative forced choice task (up vs down or left vs right) avoiding any confounds linked to the use of pointing responses, therefore measuring perceptual spatial hearing abilities directly. Since blind people cannot use visual feedback of the pointed hand, they rarely point toward sound sources in everyday life. Moreover, visual impairment is associated with changes in the development of motor behavior using upper limbs (Cappagli, Cocchi, & Gori, 2017; Pardhan, Gonzalez-Alvarez, & Subramanian, 2011). Therefore, one cannot rule out that, in the previous studies that required participants to point towards sound with their arms and hands, blind people performed worse than sighted people simply due to the changes in goal directed hand movements, and not due to the changes in their spatial hearing abilities[1] (Finocchietti, Cappagli, & Gori, 2015; Lewald, 2002, 2013; Vercillo, Tonelli, & Gori, 2018; Voss, Tabry, & Zatorre, 2015; Zwiers et al., 2001).

[1] Even if blindfolding the sighted control group during testing prevents online visual feedback, this manipulation however does not address any long-term changes in reaching behaviour.

Procedure

Prior to entering the room, the participants were blindfolded. When in the room, the participants sat in the center of the apparatus with their head positioned on a chin-rest. The height of the chinrest was fixed, and the participant could adjust the height of the chair for her/his comfort. This procedure was adopted to ensure that all loudspeakers along the horizontal and vertical planes were at equally distant from participant's ears (see Figure 1). The distance between the participant and the apparatus was 1.10 m. A response panel (15.5 x 9.5cm) was positioned in front of the chinrest.

During the experimental session, the sounds were presented from a single plane (i.e., horizontal or vertical) at a time, with the starting plane being counterbalanced across participants. Prior to starting the task, the experimenter informed the participant about which plane the sounds would be presented from. Within each plane, three different portions of space (each consisting of 11 contiguous/adjacent loudspeakers) were successively assessed, in a random order. Along the horizontal plane, sounds could be presented either from the left, central or right area (centered on the loudspeakers at -36°, 0° and +36°, respectively), whereas along the vertical plane, sounds could be presented either from the upper, central or lower area (centered at +36° above the center, 0° and -36° below the center, respectively; see Figure 1). The participant was informed about the upcoming stimulated area by a 100 ms alerting beep from the corresponding area that preceded the presentation of the actual set of experimental trials (10 for each area). Moreover, the position of the participant with regard to the acoustical apparatus was manipulated six times across the session, so that the participant performed the task either by facing the acoustical apparatus or with her/his back turned.

On each trial, a reference sound and a target sound, each lasting 100 ms, were presented successively with a 150 ms interval between them and followed by a 1200 ms response gap. In case a response was not provided during the response gap period, the trial was counted as a miss and the following trial automatically started. The reference sound was always played from the central speaker of the corresponding area, while the target sound was randomly played from one of the 10 contiguous speakers (ranging from ±5 to ±1 with regard to the centre/reference). Participants were instructed to indicate the location of the target second sound relative to the first reference sound in the pair of auditory stimuli (i.e., pressing left or right button response for sounds presented along the horizontal plane; pressing up or down button response for indicating for sounds presented along the vertical plane). Participants responded by pressing one of the keys (the left, right, up or down button, respectively) of the button panel. Each speaker location (10) of each area of space (6: 3 vertical and 3 horizontal) were stimulated 10 times. In total, participants were presented with 2400 trials (10 repetitions x 10 speaker locations x 2 participant positions x 2 planes x 3 areas). Before the experimental session, the participants performed a short training, in both vertical and horizontal plane. In between the experimental blocks, participants were allowed to take a break. In total, the session lasted for about 70 minutes.

The experiments were not formally preregistered. Experimental scripts, analysis scripts, and data may be found at this project's Open Science Framework page (https://osf.io/tav35/).

Data Analysis

To test for the effect of spatial arrangement of sounds on auditory localization performance, psychometric curves were fitted to the proportion of "right" or "up" responses for the horizontal and vertical axes, respectively. For each participant, the proportion of "right"/"up" responses was calculated as a function of the location of the target sound relative to the reference sound (i.e., ±5 to ±1), separately for each condition. Condition here is defined as a unique combination of levels of the factors Plane (horizontal vs. vertical), Position (front vs. back), and Area (i.e., left, center, right for the horizontal plane; up, center, down for the vertical plane). For each condition, proportion of "right" or "up" responses were fit using cumulative normal function, through maximum likelihood estimation (fitting procedures were performed in R through the *Quickpsy* package; Linares and Lopez-Moliner 2016; R_Core_Team 2017). In addition, the goodness-of-fit for each subject and each condition, was assessed by using bootstrap to calculate the p-value of the deviance (N=500). First, the psychometric function (i.e. the fit) was used for generating 500 bootstrap samples, and for each sample, the best fit and the deviance were calculated. The distribution of the deviances was used to calculate the probability of obtaining a value of the deviance larger than the deviance evaluated for the original data (the fit was considered as a poor/bad fit if the p-value was less than 0.05). For spatial location discrimination the one threshold score per subject and per condition (the difference in space required to shift the performance from 50% to 75%) and point of subjective equality (PSE: the mean of psychometric function) were extracted from the fitted function. We identified two types of outlying values, and we excluded them from further analyses (8.3% in total). The first type is constituted by the conditions for which a poor goodness of fit, evaluated through a bootstrapping procedure, resulted from the psychophysical models (5.9%). The second type of outlying value being for each participant threshold values deviating more than three standard deviations from the mean of that condition (2.4% of the data).

The threshold values extracted from the psychometric curves were submitted to a Linear Mixed-Models (LMM), as computed through the *lme* function for R (*nlme* package, Pinheiro, Bates, Debroy, Sarkar D, & R Core Team, 2014 combination with *lmerTest* package, Kuznetsova, Brockhoff, & Christensen, 2017). An LMM was performed on the whole dataset, with Plane, Position and Group as fixed effects, and Subject as a random effect. To consider the high variability in the vertical plane threshold values compared to the horizontal plane, option of different variances for each level of Plane was allowed. Then, two LMMs were computed on the thresholds reported for the horizontal and vertical plane separately, with Area, Position and Group as fixed effects and Subject as a random effect. We computed the test of significance of the different factors (Satterthwaite degrees of freedom approximation method) for each LMMs in order to evaluate the global effects of the predictors. False discovery rate (FDR) correction was applied for multiple post-hoc comparisons. Note that due the complexity of calculating "true" degrees of freedom in LMMs, we used the Satterthwaite approximation approach and the denominator degrees of freedom are determined by the grouping level at which the term is estimated (Pinheiro & Bates, 2000). A similar approach to the threshold values, was adopted to analyze PSE measures. PSE analysis as well as their visualization (including individual subject estimates of PSE) were presented in the supplemental material (see Supplemental Analyses, and Fig. S1).

In order to further analyze our data without modeling them with curve fitting, we performed 3 LMMs directly on the proportion of correct responses (Moscatelli et al., 2012). We not only replicate our main results but, if anything, we actually observed a gain in the statistical power of our main group differences (see Supplemental Analyses).

Results

Results of the two groups are shown in Figure 2, separately for each experimental condition. The individual threshold and PSE values across horizontal and vertical conditions dot plot are shown in Figure S1.

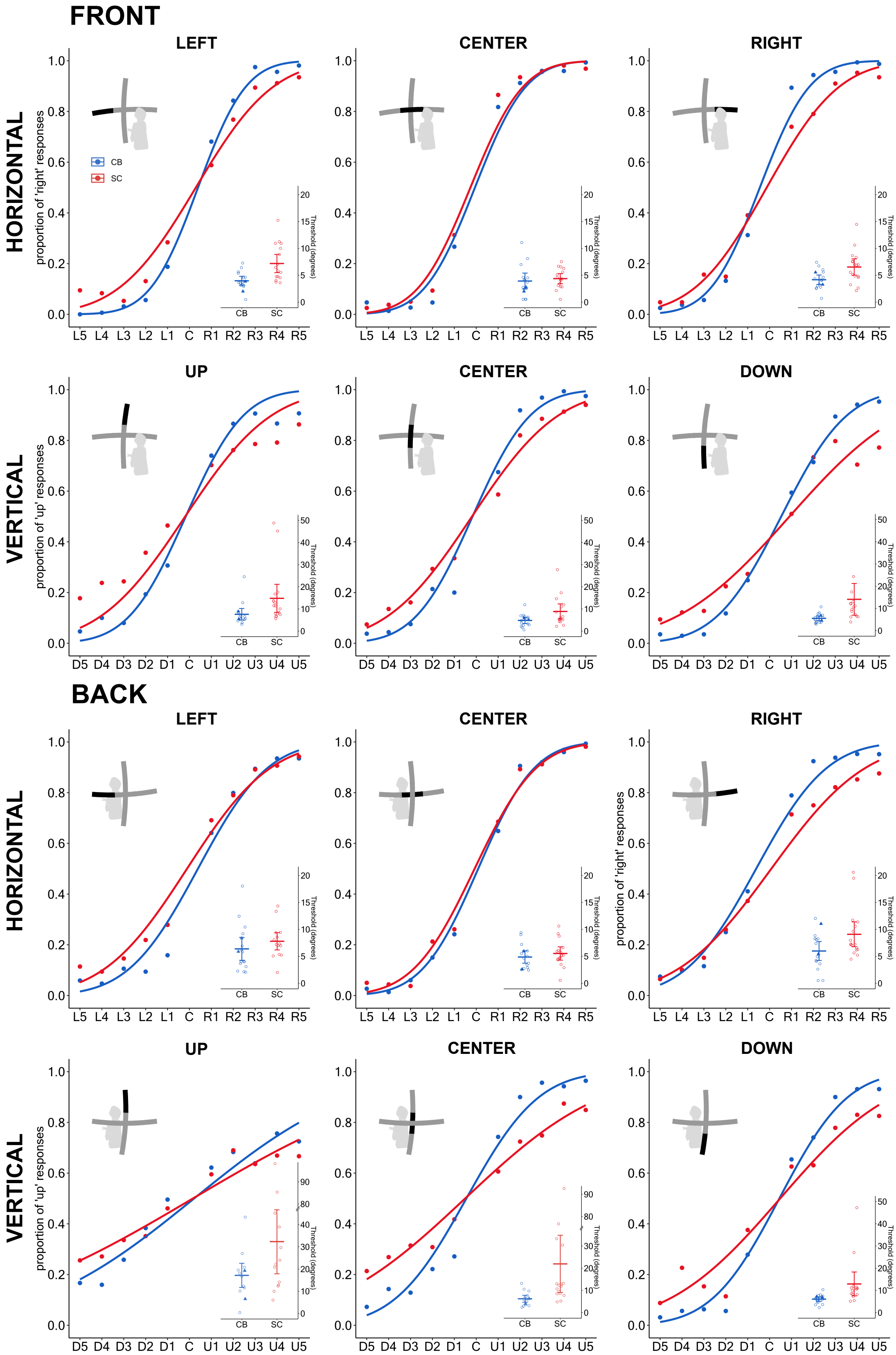

Fig. 2. Results of the minimal audible angle task reported for the two groups, separately for each experimental condition. Fitting representation is at the group level for illustration purposes only. Dot plots report the individual threshold values in degrees of angle with mean (thick bar) and ± standard deviation for each group. The filled triangle shapes within CB group indicate the two early blind participants that were not fully blind at birth. First row: frontal position horizontal plane

for each area (left, center, and right, respectively); second row: frontal position vertical plane for each area (up, center, down, respectively), third row: back position horizontal plane for each area (left, center and right); fourth row: vertical plane for each area (up, center, down respectively). Plots show the psychometric curves fitted to the proportion of right (horizontal plane) or up (vertical plane) responses.

Thresholds

In the first LMM, we analysed the auditory localization performance of CB and SC by considering Plane, Position and Group as fixed effects, and Subject as a random effect (marginal R^2 = 0.72; conditional R^2 = 0.84). In the model, within plane spatial areas (e.g. left, center, and right) were concatenated in order to create a Plane predictor. This analysis revealed a significant effect of Group (F = 6.44, p = .016), indicating overall lower thresholds (i.e., superior auditory localization performance) of CB compared to SC. The effect of Position was also significant (F = 20.8, p < .001) showing better performance when participants were facing the speakers. The significant main effect of Plane (F = 43.35, p < .001) showed that the auditory localization task was easier in the horizontal plane compared to the vertical plane. The observed significant Plane by Group interaction (F = 14.84, p < .001) demonstrated that despite the performance of the two groups differ significantly both in horizontal (t(31.9) = -2.25, p = .03) and vertical (t(199.2) = -4.57, p < .001) planes; the group difference was stronger in the vertical plane(pair-wise t-test p values adjusted with FDR correction method for 2 tests). A significant interaction between Plane and Head (F = 5.81, p = .017) suggested that even if performance drops in the back space for both horizontal and vertical planes, in the vertical plane localisation is affected the most (horizontal plane, t(160.1) = -4.02, p < .001; vertical plane, t(173.3) = -3.19, p = .002, pair-wise t-test p values adjusted with FDR correction method for 2 tests).

To further investigate the effect of spatial areas (e.g. left, center, and right in the horizontal plane) in auditory localization, the threshold values were entered into two LMMs for each plane separately. Group, Position and Area predictors submitted as fixed effects and the subjects as random effect (marginal R^2 = 0.20; conditional R^2 = 0.56). In the model for the horizontal data, the global main effects of Group, Position and Area were significant. The main effect of Group shows that the CB were overall more proficient than the SC (F = 5.45, p = .026). The main effect of Position (F = 19.89, p < .001) shows an advantage for localizing sounds coming from the front. Post-hoc comparisons (FDR correction method for 3 pair-wise t-tests) on the main effect of Area (F = 13.76, *p* < .001) showed that the discrimination thresholds were overall significantly lower for the central area compared to the two peripheral ones (left vs. center, *t*(147.7) = 4.85, *p* < .001; center vs. right, *t*(147.6) = 4.14, *p* < .001; left vs. right, *t*(147.3) = .7, *p* = 0.49). The interaction between Area and Group, (*F* = 3.18, *p* = .045) indicated a better accuracy of CB at localizing sounds in the peripheral areas compared to the SC (left area, *t*(56.7) = -2.47, *p* = .028; center area *t*(57.83) = -.71, *p* = .5; right area, *t*(55.8) = -2.84, *p* = .023; FDR correction method for 3 pair-wise t-tests).

The LMM computed on the vertical data (marginal R^2 = 0.22; conditional R^2 = 0.67). also showed a significant global effect of Group (*F* = 7.23, *p* = .01) revealing overall better performance in the blind group. We also observed a main effect of Position (*F* = 19.68, *p* < .001) better localization for sounds coming from the front. Post-hoc comparisons (FDR correction method for 3 pair-wise t-tests) on the main effect of Area (*F* = 7.58, *p* < .001) showed that the thresholds were overall higher when localizing sounds in the upper area compared to the center, (*t*(133.8) = 4.01, *p* < .001), and upper area compared to the down area, down (*t*(134.2) = -3.9, *p* < .001), with no differences in center vs. down (*t*(133.4) = -0.15, *p* = 0.8). The significant interaction between Position and Area (*F* = 7.6, *p* < .001) is due to the absence of different between front and rear space in the down area (center area, t(134.9) = -2.45, *p* = .023; up area, t(135.6) = -5.26, *p* < .001; pair-wise t-test *p* values adjusted with FDR correction method for 3 tests).

Point of Subjective Equality (PSE)

The Point of Subjective Equality (PSE) is the test location that is perceived to be the equal to the reference stimulus location for each "space". LMM analyses on PSE were carried out separately for each plane separately. In summary, the results revealed a higher tendency to respond "left" when sounds were presented in the left area of horizontal space, a bias that was exacerbated in blind people (Cattaneo et al., 2011) (see Supplemental Analyses).

DISCUSSION

Several studies have suggested that vision may scaffold the development of spatial abilities in the remaining senses (Knudsen, 2002) and that, therefore, the lack of vision since birth may prevent the optimal development of spatial hearing skills (Gori et al., 2014). In striking contrast with this view, our results are unequivocal in showing that early visual deprivation triggers a general enhancement of auditory spatial abilities. We therefore conclude that vision is not essential to calibrate the development of auditory spatial abilities (Gori et al., 2014), but rather demonstrate that the enhanced reliance on auditory cues in early blind people induces an improvement in auditory localization skills (Collignon et al., 2009).

Our findings contrast with previous studies showing an impairment of early blinds' spatial hearing abilities (Finocchietti et al., 2015; Gori et al., 2014; Lewald, 2002, 2013; Vercillo, Burr, & Gori, 2016; Voss et al., 2015; Zwiers et al., 2001). This discrepancy might be explained by considering the experimental paradigms used in those conflicting studies. First, a series of studies showing deficits in blind participants when compared to SC have relied on a spatial bisection task (Gori et al., 2014; Vercillo et al., 2016). Spatial bisection tasks might be impaired in early blind participants for two reasons that are independent of pure perceptual auditory spatial skills. First, spatial bisection tasks induce a mandatory conflict between space and time since shorter/longer spatial intervals have the same duration. Early blind people, due to their acute auditory skills (as demonstrated here) may be especially sensitive to such spatio-temporal incongruencies resulting in altered performance (Gori, Amadeo, & Campus, 2018). Second, spatial bisection task requires a metric representation of external space (Vercillo et al., 2018). Indeed, early blind people have qualitative alterations in their perception of external space (Crollen et al., 2017), which may explain their specific difficulties in resolving spatial bisection tasks independently of their intrinsic spatial hearing abilities (Collignon et al., 2009). Supporting this view, it was shown that severe deficits of early blind participants to localize brief auditory stimuli with respect to external acoustic landmarks (using a spatial bisection task) can be simply alleviated when participants had to localize the exact same sounds with respect to their own hand (using a body-centered reference frame; Vecillo et al., 2018). These results suggest that the spatial deficit of early blind individuals in the spatial bisection task is not perceptual in nature but rather the by-product of an altered representation of metric relationships in external space (Crollen, Spruyt, Mahau, Bottini, & Collignon, 2019; Vercillo et al., 2018). In contrast, the minimum audible angle task can be proficiently performed by relying on a mere topographical representation of sounds and therefore assess the capability to perceptually localize sounds in space without being confounded by advanced metric computations in the external space.

Another crucial difference between our paradigm and previous studies having shown poorer performance in CB related to the method used to provide a response on the location of sounds. Several previous studies have required the participants to point towards the source of sounds either with their hand or head (Finocchietti et al., 2015; Lewald, 2013; Vercillo et al., 2018; Voss et al., 2015; Zwiers et al., 2001), which is an action particularly unnatural to perform by blind participants who rarely points toward the source of events in the absence of visuo-motor guidance. Moreover, visual impairment is associated with changes in the development of motor behavior using upper limbs (Pardhan et al., 2011). Furthermore, pointing prompts the use of an allocentric representation of space, which, as explained above, is not the default reference frame used by blind individuals (Crollen et al., 2019; Vercillo et al., 2018). Consequently, a higher performance of sighted (vs. blind) individuals might artificially emerge in tasks using pointing to provide a response to the location of sounds, and therefore would not assess pure perceptual auditory localization abilities *per se*.

Although early visual deprivation enhances auditory localization abilities overall, this perceptual enhancement was particularly marked for sounds presented in the peripheral areas (King & Parsons, 1999; Josef P. Rauschecker & Kniepert, 1994; Röder et al., 1999; Voss et al., 2004). Such preferential enhancement in the auditory periphery could simply relate to the fact that sounds are more difficult to localize in the periphery therefore opening more possibilities for experience-dependent improvement and therefore to the expression of between-group differences. Second, preferential enhancement in the periphery may relate to the fact that anatomical projections from the auditory cortex to the primary visual cortex in primates preferentially map onto the visual periphery (Falchier, Clavagnier, Barone, & Kennedy, 2002). The absence of vision might result into a strengthening of these connections, thus underlying the behaviorally observable enhancement of peripheral sensory fields representation. Another possibility is that peripheral sounds, in addition to interaural level difference and interaural temporal difference cues, rely more strongly on information provided by spectral cues (Middlebrooks & Green, 1991). The more proficient localization of peripheral stimuli would thus be explained by the superiority of CB at processing spectral cues (Doucet et al., 2005; Lessard et al., 1998).

Assessing spatial hearing abilities at the back of the participant offers the unique opportunity to probe the relationship between visual experiences and auditory localization skills under a condition where neither of the two groups could rely on any direct sensory feedback during development. As expected, our results confirmed in sighted participants that localizing sounds derived from sources straight in front of the participant are much easier compared to sound localization in the back (Makous & Middlebrooks, 1990; Middlebrooks & Green, 1991). More precisely, SC were particularly impaired when localizing sounds located in the upper portion of rear space. (Makous & Middlebrooks, 1990; Oldfield & Parker, 1984). Interestingly, this difference between frontal and rear sounds was less prominent in CB who again showed better performance than sighted controls. This result is instrumental in showing that the difference between blind and sighted people does not only manifest in frontal regions where sighted typically have direct visual cues to calibrate the exact position of sound sources in external spaces, but also in situations where both the groups do not have such instantaneous visual calibration.

What are the effects that could drive such enhanced perceptual skills in CB?
Blind individuals rely more on the spatial hearing ability in navigating their environment, it is likely that perceptual training sharpens their auditory spatial skills (King, 2015). Such perceptual training effects may also induce, and potentially be supported by, changes in the neurobiology of spatial hearing abilities. The enhanced auditory skills could stem from either the plasticity within the auditory regions or through the recruitment of functionally related occipital regions that lack their typical/intrinsic visual input (Rauschecker & Harris, 1983). Previous studies have shown that regions typically dedicated to visuo-spatial processing, like for instance the right dorsal occipito-parietal cortex, show enhanced responses when CB, compared to SC, localize sounds in space (Collignon et al., 2011). A study using transcranial magnetic stimulation (TMS) found that focally and transiently disrupting the activity of the right the middle/superior occipital gyrus significantly altered auditory spatial localization abilities in the early blind, while leaving pitch and intensity perception unaffected (Collignon, Lassonde, Lepore, Bastien, & Veraart, 2007). Finally, superior auditory localization abilities of early blind individuals have been shown to correlate with the enhanced recruitment of the occipital cortex (Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005). However, elucidating how brain plasticity link to enhanced auditory spatial skills in blind people might be less trivial than a simple linear relationship between spatial hearing performance and occipital reorganization since recent studies have shown that the lack of vision triggers a large-scale reorganization (increase and decreased involvement) in the network dedicated to spatial hearing (Collignon et al., 2009; Dormal, Rezk, Yakobov, Lepore, & Collignon, 2016). Further studies are therefore needed to relate the superiority of CB in auditory localization to the underlying neuroplastic mechanisms at the level of brain networks.

Authors contributions: C. Battal and O. Collignon developed the study concept and design. G. Bertonati and C. Battal acquired the data. F. Falagiarda and C. Battal performed the data analysis under the supervision of O. Collignon. V. Occelli, C. Battal and O. Collignon drafted the paper and all authors approved the final version of the manuscript.

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Supplementary material

Table S1. Demographic and clinical data for the CB participants.

Code	Age	Gender	Etiology	Blindness onset	Light perception
CB 1	28	M	Retinopathy of prematurity	Birth-3 y/o*	No
CB 2	36	M	Retinopathy of prematurity	Birth	No
CB 3	35	F	Retinopathy of prematurity	Birth	Yes
CB 4	27	F	Retinitis pigmentosa	Birth	Yes
CB 5	46	M	Atrophy of optic nerve	Birth	Yes
CB 6	45	M	Congenital glaucoma	Birth	No
CB 7	44	M	Congenital retinopathy	Birth	No
CB 8	34	F	Retinopathy of prematurity	Birth	Yes
CB 9	40	M	Leber congenital amaurosis	Birth	Yes
CB 10	27	F	Bilateral agenesia optic nerve	Birth	No
CB 11	29	F	Retinopathy of prematurity	Birth	Yes
CB 12	33	M	Retinopathy of prematurity	Birth	No
CB 13	20	F	Leber congenital amaurosis	Birth	Yes
CB 14	27	M	Retinopathy of prematurity	Birth	No
CB 15	26	F	Bilateral microphthalmia	Birth	Yes
CB 16	30	F	Congenital glaucoma	Birth	No
CB 17	27	M	Infection at birth	Birth-3 y/o*	No

***full blindness at 3 y/o but massive visual impairments were present since birth preventing visually guided behaviour and the development of visual abilities.

Table S2. Post-hoc tests of interactions in the planes, horizontal and vertical planes LMM. The abbreviations refer to congenitally blind (CB) and sighted control (SC) groups, horizontal (hor), vertical (ver) planes, horizontal plane center area (ctrh), vertical plane center area (ctrv), and the numbers represent position (1) and back position (2). For the multiple comparison corrections, we adopted FDR and only applied to the certain pairwise t-tests that were defined as contrast of interest indicated in the table as a column. In case of contrast of no interest (indicated with 0), the p value correction for multiple comparison was not applied and was shown as not available (NA). The df column represents degree of freedom, while df-Satterthwaite column represents the degree of freedom with Satterthwaite approach.

Post-hoc Pairwise comparison of Plane and Group interaction

contrast	*estimate*	*SE*	*df*	*t.ratio*	*p.value*	*Contrast of Interest*	*p.value Corrected (FDR)*	*df- satterthwaite*
hor,CB - ver,CB	-0,697	0,355	332	-1,966	0,050	0	NA	185,178
hor,CB - hor,SC	-0,461	0,205	32	-2,252	0,031	1	0,031	31,836
hor,CB - ver,SC	-3,096	0,397	32	-7,799	0,000	0	NA	188,193
ver,CB - hor,SC	0,237	0,399	32	0,593	0,557	0	NA	188,705
ver,CB - ver,SC	-2,399	0,524	32	-4,575	0,000	1	0,000	199,183
hor,SC - ver,SC	-2,635	0,352	332	-7,486	0,000	0	NA	185,276

Post-hoc Pairwise comparison of Plane and Head interaction

contrast	*estimate*	*SE*	*df*	*t.ratio*	*p.value*	*Contrast of Interest*	*p.value Corrected (FDR)*	*df- satterthwaite*
hor,1 - ver,1	-1,067	0,344	332	-3,097	0,002	0	NA	185,489
hor,1 - hor,2	-0,367	0,091	332	-4,021	0,000	1	0,000	160,139
hor,1 - ver,2	-2,633	0,362	332	-7,281	0,000	0	NA	184,451
ver,1 - hor,2	0,700	0,345	332	2,030	0,043	0	NA	186,073
ver,1 - ver,2	-1,566	0,491	332	-3,188	0,002	1	0,002	173,269
hor,2 - ver,2	-2,266	0,362	332	-6,262	0,000	0	NA	184,992

Post-hoc Pairwise comparison of the interaction between Area and Group in the horizontal plane

contrast	*estimate*	*SE*	*df*	*t.ratio*	*p.value*	*Contrast of Interest*	*p.value Corrected (FDR)*	*df- satterthwaite*
ctrh,CB - left,CB	-0,255	0,146	147	-1,747	0,083	0	NA	147,511
ctrh,CB - right,CB	-0,227	0,149	147	-1,531	0,128	0	NA	147,959
ctrh,CB - ctrh,SC	-0,166	0,231	32	-0,718	0,478	1	0,478	57,796
ctrh,CB - left,SC	-0,823	0,232	32	-3,546	0,001	0	NA	58,739
ctrh,CB - right,SC	-0,876	0,229	32	-3,822	0,001	0	NA	56,496
left,CB - right,CB	0,027	0,144	147	0,190	0,849	0	NA	146,898
left,CB - ctrh,SC	0,089	0,228	32	0,390	0,699	0	NA	55,711
left,CB - left,SC	-0,568	0,230	32	-2,474	0,019	1	0,028	56,650
left,CB - right,SC	-0,622	0,227	32	-2,740	0,010	0	NA	54,417

right,CB - ctrh,SC	0,062	0,230	32	0,268	0,790	0	NA	57,081
right,CB - left,SC	-0,595	0,231	32	-2,575	0,015	0	NA	58,022
right,CB - right,SC	-0,649	0,228	32	-2,840	0,008	1	0,023	55,783
ctrh,SC - left,SC	-0,657	0,146	147	-4,509	0,000	0	NA	147,161
ctrh,SC - right,SC	-0,711	0,142	147	-5,012	0,000	0	NA	146,914
left,SC - right,SC	-0,054	0,144	147	-0,374	0,709	0	NA	147,183

Post-hoc Pairwise comparison of the interaction between Area and Head in the vertical plane

contrast	*estimate*	*SE*	*df*	*t.ratio*	*p.value*	*Contrast of Interest*	*p.value Corrected (FDR)*	*df- satterthwaite*
ctrv,1 - down,1	-0,810	0,591	137	-1,371	0,173	0	NA	134,035
ctrv,1 - up,1	-0,821	0,593	137	-1,384	0,169	0	NA	134,559
ctrv,1 - ctrv,2	-1,481	0,605	137	-2,448	0,016	1	0,023	134,935
ctrv,1 - down,2	-0,801	0,596	137	-1,343	0,182	0	NA	134,271
ctrv,1 - up,2	-4,162	0,638	137	-6,527	0,000	0	NA	135,314
down,1 - up,1	-0,011	0,588	137	-0,019	0,985	0	NA	134,367
down,1 - ctrv,2	-0,671	0,600	137	-1,119	0,265	0	NA	134,726
down,1 - down,2	0,009	0,591	137	0,015	0,988	1	0,988	134,134
down,1 - up,2	-3,353	0,632	137	-5,301	0,000	0	NA	135,149
up,1 - ctrv,2	-0,660	0,597	137	-1,105	0,271	0	NA	134,123
up,1 - down,2	0,020	0,591	137	0,034	0,973	0	NA	134,052
up,1 - up,2	-3,342	0,635	137	-5,261	0,000	1	0,000	135,576
ctrv,2 - down,2	0,680	0,602	137	1,129	0,261	0	NA	134,412
ctrv,2 - up,2	-2,682	0,645	137	-4,157	0,000	0	NA	135,647
down,2 - up,2	-3,362	0,641	137	-5,247	0,000	0	NA	135,926

Supplemental Analyses

Data analysis on PSE values

The PSE values extracted from the psychometric curves were submitted to a Linear Mixed-Models (LMM), as computed through the *lme* function for R (*nlme* package, Pinheiro, Bates, Debroy, Sarkar D, & R Core Team, 2014 combination with *lmerTest* package, Kuznetsova, Brockhoff, & Christensen, 2017). Two separate LMMs were computed on the thresholds reported for the horizontal and vertical plane separately, with Area, Position and Group as fixed effects and Subject as a random effect. We computed the test of significance of the different factors (Satterthwaite degrees of freedom approximation method) for each LMMs in order to evaluate the global effects of the predictors. False discovery rate (FDR) correction was applied for multiple post-hoc comparisons.

Results on PSE values

The point of subjective equality is the test location that is perceived to be the equal to the reference stimulus location for each "space". Note that PSE shifts to the left/down (smaller than zero) mean that a larger range of locations is perceived as being to the right/up of reference speaker (e.g. midline of a given area), and vice versa for a rightward/upward shift in PSE.

In the horizontal plane, an LMM was computed with Area, Position and Group as fixed effects, and Subject as a random effect (marginal $R^2 = 0.12$; conditional $R^2 = 0.15$). This analyze revealed a significant main effect of Area ($F = 6.44$, $p = .002$). Post-hoc comparisons showed a stronger tendency to respond 'left' when localizing sounds in the left area compared to the center, ($t(152.6) = 2.42$, $p = .025$), and in the left area compared to the right ($t(151.5) = 3.44$, $p = .002$), with no differences in the other comparison between right vs. center ($t(153) = -.99$, $p = 0.33$). We also observed a significant Arm by Group interaction ($F = 4.49$, $p = .013$). Pairwise t-tests across group separately for each area, showed significant group differences only in right area (left area: $t(144) = 1.47$, $p = .2$; center area: $t(146) = .46$, $p = .7$; right area: $t(142.9) = -2.58$, $p = .04$) (FDR correction method for 3 pair-wise t-tests). To explore further the potential origin of the interaction, we carried out pairwise comparison between areas in each group separately. These post-hoc analyses revealed that only in the CB group the left area showed more leftward bias compared to the right area ($t(151.2) = 4.51$, $p < .001$) (FDR correction method for 6 pair-wise t-tests). This result suggest that the leftward bias observed in both groups when sounds are presented in the left area (see above) is slightly exacerbated in blind individuals.

In the vertical plane, the LMM computed with Area, Position and Group as fixed effects, and Subject as a random effect (marginal $R^2 = 0.05$; conditional $R^2 = 0.28$) revealed significant main effect of Area ($F = 3.75$, $p = .026$). Post-hoc comparisons showed stronger tendency to respond "down" when localizing sounds in the down area compared to the center ($t(140.2) = 2.19$, $p = .045$) and up ($t(141.8) = 2.53$, $p = .036$) areas. No interaction effect was observed.

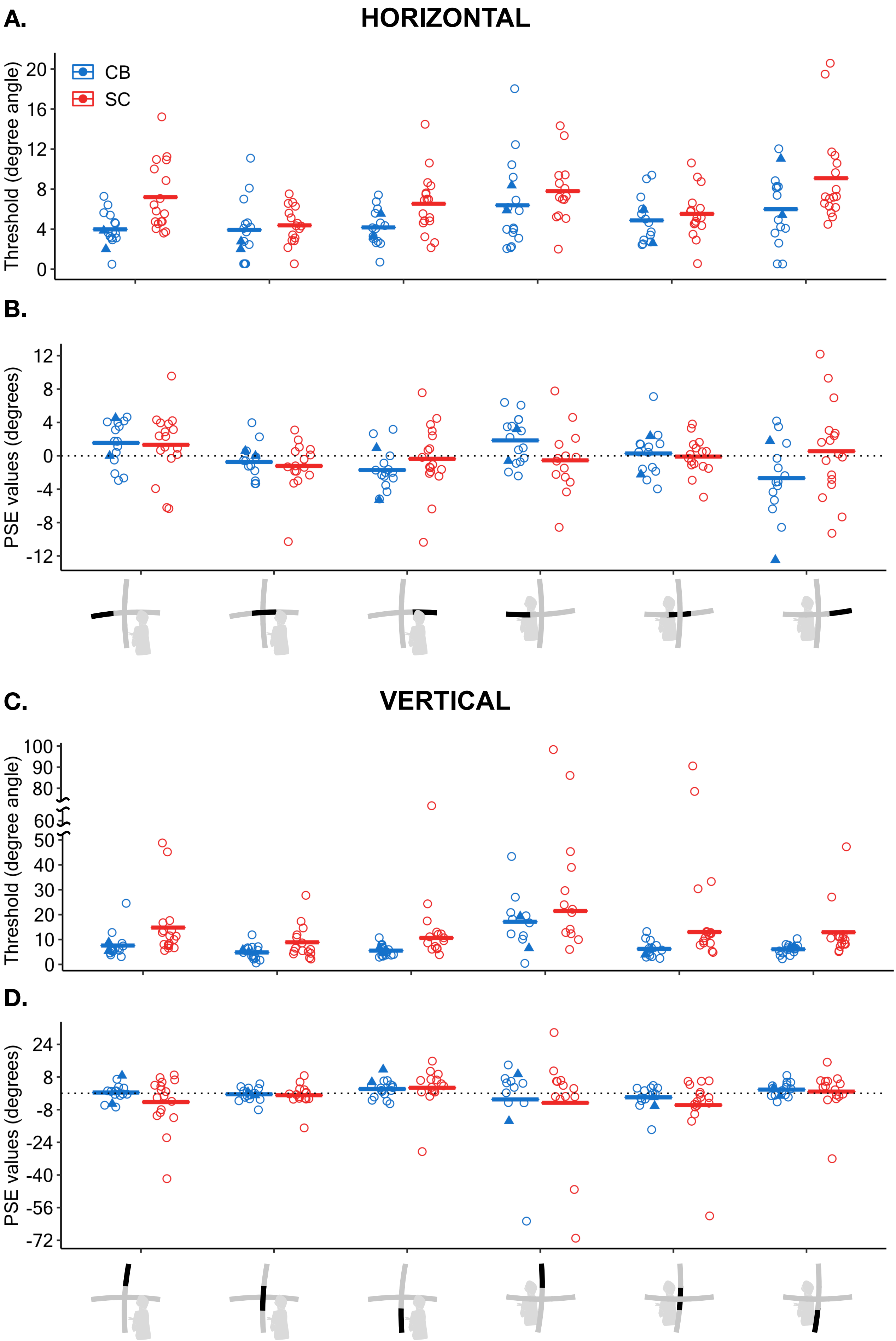
A.
HORIZONTAL
CB
SC
Threshold (degree angle)
0
4
8
12
16
20
B.
PSE values (degrees)
12
8
4
0
-4
-8
-12
C.
VERTICAL
Threshold (degree angle)
100
90
80
60
50
40
30
20
10
0
D.
PSE values (degrees)
24
8
-8
-24
-40
-56
-72

Figure S1. Psychometric curve fitting threshold and PSE values across groups and conditions. Results of the minimal audible angle task reported for the two groups, separately for each experimental condition. Dot plots report the individual threshold and PSE values in degrees of angle with mean (thick bar) for CB and SC group (in blue and red respectively). The filled triangle shapes within CB group indicate two early blind participants. A. Individual threshold values in horizontal plane for 6 conditions (front position left, center, and right, and back position left, center, and right, respectively). B. Individual PSE values in horizontal plane for 6 conditions (front position left, center, and right, and back position left, center, and right, respectively). C. Individual threshold values in vertical plane for 6 condition (front position up, center, down, and back position up, center, down, respectively). D. Individual PSE values in vertical plane for 6 condition (front position up, center, down, and back position up, center, down, respectively).

Data analysis on proportion of correct responses

For each condition, the proportion of correct responses were directly fitted to generalised mixed models (Moscatelli et al., 2012). We used a mixed effect probit model computed through the *glmer* function for R (lme4 package, Bates et al., 2015). An GLMM was performed on the whole dataset, with Plane, Position, Group, and Speaker as fixed effects, and Subject as a random effect. Then, two GLMMs were computed on the thresholds reported for the horizontal and vertical plane separately, with Area, Position, Group and Speaker as fixed effects and Subject as a random effect. We calculated Analysis of Deviance Tables (using Type II Wald Chi-Square tests) for the models using the car package "Anova" function (Fox and Weisberg, 2019). For significant interactions, we performed post hoc comparisons using the emmeans package (Lenth 2019), which computes, and contrasts estimated marginal means. We adopted FDR p adjustment, contrasts with $p < 0.05$ were considered as significant (corrected p values are reported).

Results on proportion of correct responses

Results of the proportion of correct responses across five different speaker distance and two groups are shown in Figure S2, separately for each experimental condition. CB group showed consistently higher auditory localization performance across conditions, even in a smaller scale, across speakers.

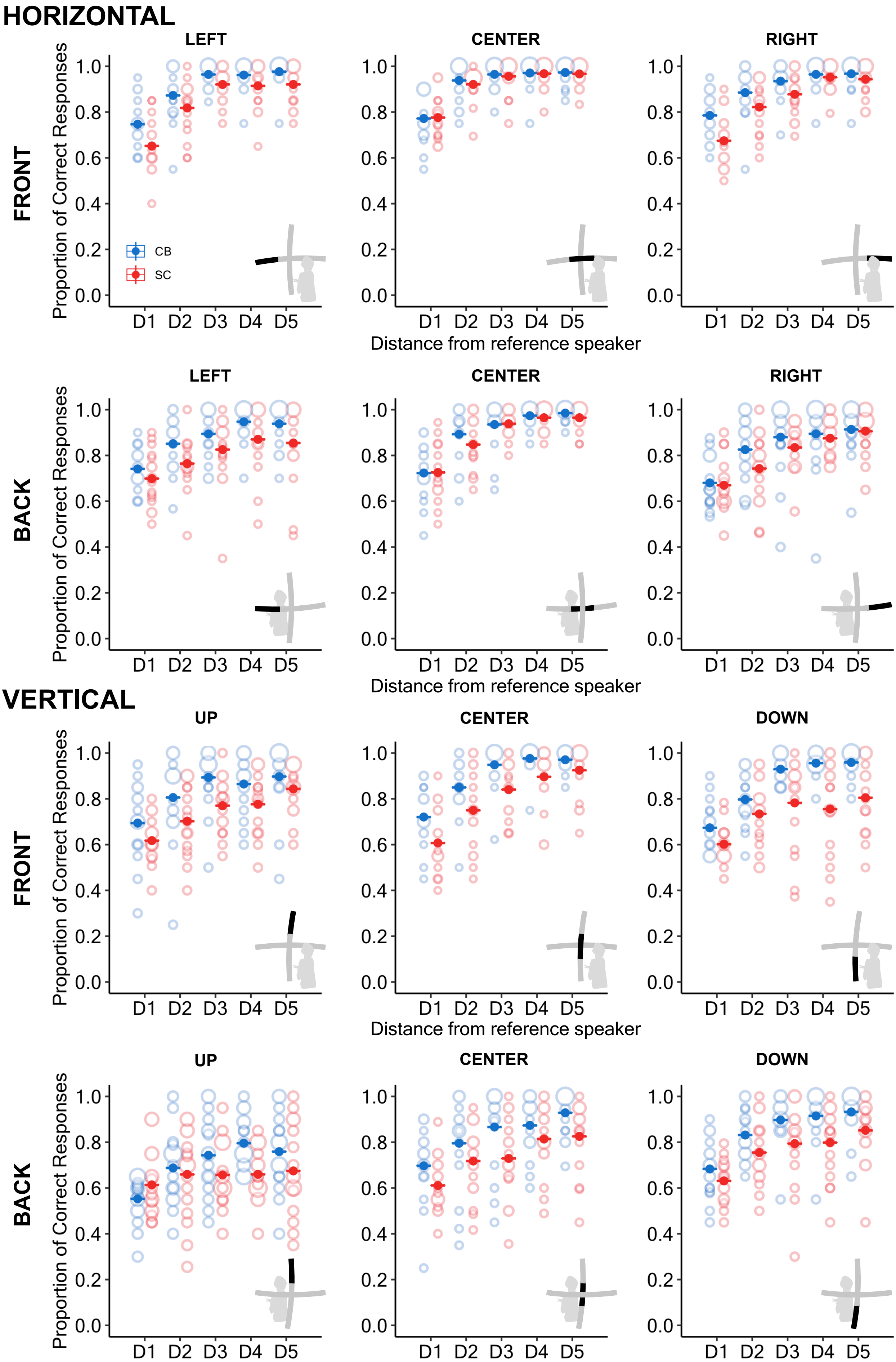
HORIZONTAL
FRONT
BACK
VERTICAL
LEFT
CENTER
RIGHT
UP
DOWN
Proportion of Correct Responses
Distance from reference speaker
D1 D2 D3 D4 D5
0.0 0.2 0.4 0.6 0.8 1.0
CB
SC

Fig. S2. Results of the minimal audible angle task reported for the two groups, separately for each experimental condition. Balloon plots report the count of occurrences of proportion of correct responses across the speaker distances from the reference speaker with mean (opaque horizontal thick bar and circle) for each group. CB group is represented in blue, while SC group is represented in red. The proportion of the correct responses across the same speaker distances from the left/right position respective to the central reference speaker were grouped for illustration purpose only (e.g. L5 – R5, L4 – R4, L3 – R3, L2 – R2, L1 – R1) and represented with D1: distance 1, D2: distance 2, D3: distance 3, D4: distance 4, D5: distance 5. The size of the balloons represents the ratio/number of participants sharing the same proportion of correct responses (i.e. bigger the balloon size, more occurrences of the same proportion of correct responses across participants). First row: frontal position horizontal plane for each area (left, center, and right, respectively); second row: back position horizontal plane for each area left, center, and right, respectively), third row: front position vertical plane for each area (up, center, down); fourth row: back position vertical plane for each area (up, center, down respectively).

In the first GLMM, we analysed the auditory localization performance of CB and SC by considering Plane, Position, Group and Speaker as fixed effects, and Subject as a random effect. In the model, within plane spatial areas (e.g. left, center, and right) were concatenated in order to create Plane predictor. This analysis revealed a significant main effect of Group (χ^2 = 10.75, P = 0.001), Planes (χ^2 = 604.35, P < 0.001), Position (χ^2 = 189.83, P < 0.001) indicating that behavioural accuracy of CB was better than SC group, the horizontal conditions are easier than the vertical conditions, and auditory localisation in the front space is easier than in the back space. Furthermore, significant interaction of Plane x Group and Group x Position suggested that even if, localizing sounds is easier in the horizontal plane (compared to the vertical plane) and in the front space (compared to the back space), nevertheless, the group difference is more on the front space and in the vertical plane.

To further investigate the effect of spatial area (e.g. left, center, and right in the horizontal plane) in auditory localization, the proportion of correct response values were entered into two GLMMs for horizontal and vertical planes separately. Group, Position, Area and Speaker predictors submitted as fixed effects and the subjects as random effect. In the model for the horizontal data, the global main effects of Group, Position and Area were significant. The main effect of Group shows that the CB were overall more proficient than the SC (χ^2 = 5.27, P = 0.022). The main effect of Position (χ^2 = 86.22, P < 0.001) shows an advantage for localizing sounds coming from the front. Post-hoc comparisons on the main effect of Area (χ^2 = 136.39, P < 0.001) showed that the performances were overall significantly higher for the central area compared to the two peripheral ones. The significant interaction between Area and Group, ($\chi^2 = 17.52$, $P < 0.001$) indicated a better accuracy of CB at localizing sounds in the peripheral areas.

The GLMM computed on the vertical data also showed a significant global effect of Group ($\chi^2 = 11.6$, $P = 0.001$) revealing overall better performance in the blind group. We also observed a main effect of Position ($\chi^2 = 88.26$, $P < 0.001$) better localization for sounds coming from the front. Post-hoc comparisons on the main effect of Area ($\chi^2 = 169.32$, $P < 0.001$) showed that the auditory localization performances were overall lower when localizing sounds in the upper area compared to the center and lower areas. The significant interaction between Area and Position ($\chi^2 = 65.52$, $P < 0.001$) is due to the higher difficulty at localizing sounds in upper and center areas in the dorsal space. The significant interaction of Group and Position ($\chi^2 = 9.88$, $P = 0.002$) is due to the group difference is more prominent on the front space.

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