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Early Visual Deprivation Severely Compromises the Auditory Sense of Space in Congenitally Blind Children

Tiziana Vercillo,

Department of Psychology, University of Nevada

David Burr, and

Department of Neuroscience, University of Florence and CNR Institute of Neuroscience, Pisa, Italy

Monica Gori

U-VIP Unit for Visually Impaired People, Fondazione Istituto Italiano di Tecnologia, Genoa, Italy

Abstract

A recent study has shown that congenitally blind adults, who have never had visual experience, are impaired on an auditory spatial bisection task (Gori, Sandini, Martinoli, & Burr, 2014). In this study we investigated how thresholds for auditory spatial bisection and auditory discrimination develop with age in sighted and congenitally blind children (9 to 14 years old). Children performed 2 spatial tasks (minimum audible angle and space bisection) and 1 temporal task (temporal bisection). There was no impairment in the temporal task for blind children but, like adults, they showed severely compromised thresholds for spatial bisection. Interestingly, the blind children also showed lower precision in judging minimum audible angle. These results confirm the adult study and go on to suggest that even simpler auditory spatial tasks are compromised in children, and that this capacity recovers over time.

Keywords

visual deprivation; auditory perception; spatial perception

Visual deprivation impacts strongly on the functional organization of the brain, especially if it occurs early in life, when cortical plasticity is maximal. The premature loss of vision causes functional reorganization of the visual cortex, which can become colonized by other sensory modalities and be activated by nonvisual stimuli (Collignon et al., 2013; Collignon et al., 2011; Rauschecker, 1995; Voss & Zatorre, 2012). The neural colonization is accompanied by improvement of many auditory and tactile abilities in congenitally blind adults. Tactile spatial acuity has been reported to be superior in the blind than in the sighted (Van Boven, Hamilton, Kauffman, Keenan, & Pascual-Leone, 2000), with the enhancement of acuity seeming to result from tactile experience (Wong, Gnanakumaran, & Goldreich, 2011). Similarly, blind adults can map auditory events with equal or better accuracy than

sighted subjects (Doucet et al., 2005; Lessard, Paré, Lepore, & Lassonde, 1998; Roder et al., 1999; Voss et al., 2004). These enhanced sensory abilities have been ascribed to changes within the auditory and tactile pathways (Cohen et al., 1997; Elbert et al., 2002) and also to the colonization of the visual cortex from the remaining sensory modalities (Collignon et al., 2013; Collignon et al., 2011; Collignon, Voss, Lassonde, & Lepore, 2009; Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005), supporting the hypothesis of sensory substitution (Rauschecker, 1995).

However, there have also been reports of negative effects of prolonged visual deprivation in perceptual tasks. A recent study investigated local versus global processing in naming and haptic drawing tasks in a group of blind and sighted children and reported that analytical strategies predominate over holistic strategies in haptic perception in blind children of around 10 years of age (Puspitawati, Jebrane, & Vinter, 2014). Children explored tactile “Navon” patterns composed of a large global figure made up of smaller local shapes, and had to name or draw the perceived shape. Young blind children failed to recognize the global pattern, focusing more on the local features that composed the figure. This study suggests that blind children find it difficult to understand part-whole relationship in the haptic modality. Millar (1976) investigated spatial representation in two experiments of mental rotation of a raised line and found impairment in blind children from 6–11 years of age in recall tests. These studies suggest that early visual deprivation affects the development of spatial processing, at least in the haptic modality. Moreover, physiological research has reported effects of visual deprivation on the functional organization of some subcortical structures. For example, the maturation of auditory spatial response properties of neurons in the superior colliculus is affected by visual deprivation, suggesting that vision plays an important role in developing these spatial representations (King & Carlile, 1993; Knudsen & Brainard, 1991; Wallace & Stein, 1997; Withington-Wray, Binns, Dhanjal, Brickley, & Keating, 1990). Indeed, tasks such as orienting and localization involve the superior colliculus and the “dorsal stream,” projecting to the parietal lobe that is essential for the perception and interpretation of spatial relationships (Goodale & Milner, 1992). Additionally, psychophysical studies have shown that visual information may be used to calibrate auditory spectral pinna cues. Zwiers, Van Opstal, and Cruysberg (2001) reported poor localization in early blind adults on the elevation plane, where binaural cues are poor and the benefits of vision are normally maximal, and Zwiers, Van Opstal, and Paige (2003) described auditory spatial distortion in sighted individuals after adaptation to a compressed visual space.

Recently, Gori et al. (2014) reported severe deficits in auditory spatial bisection along the horizontal plane in congenitally blind individuals. In their study a group of congenitally blind adults performed two spatial auditory tasks: space bisection and minimum audible angle. Blind individuals showed a massive impairment in the spatial bisection task, where they had to compare the relative distance between an auditory target and two fixed auditory landmarks to determine its spatial position. On the contrary, their performance in the minimum audible angle task, where they had to understand which sound of a sequence of two was more on their right side, was similar to controls. This latter task requires a spatial judgment that might be more anchored to an egocentric reference frame rather than an external reference frame as the one provided by the two auditory landmarks. The authors

suggested that early visual deprivation might compromise the visual calibration of the auditory system, hindering the creation of complex auditory representations of Euclidean space. They pointed to the importance of visual experience and cross-sensory interaction in the creation and calibration of complex auditory maps. On the other hand, the unimpaired performance in the minimum audible angle suggests that simpler visual maps can develop even without visual information.

In the current study we investigated whether congenitally blind children show the same impairment in understanding and representing spatial relations between multiple sound sources, and perhaps even in simple auditory localization. Although auditory spatial perception has been widely investigated in congenitally blind adults, less effort has been spent in understanding how this sense of space changes during development in the blind. We tested congenitally blind and sighted children in the same spatial tasks used by Gori et al. (2014) and found strong deficits for blind children suggesting that the absence of vision induces a severe impairment in the development of auditory spatial abilities.

Method

We analyzed the performance of blind and sighted children on two spatial tasks: space bisection and minimum audible angle. Eight congenitally blind children performed both tasks (mean age, 10.9 ± 0.8 years of age; 6 females, 2 males, see supplemental material for additional details about pathology and residual vision). We compared their thresholds with those of a group of 52 age matched sighted children (sixteen 8-year-olds, twenty-four 10-year-olds and thirteen 13-year-olds; 31 females and 21 males) for the minimum audible angle, and with those of a group of 29 children (fourteen 9-year-olds, ten 10-year-olds, and five 12-year-olds; 21 females and 8 males) for the space bisection task. All participants had normal hearing. Blind children were recruited from the Institute David Chiossone in Genoa, Italy. None of the congenitally blind subjects had cognitive impairments; none have ever had functional vision, or even rudimentary sensitivity for brightness differences, except for one 11-year-old child who had some residual vision (low-level bright light detection) who is represented by a diamond symbol. Sighted children were recruited from elementary and intermediate schools in Genoa, Italy.

Methods and procedures were the same to those used by Gori, Sandini, and Burr (2012) and Gori et al. (2014). All sighted participants were blindfolded before entering the experimental room. Participants sat in a silent room, 180 cm from the center of an array of 23 speakers spanning $\pm 25^\circ$ of visual angle (with 0 representing the central speaker, negative values locations on the left, and positive values right). Each speaker was separated 2.2° from each other.

Auditory stimuli for all of the experiments were 500 Hz tones of 75 ms duration at 60 dB Sound Pressure Level (SPL). Since Gori et al. (2014) found no differences in spatial precision in localization of 500 and 3000 Hz sounds and pink noise (ranging from 0 to 5 kHz) in either sighted or blind individuals, we used the same experimental procedure to better compare the results between the two studies. For the space bisection task (Figure 1a), three sounds were played successively at 500 ms intervals. The locations of the first and the

third sounds were fixed at -25° and $+25^\circ$ (left and right of the subject). The second sound was placed in between the others, and subjects had to verbally report whether it seemed to be closer to the first or the third sound. The location of the second “probe” sound was determined by the QUEST algorithm (Watson & Pelli, 1983), which positioned this sound near the best estimate of perceptual midpoint. This procedure uses efficient Bayesian methods to estimate threshold from all trials to date. We presented the next trial at this predicted position, perturbed by Gaussian jitter. For the minimal audible angle experiment (Figure 1b), only two sounds were presented, successively at 500 ms intervals, one (randomly either first or second) located at 0° , and the other either left or right of it, at a separation controlled by the adaptive QUEST algorithm. Participants had to verbally report which of the two stimuli was more on the right.

As in the study from (Gori et al., 2014), we also tested seven out of eight blind children and another group of 42 sighted children (mean age, 9 ± 0.36 years old) in a temporal bisection task (Figure 1c). Children were positioned in front of a single speaker and listened to a sequence of three sounds (driven by a well-calibrated National Instrument Support Interface), and reported whether the second (probe) stimulus appeared *temporally* closer to the first or to the third sound. The total duration of the stimulation was 1,000 ms. The timing of the second stimulus was regulated by a QUEST algorithm, following the procedure described above.

The group of congenitally blind children performed 60 trials in a trial block for each task, while sighted children participated in only one of the tasks. We ensured long breaks between the three tasks for the blind children to avoid any effect of fatigue and/or inattentiveness, and the order of the three tasks was randomized. The duration of each trial block was about 15 min. We involved all the children in a short training session, to make them familiar with the task and to be sure that they understood the task correctly. We asked children to keep their head steady for the duration of the experiment. We did not measure head movements directly, to reduce the invasiveness of the experiment, but the experimenter was continually monitoring the head position of the children during the test. If the head turned, the child was encouraged to correct the position. The families of the children gave informed consent before the test. The study was approved by the ethics committee of the local health service (Comitato Etico, ASL3, Genova).

Data were fitted by cumulative Gaussian distributions (error functions). Following standard psychophysical procedure (Kingdom & Prins, 2010), discrimination thresholds were taken to be the standard deviation of these distributions.

Results

Figure 2 shows the average thresholds (geometric mean) for three different tasks, averaged over all ages. As previously reported by Gori et al. (2014) the performance of blind participants was considerably impaired in the bisection task, in which subjects had to report the relative position of a sound with respect to other two auditory stimuli. The average thresholds for the congenitally blind were $17 \pm 2^\circ$ of visual angle, nearly four times higher than those of sighted children ($4.9 \pm 0.3^\circ$), a highly significant difference (one-tailed

unpaired t -test, $t_{35} = 7.13$, $p < .001$). Interestingly, young blind participants also had lower precision than sighted children in the minimum audible angle task (Figure 2b), although the difference was less marked, only about 50%. Average thresholds for the two groups of young participants were $18 \pm 2.5^\circ$ and $12 \pm 0.7^\circ$, respectively (one-tailed unpaired t -test, $t_{58} = 2.84$, $p < .01$). On the contrary, the two groups of children performed the temporal task with similar precision: average thresholds for the congenital blind children were 89 ± 29 ms, not statistically different from those of sighted children, 82 ± 10 ms (one-tailed unpaired t -test, $t_{40} = 0.66$, $p = .37$). The performance of congenitally blind children was severely impaired only in the spatial tasks.

Unexpectedly, we also found that sighted children performed the space bisection task with better precision, that is, lower thresholds, than the minimum audible angle task (one-tailed unpaired t -test, $t_{79} = 6.66$, $p < .001$) suggesting that different mechanisms might be involved in the processing of the two spatial tasks.

Figure 3 shows individual thresholds of congenitally blind children (filled gray symbols) and average thresholds (geometric mean: black symbols) of the sighted control group in the space bisection (Figure 3a) and in the minimum audible angle task (Figure 3b). Four blind children performed both tasks at chance level, to which we assigned an arbitrary threshold of 25° , half the total separation of the speakers. The performance of sighted children clearly improves with age in both of the spatial tasks. In the space bisection task there is a reduction of the thresholds of $\sim 3^\circ$ of visual angle, with 9-year-old sighted children performing the task with a standard deviation of $6.5 \pm 0.6^\circ$ of visual angle, and 12-year-old sighted children with a standard deviation of $3.9 \pm 0.6^\circ$ of visual angle (see Figure 3a). A linear regression model confirmed a strong correlation between thresholds and age (adj. $R^2 = 0.32$; $p = .001$). As expected, we did not find the same improvement in precision for the same task in the group of blind children (adj. $R^2 = 0.07$; $p = .25$).

Interestingly, we reported a similar pattern of results also for the minimum audible angle task: the average thresholds of the sighted children decrease from $13.9 \pm 1^\circ$ in the 8-year-olds to the $8 \pm 1^\circ$ in the 13-year-olds, but again thresholds did not change with age in the group of congenitally blind children (Figure 3b). A linear regression model on individual data revealed a correlation between thresholds and age in the sighted (adj. $R^2 = 0.18$; $p < .001$) but not in the blind group of children (adj. $R^2 = 0$; $p = .45$). Maybe the lack of correlation in blind children simply reflected the smaller sample size and age range of this group.

Figure 3 also reports the average thresholds (geometric mean: empty gray circles) measured in the young adults ($n = 6$, mean age 23 years) and adults ($n = 3$, mean age 56 years) congenitally blind and in the young adults ($n = 15$, mean age 23 years) and adults ($n = 12$, mean age 41 years) sighted subjects in a previous experiment conducted in our laboratory. Black and gray arrows falling outside the axis indicate geometric average thresholds for sighted and blind adults, respectively, and black and gray arrows falling inside the axis indicate geometric average thresholds for the sighted and blind children. In the space bisection task, the average thresholds for all the blind participants are far higher than those

of young and adult sighted participants. Conversely, in the minimum audible angle, the performance of blind participants was impaired only at the youngest ages.

Summarizing, congenitally blind individuals of all ages showed a severe deficit in understanding and evaluating spatial relations between sounds. Their performance was strongly impaired compared with the sighted participants.

Figure 3c plots bisection thresholds against minimal audible angle for congenitally blind children. The two measures clearly correlate with each other (adj. $R^2 = 0.91$; $p < .001$), suggesting common mechanisms. However, the correlation cannot be explained by age, because the partial correlation coefficient with age factored out remained high ($r = .96$). Interestingly, reanalyzing the data of Gori, Sandini, Martinoli, & Burr (2010), we found no similar correlation between the thresholds of the two spatial tasks in blind adults (adj. $R^2 = 0$; $p = .43$).

Discussion

The results reported here are broadly in line with those of Gori et al. (2014), confirming that like adults, congenitally blind children have difficulties in processing spatial relationships between sounds (spatial bisection task). Unlike adults, however, the blind children were also significantly worse than sighted controls in the simpler minimal audible angle task, but the difference was much less: 50% rather than 400%. These results are in line with electrophysiological studies showing that early visual deprivation (by dark rearing) causes disordered development of auditory spatial maps in the superior colliculus of cats and ferrets (King, 1999; King & Carlile, 1993; King, Schnupp, & Thompson, 1998).

Interestingly, performance in the two tasks were highly correlated in the congenitally blind children, but not in adults. This suggests that there may be a generalized auditory spatial deficit in the developing individual, which changes into a distinctive deficit restricted to complex auditory spatial configuration in the adult age. The correlation could not be explained by chronological age, suggesting differential development in these children.

Ashmead et al. (1998) reported that blind children localized sound sources well, better than typical controls. However, the population of children tested in their study also comprised children who became blind at relatively old ages, and also many children with light perception or even pattern vision and they ranged in age from 6 to 20 years. In our study, we have only tested young congenitally blind children to clarify the importance of visual exposure in the first period of life for auditory spatial perception and to explore possible difference localization abilities between children and adults.

These results may seem to contrast with studies reporting higher precision and accuracy for blind individuals in localization of single sound sources (Lessard et al., 1998; Roder et al., 1999). However, in our previous study (Gori et al., 2014) we confirmed that in simple localization tasks blind adults were no worse than sighted controls. The current study suggests that younger blind children also show deficits in minimal audible angle, but this is not at odds with the literature.

How can we explain the poorer thresholds in the blind? Elsewhere we have argued that a fundamental role for cross-sensory interactions is cross-sensory calibration (Burr & Gori, 2012; Gori, Del Viva, Sandini, & Burr, 2008; Gori, Sandini, et al., 2012; Gori et al., 2010). In the case of vision and audition, there is considerable evidence that for spatial localization, the visual system calibrates audition. This was first shown by Knudsen and Knudsen (1989) by rearing young owls with distorting prisms: auditory localization became aligned with the distorted visual sense, and the effect persisted for some time even after removal of the prisms. Auditory spatial mislocalization has also been demonstrated in humans, after adapting for relatively short periods to nonaligned audio-visual stimuli (Recanzone, 1998; Zwiers et al., 2003).

A clear prediction of the cross-sensory calibration hypothesis is that when the perceptual system responsible for the calibration is compromised (in this case, vision), this will impact on the system to be calibrated (auditory space perception). Thus, despite the fact that blind adults often show enhanced sensory capacities in other modalities (Doucet et al., 2005; Goldreich & Kanics, 2003; Lessard et al., 1998; Roder et al., 1999), if the auditory spatial map is not well calibrated we may expect it to be compromised, both in children and in adults. We show that thresholds are considerably compromised, particularly for spatial bisection, where it is necessary to build up a spatial representation of three distinct stimuli over the course of the trial, and determine their spatial relationships. It is interesting that in the younger age group, even the simple spatial discrimination was compromised compared with the sighted group, but the deficit was far less than for the bisection. That this difference disappears in adulthood suggests that, while cross-sensory calibration from vision is paramount, even in the absence of vision some improvement in auditory spatial representation is possible, at least for the more simple tasks.

The results of this study fit well with other research from our group. We have previously shown specific deficits in blind children, deficits in haptically judging the orientation of stimuli, but not their size (Gori et al., 2010). Again, this was a direct prediction of a developmental study showing that in young children, the haptic system dominates visuo-haptic size perception while vision dominates visuo-haptic orientation perception (Gori et al., 2008). Conversely, we showed that patients suffering from cerebral palsy, with compromised haptic perception, showed poorer thresholds for visual size, but not orientation judgments (Gori, Tinelli, Sandini, Cioni, & Burr, 2012).

A developmental study by Gori et al. (2012) reported auditory dominance in children for temporal discrimination, and visual dominance for spatial discrimination, rather than audio-visual integration (as is observed in adults: (Alais & Burr, 2004)). We attributed the dominance to sensory calibration, which precludes multisensory integration. The idea that the visual modality is the best candidate for cross-sensory calibration in the spatial domain is also supported by the phenomenon of the “ventriloquist effect” (Mateeff, Hohnsbein, & Noack, 1985; Warren, Welch, & McCarthy, 1981), in which the capture of sound by vision has been explained by sensory cue integration, where the cue is weighted on the statistical reliability (Alais & Burr, 2004).

Although unsighted children were significantly worse than sighted children in both the spatial tasks, they showed similar performance in the temporal bisection task. This is an interesting control experiment, as it shows that the spatial deficit did not result from a difficulty in understanding the task. It also shows that the auditory deficits in the blind are specific to spatial localization, not to all aspects of audition. Audition is more precise than vision in temporal judgments, in both adults (Burr, Banks, & Morrone, 2009) and children (Gori, Sandini, et al., 2012), so should not suffer from lack of vision. This result agrees with many other studies showing that several auditory skills, including pitch discrimination and auditory memory, are not disrupted in the blind, and may even be enhanced (Gougoux et al., 2004; Röder, Rösler, & Neville, 2001).

A good deal of previous research has reported haptic spatial deficits in congenitally blind children. For example, Millar (1976) reported severe impairment in blind children from 6–11 years of age in mental rotation tests. Moreover, Puspitawati et al. (2014) reported that blind children younger than 10 years of age had difficulties in understanding part-whole relationship in haptic perception, with local strategies predominating over holistic strategies. Results from our study confirm the spatial deficit in congenital blind children reporting, for the first time, a strong impairment also in the auditory modality.

One possible explanation for the poorer performance on the spatial tasks, particularly spatial bisection (which requires integration of information over 1 s) may be that the blind have compromised spatial memory. This hypothesis receives support from previous research reporting difficulties in blind adults in the simultaneous processing of multiple representations (Puspitawati et al., 2014) and in blind children in spatial recalling (Millar, 1976). However, it is unlikely that the blind suffer from a generalized lack of sensory memory, as they showed no compromise in the temporal bisection task. Nevertheless, the notion of spatial memory in the blind is a very interesting issue that deserves further investigation.

While the visual system handles multiple sources of information and represents object position in external frames of reference, the auditory system probably does not use landmarks or marked boundaries. Thus visual information might provide a contextual frame of reference to encode stimuli in allocentric (relative to external objects), rather than egocentric (relative to the observer), coordinates (Pasqualotto & Proulx, 2012). This hypothesis is supported by the fact that blind individuals fail to estimate spatial relationship between objects (Postma, Zuidhoek, Noordzij, & Kappers, 2008; Vecchi, Tinti, & Cornoldi, 2004). For example, their spatial perception seems to be based on route knowledge rather than absolute representation (Bigelow, 2001). Moreover, they do not remap tactile stimuli into external frames of references modulated by visual input (Röder, Rösler, & Spence, 2004). The spatial tasks that we used in our study required estimation of spatial relations between sounds. In particular, to perform the space bisection task subjects have to evaluate the location of a sound source in an external reference frame characterized by the two standard sounds. The minimum audible angle task, on the contrary, does not necessarily require an external frame of reference, because participants only had to report which sound was located more to the right, for which they could use their body as a reference. Possibly,

during the development, blind individuals learn how to compensate for a lacking allocentric localization by substituting with an egocentric frame.

Clarifying the effects of visual deprivation on spatial abilities is obviously of benefit in understanding and eventually helping blind people function well in the world. Our study furnishes new evidence that cross-sensory calibration is important for normal perceptual development, and encourages new technological approaches for aiding the blind.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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References

- Alais D, Burr D. The ventriloquist effect results from near-optimal bimodal integration. *Current Biology*. 2004; 14:257–262. DOI: 10.1016/j.cub.2004.01.029 [PubMed: 14761661]
- Ashmead DH, Wall RS, Ebinger KA, Eaton SB, Snook-Hill MM, Yang X. Spatial hearing in blind children with visual disabilities. *Perception*. 1998; 27:105–122. [PubMed: 9692091]
- Bigelow A. Blind and sighted children’s spatial knowledge of their home environments. *International Journal of Behavioural Development*. 2001; 19:797–816. DOI: 10.1177/016502549601900407
- Burr D, Banks MS, Morrone MC. Auditory dominance over vision in the perception of interval duration. *Experimental Brain Research*. 2009; 198:49–57. DOI: 10.1007/s00221-009-1933-z [PubMed: 19597804]
- Burr, D.; Gori, M. Multisensory integration develops late in humans. The neural bases of multisensory processes. Murray, MM.; Wallace, MT., editors. Boca Raton, FL: Taylor & Francis; 2012. p. 345-362.
- Cohen LG, Celnik P, Pascual-Leone A, Corwell B, Falz L, Dambrosia J, Hallett M. Functional relevance of cross-modal plasticity in blind humans. *Nature*. 1997; 389:180–183. DOI: 10.1038/38278 [PubMed: 9296495]
- Collignon O, Dormal G, Albouy G, Vandewalle G, Voss P, Phillips C, Lepore F. Impact of blindness onset on the functional organization and the connectivity of the occipital cortex. *Brain: A Journal of Neurology*. 2013; 136:2769–2783. DOI: 10.1093/brain/awt176 [PubMed: 23831614]
- Collignon O, Vandewalle G, Voss P, Albouy G, Charbonneau G, Lassonde M, Lepore F. Functional specialization for auditory-spatial processing in the occipital cortex of congenitally blind humans. *PNAS Proceedings of the National Academy of Sciences of the United States of America*. 2011; 108:4435–4440. DOI: 10.1073/pnas.1013928108
- Collignon O, Voss P, Lassonde M, Lepore F. Cross-modal plasticity for the spatial processing of sounds in visually deprived subjects. *Experimental Brain Research*. 2009; 192:343–358. DOI: 10.1007/s00221-008-1553-z [PubMed: 18762928]
- Doucet ME, Guillemot JP, Lassonde M, Gagné J-P, Leclerc C, Lepore F. Blind subjects process auditory spectral cues more efficiently than sighted individuals. *Experimental Brain Research*. 2005; 160:194–202. DOI: 10.1007/s00221-004-2000-4 [PubMed: 15309355]
- Elbert T, Sterr A, Rockstroh B, Pantev C, Müller MM, Taub E. Expansion of the tonotopic area in the auditory cortex of the blind. *The Journal of Neuroscience*. 2002; 22:9941–9944. [PubMed: 12427851]
- Goldreich D, Kanics IM. Tactile acuity is enhanced in blindness. *The Journal of Neuroscience*. 2003; 23:3439–3445. [PubMed: 12716952]

- Goodale MA, Milner AD. Separate visual pathways for perception and action. *Trends in Neurosciences*. 1992; 15:20–25. DOI: 10.1016/0166-2236(92)90344-8 [PubMed: 1374953]
- Gori M, Del Viva M, Sandini G, Burr DC. Young children do not integrate visual and haptic form information. *Current Biology*. 2008; 18:694–698. DOI: 10.1016/j.cub.2008.04.036 [PubMed: 18450446]
- Gori M, Sandini G, Burr D. Development of visuo-auditory integration in space and time. *Frontiers in Integrative Neuroscience*. 2012; 6:77.doi: 10.3389/fnint.2012.00077 [PubMed: 23060759]
- Gori M, Sandini G, Martinoli C, Burr D. Poor haptic orientation discrimination in nonsighted children may reflect disruption of cross-sensory calibration. *Current Biology*. 2010; 20:223–225. DOI: 10.1016/j.cub.2009.11.069 [PubMed: 20116249]
- Gori M, Sandini G, Martinoli C, Burr DC. Impairment of auditory spatial localization in congenitally blind human subjects. *Brain: A Journal of Neurology*. 2014; 137:288–293. DOI: 10.1093/brain/awt311 [PubMed: 24271326]
- Gori M, Tinelli F, Sandini G, Cioni G, Burr D. Impaired visual size-discrimination in children with movement disorders. *Neuropsychologia*. 2012; 50:1838–1843. DOI: 10.1016/j.neuropsychologia.2012.04.009 [PubMed: 22569216]
- Gougoux F, Lepore F, Lassonde M, Voss P, Zatorre RJ, Belin P. Neuropsychology: Pitch discrimination in the early blind. *Nature*. 2004; 430:309.doi: 10.1038/430309a
- Gougoux F, Zatorre RJ, Lassonde M, Voss P, Lepore F. A functional neuroimaging study of sound localization: Visual cortex activity predicts performance in early-blind individuals. *PLoS Biology*. 2005; 3:e27.doi: 10.1371/journal.pbio.0030027 [PubMed: 15678166]
- King AJ. Sensory experience and the formation of a computational map of auditory space in the brain. *BioEssays*. 1999; 21:900–911. DOI: 10.1002/(SICI)1521-1878(199911)21:11<900::AID-BIES2>3.0.CO;2-6 [PubMed: 10517863]
- King AJ, Carlile S. Changes induced in the representation of auditory space in the superior colliculus by rearing ferrets with binocular eyelid suture. *Experimental Brain Research*. 1993; 94:444–455. DOI: 10.1007/BF00230202 [PubMed: 8359258]
- King AJ, Schnupp JW, Thompson ID. Signals from the superficial layers of the superior colliculus enable the development of the auditory space map in the deeper layers. *The Journal of Neuroscience*. 1998; 18:9394–9408. [PubMed: 9801378]
- Kingdom, FAA.; Prins, N. *Psychophysics: A practical introduction*. London, UK: Academic Press; 2010.
- Knudsen EI, Brainard MS. Visual instruction of the neural map of auditory space in the developing optic tectum. *Science*. 1991; 253:85–87. DOI: 10.1126/science.2063209 [PubMed: 2063209]
- Knudsen EI, Knudsen PF. Visuomotor adaptation to displacing prisms by adult and baby barn owls. *The Journal of Neuroscience*. 1989; 9:3297–3305. [PubMed: 2795163]
- Lessard N, Paré M, Lepore F, Lassonde M. Early-blind human subjects localize sound sources better than sighted subjects. *Nature*. 1998; 395:278–280. DOI: 10.1038/26228 [PubMed: 9751055]
- Mateeff S, Hohnsbein J, Noack T. Dynamic visual capture: Apparent auditory motion induced by a moving visual target. *Perception*. 1985; 14:721–727. DOI: 10.1068/p140721 [PubMed: 3837873]
- Millar S. Spatial representation by blind and sighted children. *Journal of Experimental Child Psychology*. 1976; 21:460–479. DOI: 10.1016/0022-0965(76)90074-6 [PubMed: 939949]
- Pasqualotto A, Proulx MJ. The role of visual experience for the neural basis of spatial cognition. *Neuroscience & Biobehavioral Reviews*. 2012; 36:1179–1187. DOI: 10.1016/j.neubiorev.2012.01.008 [PubMed: 22330729]
- Postma A, Zuidhoek S, Noordzij ML, Kappers AM. Haptic orientation perception benefits from visual experience: Evidence from early-blind, late-blind, and sighted people. *Perception & Psychophysics*. 2008; 70:1197–1206. DOI: 10.3758/PP.70.7.1197
- Puspitawati I, Jebrane A, Vinter A. Local and global processing in blind and sighted children in a naming and drawing task. *Child Development*. 2014; 85:1077–1090. DOI: 10.1111/cdev.12158 [PubMed: 24016216]
- Rauschecker JP. Compensatory plasticity and sensory substitution in the cerebral cortex. *Trends in Neurosciences*. 1995; 18:36–43. DOI: 10.1016/0166-2236(95)93948-W [PubMed: 7535489]

- Recanzone GH. Rapidly induced auditory plasticity: The ventriloquism aftereffect. *PNAS Proceedings of the National Academy of Sciences of the United States of America*. 1998; 95:869–875. DOI: 10.1073/pnas.95.3.869
- Röder B, Rösler F, Neville HJ. Auditory memory in congenitally blind adults: A behavioral-electrophysiological investigation. *Cognitive Brain Research*. 2001; 11:289–303. DOI: 10.1016/S0926-6410(01)00002-7 [PubMed: 11275490]
- Röder B, Rösler F, Spence C. Early vision impairs tactile perception in the blind. *Current Biology*. 2004; 14:121–124. DOI: 10.1016/j.cub.2003.12.054 [PubMed: 14738733]
- Röder B, Teder-Sälejärvi W, Sterr A, Rösler F, Hillyard SA, Neville HJ. Improved auditory spatial tuning in blind humans. *Nature*. 1999; 400:162–166. DOI: 10.1038/22106 [PubMed: 10408442]
- Van Boven RW, Hamilton RH, Kauffman T, Keenan JP, Pascual-Leone A. Tactile spatial resolution in blind braille readers. *Neurology*. 2000; 54:2230–2236. DOI: 10.1212/WNL.54.12.2230 [PubMed: 10881245]
- Vecchi T, Tinti C, Cornoldi C. Spatial memory and integration processes in congenital blindness. *Neuroreport*. 2004; 15:2787–2790. [PubMed: 15597055]
- Voss P, Lassonde M, Gougoux F, Fortin M, Guillemot JP, Lepore F. Early- and late-onset blind individuals show supra-normal auditory abilities in far-space. *Current Biology*. 2004; 14:1734–1738. DOI: 10.1016/j.cub.2004.09.051 [PubMed: 15458644]
- Voss P, Zatorre RJ. Organization and reorganization of sensory-deprived cortex. *Current Biology*. 2012; 22:R168–R173. DOI: 10.1016/j.cub.2012.01.030 [PubMed: 22401900]
- Wallace MT, Stein BE. Development of multisensory neurons and multisensory integration in cat superior colliculus. *The Journal of Neuroscience*. 1997; 17:2429–2444. [PubMed: 9065504]
- Warren DH, Welch RB, McCarthy TJ. The role of visual-auditory “compellingness” in the ventriloquism effect: Implications for transitivity among the spatial senses. *Perception & Psychophysics*. 1981; 30:557–564. DOI: 10.3758/BF03202010
- Watson AB, Pelli DG. QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics*. 1983; 33:113–120. DOI: 10.3758/BF03202828 [PubMed: 6844102]
- Withington-Wray DJ, Binns KE, Dhanjal SS, Brickley SG, Keating MJ. The maturation of the superior collicular map of auditory space in the guinea pig is disrupted by developmental auditory deprivation. *The European Journal of Neuroscience*. 1990; 2:693–703. DOI: 10.1111/j.1460-9568.1990.tb00459.x [PubMed: 12106287]
- Wong M, Gnanakumaran V, Goldreich D. Tactile spatial acuity enhancement in blindness: Evidence for experience-dependent mechanisms. *The Journal of Neuroscience*. 2011; 31:7028–7037. DOI: 10.1523/JNEUROSCI.6461-10.2011 [PubMed: 21562264]
- Zwiers MP, Van Opstal AJ, Cruysberg JR. A spatial hearing deficit in early-blind humans. *Journal of Neuroscience*. 2001; 21:141–145.
- Zwiers MP, Van Opstal AJ, Paige GD. Plasticity in human sound localization induced by compressed spatial vision. *Nature Neuroscience*. 2003; 6:175–181. DOI: 10.1038/nn999 [PubMed: 12524547]

Figure 1.

The speaker array used in this experiment (left panel). (a) Space bisection task. Three sounds were presented in sequence, at 500 ms intervals: the first and the third at -25° and $+25^\circ$, respectively, the second (the probe) over a 23° range between these two. Participants reported whether the location of the probe stimulus sounded spatially closer to the first or the third sound. (b) Minimum audible angle task. Two auditory stimuli were presented: the standard always at 0° , and the probe ranging over $\pm 25^\circ$ of visual angle. Participants reported which of the two sounds was located more to the right side of space. (c) Temporal bisection task. Three sounds were presented from a central speaker. Subjects reported whether the second stimulus appeared temporally closer to the first or to the third. The total duration of the stimulation was 1000 ms.

Figure 2.

Geometric mean for blind (gray bars) and sighted (black bars) children for the three tasks: (a) space bisection, (b) minimum audible angle, and (c) temporal bisection. Thresholds are higher for congenitally blind than those of sighted children in both the spatial tasks especially in the space bisection, while there are no differences between the two groups in the temporal bisection.

Figure 3.

Individual thresholds. (a) Thresholds for space bisection as a function of age. Each gray filled symbol represents an individual blind child (the inverted triangle represents the 11-year-old child with low residual vision). Gray empty circles represent the geometric means of congenitally blind adults from Gori et al. (2014), and black symbols represent the geometric means of sighted participants. Arrows show average thresholds for each group of subjects: black and gray external arrows for sighted and blind adults and black and gray internal arrows for the sighted and blind children. Average thresholds for all the blind participants are far higher than those of young and adult sighted participants. (b) Thresholds for minimum audible angle, as a function of age. Conventions as for (a). (c) Space bisection thresholds plotted against minimum audible angle, for the congenitally blind (symbol code as above). The black dashed line shows the linear fit to the data (give numbers here).