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Early visual deprivation prompts the use of body-centered frames of reference for auditory localization

Tiziana Vercillo[a,*], Alessia Tonelli[b], Monica Gori[b]

[a] Department of Psychology, University of Nevada, Reno, NV, United States
[b] U-VIP Unit for Visually Impaired People, Fondazione Istituto Italiano di Tecnologia, via Morego 30, 16163 Genoa, Italy

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ABSTRACT

The effects of early visual deprivation on auditory spatial processing are controversial. Results from recent psychophysical studies show that people who were born blind have a spatial impairment in localizing sound sources within specific auditory settings, while previous psychophysical studies revealed enhanced auditory spatial abilities in early blind compared to sighted individuals. An explanation of why an auditory spatial deficit is sometimes observed within blind populations and its task-dependency remains to be clarified. We investigated auditory spatial perception in early blind adults and demonstrated that the deficit derives from blind individual's reduced ability to remap sound locations using an external frame of reference. We found that performance in blind population was severely impaired when they were required to localize brief auditory stimuli with respect to external acoustic landmarks (external reference frame) or when they had to reproduce the spatial distance between two sounds. However, they performed similarly to sighted controls when had to localize sounds with respect to their own hand (body-centered reference frame), or to judge the distances of sounds from their finger. These results suggest that early visual deprivation and the lack of visual contextual cues during the critical period induce a preference for body-centered over external spatial auditory representations.

1. Introduction

Several studies suggest that after visual deprivation the brain might improve the sensitivity of the remaining sensory systems to compensate for the lack of visual information. Indeed, people who were born blind can localize single sound sources on the horizontal plane with similar or even higher precision than sighted individuals (Lessard, Paré, Lepore, & Lassonde, 1998; Röder et al., 1999; Voss et al., 2004). Moreover, they are more sensitive to auditory spectral cues (Doucet et al., 2005), which are particularly important for sound localization on the vertical plane. It is possible that changes in auditory perception are intrinsically linked to a cortical reorganization of the visual cortex that, following sensory loss, is recruited by the remaining sensory modalities (Collignon et al., 2013). After deprivation, occipital areas preserve their functional selectivity, although it is conveyed by a different sensory input (i.e. audition, touch), showing a task-specific sensory-independent organization (Amedi, Hofstetter, Maidenbaum, & Heimler, 2017; Heimler, Striem-Amit, & Amedi, 2015). These brain regions are activated by auditory stimuli and responses in these areas to auditory stimuli appear to be organized in a topographic manner (Amedi, Merabet, Bermpohl, & Pascual-Leone, 2005; Collignon et al., 2011, 2013; Collignon, Voss, Lassonde, & Lepore, 2009; Rauschecker, 1995; Voss & Zatorre, 2012). Cortical reorganization highlights the plastic properties of the brain that can compensate for visual loss by possibly improving auditory spatial localization.

Interestingly, recent studies showed that early blind individuals fail in localizing sounds under particular auditory settings (Cappagli, Cocchi, & Gori, 2015; Finocchietti, Cappagli, & Gori, 2015; Gori, Sandini, Martinoli, & Burr, 2014; Vercillo, Burr, & Gori, 2016; Vercillo, Milne, Gori, & Goodale, 2015; Vercillo, Tonelli, & Gori, 2017; Voss, Tabry, & Zatorre, 2015; Wanet, Veraart, & Wanet, 1985). Gori et al. (2014) found a severe auditory spatial impairment in blind as compared to sighted individuals in the space bisection task, which requires the localization of an auditory stimulus relative to two other sounds. Remarkably, blind individuals performed similar to sighted controls in the minimum audible angle task, where after listening to a sequence of two sounds coming from two different spatial locations, they had to report which one of the two was located more on the right side (in agreement with previous results, see Collignon et al., 2013). A similar spatial deficit has been reported in blind children from 9 to 14 years of age (Vercillo et al., 2016) suggesting that early visual deprivation might lead to task-specific auditory deficits. However, the nature and the role

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* Corresponding author.
E-mail address: tizianavercillo@hotmail.it (T. Vercillo).

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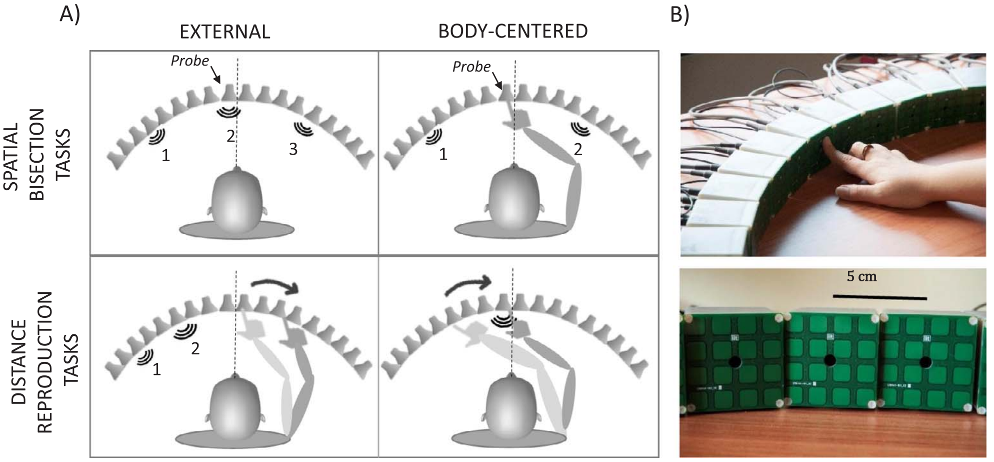

Fig. 1. (A) The upper two panels show experimental procedure for the spatial bisection tasks. In the external condition (left panel), a sequence of 3 sounds was presented and participants had to report whether the second sound was closer to the first or to the third. In the body-centered condition (right panel), participant's hand was placed on a specific speaker and a sequence of 2 sounds was presented. Participants had to report whether their finger was closer to the first or to the second sound. The lower two panels show the distance reproduction tasks. In the external condition, participant's finger was placed on a central speaker (the light grey hand shows the initial hand position) and a sequence of 2 sounds was presented on the left side of the setup. Participants reproduced the distance between the two sounds using their finger (the dark grey hand shows the final hand position). In the body-centered condition, participant's finger was placed on a speaker (like the one indicated by the light grey hand) and a sound was presented on the right side of the setup. Participants reproduced the distance between their finger and the sound using their finger (the dark grey hand shows the final hand position). (B) An image of the speakers used for the experiment.

of the impaired auditory spatial processing remains unclear.

Task-specific differences in auditory spatial processing might be related to a diverse use of body-centered and external frames of reference in early blind individuals. The spatial auditory processing relies on a variety of binaural cues and for this reason, sounds are primarily represented in head and ear-centered frames of reference. Such spatial representations of sounds are successively transformed (spatial remapping). Initially, sounds' locations are related to the eyes, facilitating the spatial alignment between auditory and visual stimuli (Cohen & Andersen, 2002; Jay & Sparks, 1987). Neurons in the lateral intraparietal area (LIP) and in the parietal reach region (PRR) encode the locations of auditory and visual stimuli in a common eye-centered reference frame (Cohen & Andersen, 2002; Deneve, Latham, & Pouget, 2001). Similarly, bimodal neurons in the superior colliculus have spatially aligned visual and auditory receptive fields and use eye-centered coordinates to specify the locations of visual and auditory stimuli (Hartline, Vimal, King, Kurylo, & Northmore, 1995; Andrew J King, 2004; Peck, Baro, & Warder, 1995). Afterward, the positions of auditory stimuli are linked to external objects (external frames of references), supporting integration across all the sensory modalities, guaranteeing perceptual constancy despite body movements, and facilitating sensory-motor interaction. External frames of reference provide spatial information for the coordinated movement of multiple effectors and for this reason, are crucial to guide actions (Cohen & Andersen, 2002). In an EEG study, Schechtman, Shrem, and Deouell (2012) revealed that the auditory cortex represents at the same time head-related and world-related reference frames, supporting the idea that sounds are represented under multiple spatial representations (Hartline et al., 1995; Jay & Sparks, 1984; Andrew J King, 2004). Without visual stimulation and without a visual representation of landmarks and marked boundaries, the spatial remapping into an external, world-centered frame of reference may not occur. Recent studies support this idea showing that the remapping of auditory and proprioceptive inputs into external coordinates is acquired during development as a consequence of visual input (Röder, Kusmierek, Spence, & Schicke, 2007) and that blind individuals are not subject to the "crossed hand illusion" (Röder, Rösler, & Spence, 2004) as they do not perceive the conflict between anatomical and external reference frames.

If the contribution of vision is crucial for the spatial remapping of sounds in external coordinates, we should expect a deficit in the early blind population for the localization of sounds in external frames of reference, but no impairment during the localization of sound sources with respect to the body (body-centered coordinates). In the present study, sighted and blind participants performed multiple spatial auditory tasks in different reference frames. By comparing their performances, we investigated whether the spatial auditory deficit previously reported in early blind individuals results from a failure in the activation of an external coordinate system and a preference for a body-centered frame of reference for sound localization.

2. Methods

2.1. Participants

We tested eight early blind (3 males, 5 females, mean age: 40.12 ± 6 years of age) and ten sighted individuals (5 males, 5 females, mean age: 34.7 ± 6 years of age). Age did not differ significantly between the two groups of participants (2-tailed independent sample *t*-test; $t_{15} = -1.16$, $p = .26$). Additional details about the age, pathology and residual vision of the blind participants are reported in the supplemental material (Table 1). All participants signed written informed consents in accordance with the Declaration of Helsinki. For the blind participants, the document was read by the experimenter and the location to sign was indicated with tactile markers. The study was approved by the ethics committee of the local health service (Comitato Etico, ASL3 Genovese, Italy).

2.2. Setup and stimuli

Participants sat in the middle of an array of 18 speakers arranged in an arc and positioned on a table. We considered the center of the array as the 0 value. Nine speakers were positioned to the right at the following positions: +5, +10, +15, +20, +25, +30, +35, +40 and +45 cm (positive values indicate rightward positions). The other nine speakers were located on the left side, at the following positions: −5, −10, −15, −20, −25, −30, −35, −40 and −45 cm (negative values indicate leftward positions). By positioning speakers not at the ear level, we might have added reverberation and affected sound perception. On the other hand, reverberation should have equally impaired the performance of both group of participants, and not only that one of the blind group. Each speaker was located 57 cm from the participant. The auditory stimuli were 300 ms white noise bursts at 70 dB of sound pressure level. We recorded motor responses by using tactile sensors directly attached to the speaker surface (Fig. 1, right panel). The experimenter, who sited on the other side of the table in front of the participants, controlled for eventual head movements.

2.3. Tasks and procedures

Before starting the experiment, blind participants explored the setup tactually, and sighted participants visually. Sighted participants were blindfolded during the experiment. Participants completed two spatial