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A Framework to Account for the Effects of Visual Loss on Human Auditory Abilities

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Abstract

Until recently, a commonly held view was that blindness resulted in enhanced auditory abilities, underpinned by the beneficial effects of cross-modal neuroplasticity. This viewpoint has been challenged by studies showing that blindness results in poorer performance for some auditory spatial tasks. It is now clear that visual loss does not result in a general increase or decrease in all auditory abilities. Although several hypotheses have been proposed to explain why certain auditory abilities are enhanced while others are degraded, these are often limited to a specific subset of tasks. A comprehensive explanation encompassing auditory abilities assessed in fully blind and partially sighted populations and spanning spatial and non-spatial cognition has not so far been proposed. The current paper proposes a framework comprising a set of nine principles that can be used to predict whether auditory abilities are enhanced or degraded. The validity of these principles is assessed by comparing their predictions with a wide range of empirical evidence concerning the effects of visual loss on spatial and non-spatial auditory abilities. Developmental findings and the effects of early- versus late-onset visual loss are discussed. Ways of improving auditory abilities for individuals with visual loss and reducing auditory spatial deficits are summarized. A new Perceptual Restructuring Hypothesis is proposed within the framework, positing that the auditory system is restructured to provide the most accurate information possible given the loss of the visual signal and utilizing available cortical resources, resulting in different auditory abilities getting better or worse according to the nine principles.

Keywords: auditory; blindness; cross-modal; spatial; neural plasticity

Introduction

Visual loss affects a wide variety of abilities across the remaining intact senses. Many abilities are enhanced following blindness. This has been demonstrated with auditory (Hotting & Roder, 2009; Kolarik, Cirstea, Pardhan, & Moore, 2014a; Voss, 2019), tactile (Goldreich & Kanics, 2003; Van Boven, Hamilton, Kauffman, Keenan, & Pascualï Leone, 2000), and olfactory (Cuevas, Plaza, Rombaux, De Volder, & Renier, 2009) tasks. Blind people have also been reported to have an enhanced ability to discriminate small changes in heat (Slimani, Ptito, & Kupers, 2015). However, other abilities have been shown to be degraded following visual loss in the auditory (Gori, Sandini, Martinoli, & Burr, 2014) and tactile (Gori, Sandini, Martinoli, & Burr, 2010) domains. It appears that loss of vision does not lead to a general increase or decrease in abilities in the intact sensory domains. Instead, some abilities are enhanced and some are degraded, and whether performance is better or worse than ñnormalò appears to be task dependent. Although a number of explanations for why specific abilities change following visual loss have been put forward, as described later in this paper, the underlying principles of what drives changes in abilities following visual loss are not yet clear. Nor is it clear what characteristics of a given ability/task are associated with enhancement or degradation.

Auditory abilities, which are the focus of the current paper, are especially important to people with full and severe visual loss, who rely heavily on sound for navigating and exploring new environments and communicating and interacting with others. In the absence of vision, auditory cues provide spatial information about sound sources and sound-reflecting objects in extrapersonal space, the region beyond reaching distance. Visual loss does not seem to affect auditory performance for very basic detection or discrimination tasks, such as the detection of pure tones in quiet (Yabe & Kaga, 2005) or the detection of changes in intensity (Voss & Zatorre, 2011). However, blindness can have substantial effects on the accuracy of judgments of the azimuth, distance and elevation of sound sources, and the impact of blindness on auditory spatial abilities in particular has been the focus of considerable research (for reviews, see Hotting & Roder, 2009; Kolarik, Moore, Zahorik, Cirstea, & Pardhan, 2016a; Théoret, Merabet, & Pascual-Leone, 2004; Voss, 2016).

The perceptual deficiency hypothesis and the perceptual enhancement hypothesis

Two primary hypotheses have been put forward to account for how and why auditory abilities are either degraded or enhanced. These are the perceptual deficiency hypothesis and the perceptual enhancement hypothesis, respectively. First proposed around sixty years ago, these hypotheses have continued to shape modern interpretations of the effects of visual loss on hearing. The perceptual deficiency hypothesis (Axelrod, 1959; Jones, 1975) is specific to spatial processing, and posits that without an intact visual signal to accurately calibrate auditory information, performance for auditory spatial tasks will be poorer than normal. This hypothesis has been supported by studies showing that blind people show deficits in the construction of internal auditory spatial maps (Gori, et al., 2014; Lewald, 2002b; Zwiers, Van Opstal, & Cruysberg, 2001); these studies are described in more detail later in this paper. The perceptual deficiency hypothesis has been used to explain the poorer auditory performance of visually impaired people in judging elevation (Lewald, 2002b; Zwiers, et al., 2001) and absolute distance (Kolarik, Pardhan, Cirstea, & Moore, 2017a), and in a spatial bisection task, which involves presentation of three successive sounds in different locations, the participant being asked to judge whether the second sound is closer to the first or the third (Gori, et al., 2014). In contrast, the compensation or perceptual enhancement hypothesis (Rice, 1970) suggests that loss of or reduced visual input leads to greater reliance on and experience with the use of auditory information compared to fully sighted people, and this, combined with compensatory processes such as recruitment of visual areas of the brain for the processing of auditory information, leads to enhanced performance (Collignon, Voss, Lassonde, & Lepore, 2009; Dormal, Rezk, Yakobov, Lepore, & Collignon, 2016; Voss, 2016; Voss & Zatorre, 2012). The perceptual enhancement hypothesis has been used to explain results showing enhanced auditory performance following blindness for judgments of sound source azimuth (Lessard, Pare, Lepore, & Lassonde, 1998), frequency discrimination (Gougoux et al., 2004), distance discrimination (Kolarik, Cirstea, & Pardhan, 2013b; Voss et al., 2004) and detection of motion (Lewald, 2013).

The application of these hypotheses has been somewhat ad hoc. It is not clear which of the two hypotheses should be applicable to any specific auditory ability/task. If certain auditory abilities can be improved following visual loss via mechanisms such as cortical reorganization, the question arises as to why all auditory abilities are not improved. Similarly, if visual signals are required to accurately calibrate auditory spatial information, why are not all auditory spatial abilities degraded following visual loss? These issues are also faced by other explanations for changes in auditory abilities with visual loss. One such explanation is in terms of reference frames (for a review, see Voss, 2016). It has been suggested that blindness results in a reduced ability to use an allocentric reference frame, where external objects or the local environment are used as a spatial reference, and greater reliance on an egocentric reference frame that uses the body as a spatial reference (Gori, et al., 2014; Vercillo, Burr, & Gori, 2016; Vercillo, Milne, Gori, & Goodale, 2015; Wersenyi, 2012). However, this explanation is problematic since there is evidence that internal representations may be solely dependent on egocentric reference frames (Filimon, 2015). A more comprehensive framework is required to account for why some auditory abilities are enhanced and others are degraded. Such a framework could then be used to predict the effects of visual loss on auditory spatial abilities that have not yet been assessed.

We next propose a series of general principles that can be used to predict whether the ability to perform any specific task is enhanced or degraded by visual loss. We note that these may not apply in all cases, but that they apply in most. To assess the validity of these principles, we assess the extent to which the predictions are valid for a wide range of auditory abilities that have been assessed to date, including abilities for localizing both active sound sources and silent objects using echolocation, and speech, music and spectral processing. Developmental findings regarding the effects of visual loss on auditory abilities are described. The effects of early- and late-onset visual loss are described, and explanations are discussed regarding the origin of individual differences in auditory abilities in people with visual loss. Lastly, possible means of reducing auditory spatial deficits brought on by visual loss are discussed, and the importance of linking laboratory research to real-life applications is highlighted.

Proposed principles determining whether enhancement or degradation occurs following blindness

The proposed principles are described below. Each is denoted by P followed by a number, to facilitate later evaluation of the principles:

P1. *Complexity.* For changes in auditory ability (for better or worse) to occur as a result of blindness, the task must be complex.

P2. *Discrimination*. The ability to discriminate small changes in sounds is improved by blindness.

P3. *Detection*. The enhancement in discrimination ability is marked when the task only requires detection of a change.

P4. *Identifying the direction of monotonic change.* Enhancement will occur when the auditory cues involved change monotonically with the variable that is to be judged.

P5. *Identifying the direction of non-monotonic change.* Enhancement will occur if the relationship between the auditory cues and the variable that is to be judged has been learned; otherwise degradation will occur.

P6. *Calibration requiring visual cues.* Blindness results in degraded performance when lack of requisite visual calibration information leads to a less precise mapping of auditory cues to the quantity to be judged.

P7. *Calibration using non-visual cues.* Blindness leads to enhanced performance for auditory cues that can be calibrated without vision.

P8. *Experience and practise.* Prolonged experience and practise using auditory cues leads to superior auditory performance for blind people.

P9. *Age of onset*. Changes in auditory ability are greater the earlier in life that vision is lost.

The next section reviews auditory spatial abilities that are enhanced following full blindness, summarizes the linking characteristics between them, and assesses the extent to which the results are consistent with principles P1 to P9.

Auditory spatial abilities that are enhanced as a result of full blindness

Relative auditory distance perception

A number of studies have shown that blindness results in an enhanced ability to judge the relative distance of sounds, e.g. to judge which of two successive sounds is closer. Ashmead et al. (1998) assessed distance discrimination for pairs of Gaussian noise bursts presented at distances between 1.55 and 1.95 m in a reverberant environment. Blind children (a mixture of early and late-onset) were significantly better able to discriminate distance than groups of sighted children or sighted adults. Voss, et al. (2004) reported that early- and late- onset blind groups were able to discriminate the distances of pairs of broadband noises presented in a reverberant environment between 3 and 4 m from the participant, whereas sighted controls were unable to discriminate the distances of the noise bursts. Kolarik, et al. (2013b) assessed distance discrimination for pairs of broadband noise bursts presented between 1 and 8 m away in virtual anechoic and reverberant environments. The blind participants were better than sighted or partially sighted groups at using two the two main auditory distance cues, level and direct-to-reverberant energy ratio (DRR)(Kolarik, Cirstea, & Pardhan, 2013a; Kolarik, et al., 2016a; Zahorik, Brungart, & Bronkhorst, 2005), to discriminate distance. These findings are consistent with P1 (complexity), P2 (discrimination), and P4 (identifying the direction of monotonic change). Overall, the findings for relative auditory distance perception are consistent with the perceptual enhancement hypothesis. They are not consistent with the perceptual deficiency hypothesis.

Echolocation

Human echolocation is the ability to emit sounds and utilize the returning echoes to obtain information regarding silent objects in the vicinity, in a similar manner to bats and dolphins (for reviews, see Kolarik, et al., 2014a; Stoffregen & Pittenger, 1995; Thaler & Goodale, 2016). Within the blind population, those who echolocate often have real-life advantages, including higher salary and higher mobility in unfamiliar places, than those who are not echolocators (Thaler, 2013). Successful echolocation depends on the ability to produce appropriate signals, such as tongue clicks, and to detect and discriminate the sound reflections (Tirado, Lundén, & Nilsson, 2019). Although both sighted and blind people are able to echolocate, blind people display enhanced skills for several aspects of echolocation, including object detection (Kolarik, Scarfe, Moore, & Pardhan, 2017c; Rice, 1969) and localization (Rice, 1969; Schenkman & Nilsson, 2010, 2011), discrimination of the spatial positions of two disks (Teng & Whitney, 2011), discrimination of object material or texture (but not density, Hausfeld, Power, Gorta, & Harris, 1982; Kellogg, 1962), judgment of size and distance (Kellogg, 1962), and shape (Hausfeld, et al., 1982), and when using sound to navigate around obstacles (Kolarik, et al., 2017c) or to walk in a straight line parallel to a wall (Strelow & Brabyn, 1982). Blind people are also more sensitive than sighted controls to non-self-generated sound echoes (Dufour, Després, & Candas, 2005; Kolarik, et al., 2013b).

Teng and Whitney (2011) showed that early-onset blindness enhanced spatial acuity for echolocation compared to sighted people. They used an auditory version of the visual Vernier acuity task to measure the spatial resolution of echolocation. Participants were presented with two vertically separated disks, at various horizontal center-to-center offsets, and were required to report if the top disk was positioned to the left or right of the bottom disk. Participants were an early-onset blind expert echolocator, and a group of sighted participants trained in the task until they reached asymptotic performance. The blind expert showed the best performance, but some sighted controls showed spatial resolution that approached that of the blind expert.

Schenkman and Nilsson (2010) played recorded bursts of noise to blind (a mix of early and late-onset) and sighted participants with an aluminum disk present at distances between 0.5-5 m, or with the disk absent. Blind participants were better able to detect the presence of the disk than sighted participants. Possible cues were: (1) the overall level was higher when the disk was present; (2) the interaction of the direct sound and the reflected sound from the disk produced spectral and temporal cues that evoked a pitch percept. In a follow-up study Schenkman and Nilsson (2011) showed that a mix of early and late-onset blind participants performed better than sighted participants when only the pitch cue was present but not when only the level cue was present, suggesting the importance of spectral and temporal information for blind people when detecting objects using echolocation.

Nilsson and Schenkman (2016) measured discrimination thresholds for interaural time differences (ITDs) and interaural level differences (ILD) in click sounds for sighted and blind people (a mix of early and late-onset blind). They included sounds with two successive clicks, simulating a leading sound and an echo, and the ITD and ILD were changed either for the leading sound or the lagging sound. ITD and ILD sensitivity were greater for the blind group than for age-matched controls in all conditions.

Schenkman, Nilsson, and Grbic (2016) measured sensitivity for detecting echoes using sounds recorded in a reverberant room, via an artificial binaural head with a loudspeaker emitting sounds from 1 m behind the head and with an aluminium disk 1 m in front of the head either present or absent. Stimuli were brief bursts of noise presented at rates from 1 to 64 bursts within 500 ms or a single 500-ms burst. Participants had to report which of two sounds, one with the disc present and one with it absent, contained an echo. The blind participants (a group with a mix of early and late-onset blindness) performed better than the sighted controls for all burst rates and for the 500-ms burst.

Kolarik, et al. (2017c) investigated the kinematics of obstacle circumvention for an early-onset blind echolocation expert, an early-onset blind group untrained in echolocation, and a sighted control group. Participants were blindfolded and had to detect and navigate around an obstacle using echolocation clicks. The obstacle was placed in a random location at the midline of the participant or to the left or right, at a distance of 1.5 or 2 m, or was absent. Blind non-echolocators navigated significantly more effectively than blindfolded sighted controls, as shown by a greater obstacle detection range, fewer collisions, lower movement times, and fewer velocity corrections (number of stops and starts, a measure of how fluid the movement is). The blind expert echolocator showed performance similar to or better than for the other groups, although the differences were not significant. The results suggest that blind people develop enhanced abilities to process sound echoes and these can be used to enhance locomotor performance, resulting in more accurate, faster and more fluid navigation using echolocation, even without extensive training or experience.

Thaler, Zhang, Antoniou, Kish, and Cowie (2020) also investigated obstacle circumvention using echolocation, and compared groups of blind expert echolocators, blind echolocation beginners, and blindfolded sighted non-echolocators. The blind groups were a mix of early and late-onset participants. In contrast to Kolarik, et al. (2017c), there were no significant differences in performance between sighted controls and blind echolocation beginners, for number of collisions, movement speed, or walking paths, but blind experts showed better performance on these measures than the other groups. The findings of Kolarik, et al. (2017c) suggest that long-term blindness itself leads to enhanced performance, whereas the findings of Thaler, et al. (2020) suggest that it is expertise, or expertise combined with blindness, that leads to enhanced performance. However, there were a number of methodological differences between the two studies that may have contributed to the differences in findings. Kolarik, et al. (2017c) utilized an obstacle covered by reflective foil to give strong echoes, whereas Thaler, et al. (2020) used a polystyrene obstacle coated with primer that probably led to less distinct echoes. Also, Thaler, et al. (2020) did not move the obstacle in the lateral direction and analyzed all trials, including collisions, whereas Kolarik, et al. (2017c) only analyzed successful (non-collision) trials. Further work is needed to clarify when enhanced sensitivity to sound echoes arising from blindness is associated with advantages in sensory-motor coordination. It is clear that the extensive experience of blind expert echolocators leads to improved performance when using echolocation for spatial tasks

(Arnott, Thaler, Milne, Kish, & Goodale, 2013; Milne, Arnott, Kish, Goodale, & Thaler, 2015; Teng, Puri, & Whitney, 2012; Teng & Whitney, 2011; Thaler, et al., 2020).

Overall, the results described in this section are consistent with P1 (complexity), P2 (discrimination), P8 (experience and practise), and the perceptual enhancement hypothesis.

Sound localization in azimuth

Auditory cues to azimuth can in principle be calibrated without visual information. For example, a blind person may be able to feel the position of a nearby sound source such as a radio. Also, for a sound source that is fixed in azimuth, the person can rotate their head to sample how the cues change with azimuth. Under these conditions, blindness may lead to enhanced performance (P5), but only if accurate calibration has been achieved. Several studies have shown that judgments of sound azimuth are indeed enhanced as a result of blindness (Després, Boudard, Candas, & Dufour, 2005a; Muchnik, Efrati, Nemeth, Malin, & Hildesheimer, 1991; Rice, 1969). This enhancement is often evident only in specific conditions, such as when listening monaurally (Doucet et al., 2005; Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005; Lessard, et al., 1998; Voss, Lepore, Gougoux, & Zatorre, 2011; Voss, Tabry, & Zatorre, 2015) or towards the side (Fieger, Röder, Teder-Sälejärvi, Hillyard, & Neville, 2006; Röder et al., 1999; Voss, et al., 2004) or back (Després, et al., 2005a). Several studies showed enhanced performance for approximately half of their blind participants only. A possible explanation for this was investigated by Voss, et al. (2015) and is discussed in more detail later in this paper.

Lessard, et al. (1998) asked participants to judge the location of broad-band noise bursts presented binaurally or monaurally (by plugging one ear) at azimuths between 0° and ±78° to sighted participants and participants with congenital visual loss who either had residual vision or were totally blind. In the monaural condition, half of the totally blind group showed highly accurate performance and localized the stimuli on the appropriate side of the head, suggesting a good ability to use monaural spectral cues for judgments of azimuth. Sighted controls, blind participants with residual vision, and half of the totally blind group showed poor performance and a bias to localize the stimuli on the side of the non-plugged ear. There were no significant differences in localization between sighted and totally blind groups under binaural conditions.

Later studies have confirmed that blind participants are often better able than sighted controls to use monaural cues to judge the azimuth of sound sources. Gougoux, et al. (2005) and Doucet, et al. (2005) presented monaural or binaural broad-band noise bursts at azimuths between 0° and ±78° to sighted participants and blind participants with a mix of early- and late-onset blindness. In both studies, approximately half of the blind group were able to localize the stimuli on the appropriate side of the head, whereas the sighted group could not. Doucet, et al. (2005) conducted further tests on the blind participants who showed good monaural localization. They found that localization errors increased in conditions designed to disrupt the use of spectral cues, by the application of acoustical paste to the pinna or by leaving the pinna unobstructed but high-pass or low-pass filtering the sounds. These results suggest that good monaural localization was underpinned by the efficient use of spectral information.

Similar findings were reported by Voss, et al. (2011) for a spectral discrimination task. They presented participants with broadband noise bursts filtered using monaural head-related transfer functions measured using a KEMAR manikin so as to simulate sounds with azimuths between 0° and ±60°. The sounds were presented via a single loudspeaker at 0° azimuth, so only spectral cues for azimuth were available. Approximately half of the early-onset blind group showed markedly better performance than the other half of that group, a late-onset blind group, and sighted controls. Overall, the results of these studies support the proposal that more efficient use of spectral information underlies the superior performance of some blind participants for the monaural localization of sounds in azimuth.

Voss, et al. (2004) measured binaural localization in azimuth for sighted, early-onset, and late-onset blind groups using a minimum audible angle (MAA) task, in which two successive sounds, a reference and a target, were presented at different spatial locations. The participant was asked to report whether the second sound was located to the left or right of the first sound (or more to the front or to the back). Voss et al. used reference stimuli presented at 0° (using test sounds to the left or the right of 0°) or 90° azimuth (using test sounds in front of or behind 90°). The sound sources were beyond reaching and touching distance and background noise was present. For the 90° reference azimuth and for the rear hemifield only, the early- and late-onset blind groups performed better than sighted controls. For the 0° reference azimuth, there were no significant differences between the groups, which was attributed to ceiling effects.

Some other studies have shown no significant differences between blind and sighted groups in localizing binaurally presented sounds in azimuth (Fisher, 1964; Leclerc, Saint-Amour, Lavoie, Lassonde, & Lepore, 2000). Similarities in group performance have been attributed to ceiling effects due to the relatively low task difficulty when localizing single sounds from a limited number of possible source locations (Leclerc, et al., 2000).

Feierabend, Karnath, and Lewald (2019) reported that blind participants (a mixture of early and late onset) performed more poorly than sighted participants when localizing sounds at azimuths between –45° and +45°. This is the only study that we are aware of showing an effect in this direction for judgments of azimuth. In this study, the participant adjusted a swivel pointer to indicate the perceived direction of the source. Possibly, the blind participants were relatively poor in judging the direction of the pointer, rather than being poor in judging the locations of the sounds themselves. However, that study also differed from other studies in other ways, for example in the use of environmental sounds (a cuckoo clock, laughing man, crying baby, barking dog, or ringing telephone) as stimuli, whereas previous studies generally presented noise bursts. Also, the heterogeneity of the blind participants in severity of visual loss, age of blindness onset, and duration of blindness, may have influenced the results.

It should be noted that there are two distinct aspects of performance when judging the direction of sounds: there may be systematic differences between the judged and actual direction (a form of bias); and there may be random variability in the judgments of any given direction. In many of the studies described above, the measure of accuracy used confounded these two aspects. It may have been the case that in the studies showing better performance of blind participants, these participants were not superior to the sighted participants in terms of biases, but they gave more consistent responses. Further research is needed to separate these two aspects of performance.

In summary, blindness usually leads to enhanced monaural localization in azimuth for sounds in peripheral space, probably because of more efficient use of monaural spectral cues. Effects of blindness on binaural localization in azimuth for frontal space have not generally been found, possibly due to ceiling effects, although one study found poorer performance for blind participants for localization of environmental sounds coming from the frontal region of space.

The results are in line with the perceptual enhancement hypothesis. The enhanced performance in the use of monaural spectral cues and binaural cues (in peripheral space) for localization in azimuth is consistent with P1 (complexity), P2 (discrimination), P4 (identifying the direction of monotonic change), P5 (identifying the direction of non-monotonic change) and P7 (calibration using non-visual cues), if it is assumed that blind participants have learned the relationship between the complex spectral cues produced by the pinna and sound source azimuth. The spectral cues may be calibrated via the ITD and ILD cues that usually accompany them or by monitoring how the spectral cues associated with a fixed sound source change when the person moves around a room or moves their head in the left-right direction.

Auditory motion perception

Several studies have shown that blind individuals have a better ability to perceive horizontal sound motion than sighted controls (Jiang, Stecker, Boynton, & Fine, 2016; Jiang, Stecker, & Fine, 2014; Lewald, 2013). Lewald (2013) presented broadband noises moving along a semi-circular loudspeaker array placed at a constant distance of 1.5 m from the participant. The minimum audible movement angle of the blind participants was approximately half the value measured for sighted controls. Early-onset and congenitally blind participants did not perform significantly differently from late-onset blind participants, suggesting that enhanced auditory motion perception does not depend critically on age of onset, inconsistent with P9.

The effect of blindness on the ability to perceive looming sounds was assessed by Schiff and Oldak (1990). A sighted group of participants either watched a film with a soundtrack of approaching objects that disappeared before reaching their position or they listened to the soundtrack only without the film. A group of early-onset blind participants took part in the soundtrack-only condition. The task was to predict when the object would have reached them, by pressing a button. The blind group was more accurate than the sighted group in the soundtrack only condition.

The studies described above support the view that blindness results in enhanced perception of auditory motion, consistent with P1 (complexity), P2 (discrimination), P3 (detection) and the perceptual enhancement hypothesis. However, the tasks used in these studies involved relatively straightforward judgments such as sound movement direction (Lewald, 2013) or time-to-arrival (Schiff & Oldak, 1990). For more difficult auditory motion encoding and reproduction tasks (e.g. Finocchietti, Cappagli, & Gori, 2015a, described in more detail below), blindness can result in poorer performance than for sighted controls, consistent with P6 (calibration requiring visual cues).

Self-localization using sound

Després, et al. (2005a) reported that blindness resulted in enhanced self-localization abilities. Sighted and congenitally blind participant groups listened to sounds played over loudspeakers at various positions in a dark anechoic room or a dark reverberant room. Participants were asked to report their own position in the room, using a plan of the room (blind participants were given a raised-relief plan). For both anechoic and reverberant rooms, the blind group were significantly more accurate at reporting their position. This is consistent with P1 (complexity), P8 (experience and practise), and the perceptual enhancement hypothesis.

Auditory spatial attention

Kujala, Lehtokoski, Alho, Kekoni, and Näätänen (1997) compared performance for early-blind and sighted participants in a bimodal divided spatial attention task. Intermixed auditory tones (delivered via headphones with an ITD of 0.5 ms and heard on the right) and tactile pulses (applied to the left index finger) were presented in a sequence together with occasional target stimuli that differed in location from the other stimuli (0 ms ITD for the auditory stimuli and left middle finger for the tactile stimuli). Participants were required to press a key as quickly as they could in response to each auditory and tactile target. Blind participants had faster reaction times for auditory targets. Similar results were found in another study investigating auditory-tactile divided spatial attention (Collignon, Renier, Bruyer, Tranduy, & Veraart, 2006): blind participants had faster reaction times than sighted participants for the auditory component of the task. Collignon, et al. (2006) suggested that a previous failure to find differences between blind and sighted participants in an auditory spatial selective attention task (Kujala et al., 1995) may have been due to attentional disengagement stemming from the ease of the task. Overall, the results are consistent with P1 (complexity) and P2 (discrimination), and the perceptual enhancement hypothesis.

Summary of results on enhanced auditory spatial abilities in the blind

In summary, consistent with the perceptual enhancement hypothesis, several auditory spatial abilities are enhanced following visual loss, including azimuthal localization in peripheral space, or using monaural cues alone, relative distance judgements, motion discrimination, self-localization, auditory selective spatial attention, and bimodal divided spatial attention. Also enhanced are a number of abilities specifically associated with echolocation, including discrimination of object material, size, and distance, object detection, walking parallel to a wall, object shape or texture discrimination, object localization accuracy, spatial acuity, ILD and ITD sensitivity, echo detection in bursts of noise, and obstacle detection range and circumvention ability. These findings are consistent with P1 (complexity), P2 (discrimination), P3 (detection), P4 (identifying the direction of monotonic change), P5 (identifying the direction of non-monotonic change), P7 (calibration using non-visual cues), P8 (experience and practise), and P9 (age of onset).

Auditory spatial abilities that are degraded as a result of full blindness

Tasks involving spatial metrics: Spatial bisection, and auditory encoding and movement reproduction

The ability to judge the position of a sound source relative to the positions of other sound sources has been explored using a spatial-bisection task (Campus, Sandini, Amadeo, & Gori, 2019; Gori, et al., 2014; Vercillo, et al., 2016; Vercillo, et al., 2015). As mentioned earlier, this involves listening to three successive sounds with different spatial locations. The participant is asked to report whether the second sound is closer to the first or the last sound. It has been argued that this task requires that auditory cues for location are used to create an internal map of the positions of objects in space; the task is then performed by comparing distances in the internal map (Finocchietti, et al., 2015a; Gori, et al., 2014). Performance for this bisection task has often been compared with that for an MAA task. The MAA task has been argued to involve simple discrimination of two sound positions based on cues such as changes in ITD or ILD; a map of space is not required (Aggius-Vella et al., 2020; Finocchietti, et al., 2015a; Gori, et al., 2014).

Several studies have shown that blindness results in poorer spatial bisection in azimuth than for sighted controls under binaural listening conditions (Campus, et al., 2019; Gori, et al., 2014; Vercillo, et al., 2016; Vercillo, et al., 2015). In contrast, blind and sighted groups show similar performance for a MAA task (Gori, et al., 2014; Vercillo, et al., 2016; Vercillo, et al., 2015; Wersenyi, 2012) or a temporal bisection task (Campus, et al., 2019). These results are consistent with P1 (complexity) and P6 (calibration requiring visual cues).

Another relatively difficult task that has been argued to require a spatial metric was used by Finocchietti, et al. (2015a). The task involved listening to a sound source that was moving in two-dimensional space and then reproducing the pattern of movement on a vertical panel located in front of the participant. Performance was compared for early- and late-onset blind and sighted participants. The early-onset blind group were less accurate than the other groups in determining the end-point sound position, and showed a bias for targets presented in the lower area of the vertical plane, located below the nose of the participant, to be perceived in space located above the nose. These results are consistent with P1 (complexity), P5 (identifying the direction of non-monotonic change), P6 (calibration requiring visual cues), and P9 (age of onset). The results are consistent with the perceptual deficiency hypothesis, but not with the perceptual enhancement hypothesis.

Sound localization in elevation

Sound localization in elevation has been reported to be degraded for blind participants (Lewald, 2002b; Voss, et al., 2015; Zwiers, et al., 2001). Zwiers, et al. (2001) investigated azimuth and elevation localization for sighted and early-blind participants, using as targets broadband noise bursts repeated every 20 ms to give a sound like a 50-Hz hum. This was done to help participants distinguish the target sound from a continuous spatially diffuse background noise that was used to increase the difficulty of the task. When the target-to-noise ratio was high, azimuth and elevation localization performance was similar for the blind and sighted groups. At lower target-to-noise ratios, performance was similar for the two groups for localization in azimuth. However, localization in elevation was poorer for the blind group.

Lewald (2002b) measured the ability of early-blind and sighted groups to judge the location of high-frequency band-pass-ýltered ñfrozenò noises (the same noise waveform on each trial) presented at elevations ranging from –30° to +30°. The groups showed similar performance in judging the relative positions of the sound sources. However, the blind group showed a deficit in judging the absolute vertical positions of the sound sources.

The judgment of elevation depends primarily on spectral cues provided by the pinna (Blauert, 1997). The results suggest that blindness adversely affects the ability to make absolute judgments of elevation using such cues. This contrasts with the findings summarized earlier showing superior performance of blind participants in judging azimuth using monaural spectral cues. A possible explanation for this was proposed by Voss, et al. (2015). They suggested that different types of spectral information were used for the two tasks; prominent spectral notches in head related transfer functions (HRTFs) are used for elevation localization, while spectral peaks are used for azimuth localization. Spectral peaks are likely to be more salient and easier to detect than spectral notches (Moore, Oldfield, & Dooley, 1989). It may also be the case that blind people can hear the changes in spectral cues associated with changes in elevation, but they have trouble relating the spectral cues to elevation because of insufficient calibration information. For localization in elevation, ITD and ILD cues are not useful for calibration unless the head is strongly tilted. Also, the positions of fixed sounds do not changed markedly in elevation relative to the listener unless the listener tilts their head in the up-down direction, which does not happen very often. Overall these results are consistent with P1 (complexity), P5 (identifying the direction of non-monotonic change), and P6 (calibration requiring visual cues). The results are consistent with the perceptual deficiency hypothesis, but not with the perceptual enhancement hypothesis.

Absolute distance judgments

In a near-anechoic environment (for example outdoors) and for a sound source of fixed level, the level at the listenerŝs ears decreases by 6 dB per doubling of the sound source distance.

Provided that the listener can estimate the level at the source, which can be done on the basis of vocal effort for speech sounds, the level at the listener's ears can be used to judge distance. In a reverberant environment, the sound level at the listener's ears decreases by less than 6 dB per doubling of distance, but an additional cue, the direct-to-reverberant ratio (DRR) in sound level, is available. Visual loss may lead to a less precise or biased relationship between level and DRR cues and perceived distance, thereby decreasing the accuracy of absolute judgements of distance (P6, calibration requiring visual cues).

Wanet and Veraart (1985) assessed the ability to judge the direction and distance of 800-Hz tones in near space, between 18 and 62 cm from the participant, for early- and late-onset blind groups, and sighted controls. Distance judgments were less accurate for the early-blind group than for the other groups, although the differences would have been non-significant if the authors had adjusted their significance levels to allow for multiple comparisons. Macé, Dramas, and Jouffrais (2012) showed that early-onset blind participants were less accurate than sighted participants at reaching towards white-noise sounds presented in peripersonal space. Lai and Chen (2006) obtained absolute distance judgments of blind (age of onset not reported) and sighted participants for a musical tone or telephone sound presented at 3 m distance. The sighted group on average made lower errors than the blind group, although the difference was not significant.

Kolarik, Cirstea, Pardhan, and Moore (2013c) obtained absolute distance judgments for speech sounds heard at virtual distances between 1.2 and 13.8 m. Normally sighted participants judged the distances of closer sounds accurately, but underestimated the distance to far sounds, as found in previous studies (for reviews, see Kolarik, et al., 2016a; Zahorik, et al., 2005). Early-blind participants underestimated the absolute distance of far sound sources, and overestimated the absolute distance of closer sound sources. This deficit was found to generalize across reverberant and anechoic environments and speech, music and noise stimuli in extrapersonal space (Kolarik, et al., 2017a).

In summary, blindness is associated with a poorer ability to judge the absolute distance of sound sources, consistent with P1 (complexity), and P6 (calibration requiring visual cues). These results are consistent with the perceptual deficiency hypothesis, but not with the perceptual enhancement hypothesis. In contrast, as described earlier, relative distance judgments tend to be more accurate for blind people, consistent with P1 (complexity), P2 (discrimination), and P3 (detection).

Inferential navigation and road crossing decisions using sound

Visual loss adversely affects navigation, impairing the ability to move safely through the environment and maintain orientation towards a destination (Veraart & Wanet-Defalque, 1987). Gait is also affected; relative to sighted people, early and late-onset blind people have a slower walking speed, shorter stride length, and longer time spent in the stance phase of gait, during which the foot remains in contact with the ground. This enables blind people to move safely and to maintain a posture with greater stability (Nakamura, 1997).

Inferential navigation requires participants to derive novel relationships between themselves and objects in the environment based on prior experience, such as completing a triangular route (Seemungal, Glasauer, Gresty, & Bronstein, 2007; Thinus-Blanc & Gaunet, 1997). Several studies have shown that blindness results in poorer inferential navigation (Gori, Cappagli, Baud-Bovy, & Finocchietti, 2017; Herman, Chatman, & Roth, 1983; Rieser, Guth, & Hill, 1986; Seemungal, et al., 2007; Thinus-Blanc & Gaunet, 1997; Veraart & Wanet-Defalque, 1987). Veraart and Wanet-Defalque (1987) tested early-onset blind, late-onset blind, and blindfolded sighted controls in a task designed to assess the accuracy of internal representations of space. Participants were guided along a route in which landmarks were indicated both with and without the use of an ultrasonic echolocation device that allowed object localization (the device was not used with the sighted controls). Participants then inferred the distance between their position and each landmark, and indicated the directions of the landmarks. Without the device, early-onset blind participants performed more poorly than the other groups for both distance and direction, indicating that early-onset blindness resulted in impaired internal representations of space, consistent with P1, 6 and 9. With the device, both blind groups improved. The results obtained without the device are consistent with a study of Rieser, et al. (1986), who reported that early-onset blindness resulted in lower sensitivity to changes in perspective structure (changes in direction and distance to stationary objects) when moving through the environment. However, this result was not replicated by Loomis et al. (1993), who suggested that mobility skills may have affected performance, and that blind participants who travel independently are likely to develop better locomotor abilities. Overall, the majority of studies support the view that early-onset blindness results in poorer performance for inferential navigation tasks using sound, consistent with P5 (identifying the direction of non-monotonic change), P6 (calibration requiring visual cues), and P9 (age of onset).

Gori, et al. (2017) explored auditory spatial shape reproduction by navigation. After hearing an experimenter move a sound source along a path that produced a shape (e.g. circle, triangle, square), early- and late-onset blind groups and sighted controls reported the shape of the path and had to reproduce the path by navigating themselves. Compared to the late-onset blind group and sighted controls, early-blind participants compressed the reproduced shape, and had difficulties correctly identifying the shape and producing the shape (e.g. a square was reported, but a circle was produced when navigating).

The ability of blind individuals to use auditory information to make road-crossing decisions was assessed by Guth, Long, Emerson, Ponchillia, and Ashmead (2013) and Hassan

(2012). Pedestrian safety when crossing a road relies substantially on accurate judgments of the time required to cross the road and the time before the next vehicle arrives (Hassan, 2012). Guth, et al. (2013) investigated road crossing judgments of a mix of early and late-onset blind and sighted controls at a roundabout. The blind group made riskier judgments, especially when traffic volume was high and the participant was positioned near the roundabout. The blind group also accepted fewer safe opportunities for crossing and were slower to make crossing judgments. Hassan (2012) assessed road-crossing decisions for sighted controls, participants with partial visual loss, and a totally blind group (age of onset not reported). When crossing decisions were based on auditory information only, the blind group made significantly less accurate decisions than the other groups. Overall, these results are consistent with P5 (identifying the direction of non-monotonic change), and P6 (calibration requiring visual cues).

In summary, several auditory spatial abilities are degraded following full visual loss, including absolute distance judgements, elevation judgements, azimuth bisection, auditory encoding and movement reproduction, inferential navigation and road-crossing decisions. Auditory abilities that are degraded by blindness generally require absolute spatial judgments or require precise internal spatial representations, such as auditory bisection and inferential navigation, consistent with P5 (identifying the direction of non-monotonic change), and P6 (calibration requiring visual cues). Findings that performance is poorer for sighted controls than for early- but not late-onset blind participants is consistent with P9 (age of onset). These results are consistent with the perceptual deficiency hypothesis, but not with the perceptual enhancement hypothesis.

Summary of enhanced and degraded auditory spatial abilities in the blind

Table 1 summarizes studies showing enhanced and degraded auditory spatial abilities for blind individuals. Neither the perceptual enhancement hypothesis nor the perceptual deficiency hypothesis are able to encompass the results across the diverse auditory spatial tasks used in these studies.

Auditory ability	Studies	Effect of blindness	Early or late-onset, or a mix
Localization in azimuth P1-2, 4-5, 7, 9			
[Binaural]	Rice (1969) C	Enhanced	Early
[Binaural]	Muchnik et al. (1991) C	Enhanced	Early
[Monaural]	Lessard et al. (1998) C	Enhanced	Early
[Binaural]	Röder et al. (1999) C	Enhanced	Early
[Binaural; Monaural; Monaural]	Voss et al. (2004; 2011; 2015) C	Enhanced	Mix; Mix; Early
[Binaural]	Després et al. (2005a) C	Enhanced	Early
[Monaural]	Doucet et al. (2005) C	Enhanced	Mix
[Monaural]	Gougoux et al. (2005) C	Enhanced	Mix
[Binaural]	Yabe & Kaga (2005) C	Enhanced	Early and Late
[Binaural]	Fieger et al. (2006) C	Enhanced	Late
[Binaural]	Chen et al. (2006) C	Enhanced	Early
[Binaural]	Feierabend et al. (2019) I	Degraded	Mix
Echolocation P1-2, 8			
Discrimination of object material, size, distance	Kellogg (1962) C	Enhanced	Late
Object detection and location	Rice (1969) C	Enhanced	Early
Walking parallel to a wall	Strelow and Brabyn (1982) C	Enhanced	Mix
Object shape or texture discrimination	Hausfeld et al. (1982) C	Enhanced	Early
Object localization accuracy	Schenkman & Nilsson (2010; 2011) C	Enhanced	Mix; Mix
Spatial acuity	Teng and Whitney (2011) C	Enhanced	Early
ILD and ITD sensitivity	Nilsson & Schenkman (2016) C	Enhanced	Mix
Detection of echoes in trains of noise bursts	Schenkman et al. (2016) C	Enhanced	Mix
Obstacle detection range and circumvention	Kolarik et al. (2017b) C	Enhanced	Early
Relative distance judgements P1-2, 4	Ashmead, et al. (1998b) C	Enhanced	Mix
	Voss et al. (2004) C	Enhanced	Early (<11 yrs) and Late (>16 yrs)
	Kolarik, et al. (2013a) C	Enhanced	Mix
Motion discrimination P1-3, 9	Schiff & Oldak (1990) C	Enhanced	Early
	Lewald (2013) C, I	Enhanced	Early and Late
	Jiang et al. (2014) C	Enhanced	Early
	Jiang et al. (2016) C	Enhanced	Early
Self-localization P8	Després, et al. (2005a) C	Enhanced	Early

Auditory selective spatial attention P1-2	Collignon et al. (2006) C	Enhanced	Early
Bimodal divided spatial attention P1-2	Kujala et al. (1997) C	Enhanced	Early
	Collignon et al. (2006) C	Enhanced	Early
Absolute distance judgement P1, 6	Wanet & Veraart (1985) C	Degraded	Early
	Macé et al. (2012) C	Degraded	Early
	Kolarik, et al. (2013b; 2017a) C	Degraded	Early
Elevation P1, 5-6	Zwiers, et al. (2001) C	Degraded	Early
	Lewald (2002) C	Degraded	Early
Azimuth bisection P1, 6	Gori et al. (2014) C	Degraded	Early
	Vercillo et al (2015; 2016) C	Degraded	Early; Early
	Campus et al (2019) C	Degraded	Early
Auditory encoding and movement reproduction P1, 5-6, 9	Finocchietti et al. (2015a) C	Degraded	Early
Inferential navigation P1, 6, 9	Herman et al. (1983) C	Degraded	Early
	Rieser et al. (1986) C	Degraded	Early
	Veraart & Wanet-Defalque (1987) C	Degraded	Early
	Seemungal et al. (2007) C	Degraded	Early
	Gori et al. (2017) C	Degraded	Early
Road crossing decisions using sound P1, 6	Guth, et al. (2013) C	Degraded	Mix
	Hassan (2012) C	Degraded	Not reported

Table 1. A summary of the spatial auditory abilities that are significantly enhanced or degraded by full blindness. Details of the studies are given in the main text. For each auditory ability, the effect of blindness (enhanced or degraded), and the group(s) (early or late-onset) showing significant differences from sighted controls are indicated. Unless specified otherwise, early-onset loss is defined here as blindness before the age of 5 years, and late-onset loss as blindness after 5 years of age. For each ability, the principles involved are denoted by P followed by a number. For each study, results consistent with the principles involved are indicated by C, and inconsistent results are indicated by I.

The effect of visual loss on non-spatial auditory abilities

Speech perception

Several studies have shown enhanced speech perception in quiet and noisy environments for blind people (Hugdahl et al., 2004; Lucas, 1984; Muchnik, et al., 1991; Niemeyer & Starlinger, 1981; Röder, Demuth, Streb, & Rösler, 2003; Rokem & Ahissar, 2009). Niemeyer and Starlinger (1981) reported better discrimination by early-onset blind than by sighted participants for speech in quiet or in background noise at 50 dB SPL. Muchnik, et al. (1991) reported better speech discrimination by early blind than by sighted controls for speech in noise presented at 40 dB above the speech reception threshold, but similar performance between groups in quiet. Rokem and Ahissar (2009) showed that speech reception thresholds were lower (better) for congenitally blind than for sighted controls for speech in quiet and in background noise at 60 dB SPL. Compared to sighted controls, early blind participants showed earlier evoked potentials when deciding whether or not a sentence was meaningful (Röder, Rösler, & Neville, 2000), were faster when performing a lexical decision task (Röder, et al., 2003), had better vowel discrimination (Ménard, Dupont, Baum, & Aubin, 2009), and had better discrimination of syllables (Hugdahl, et al., 2004). Klinge, Röder, and Büchel (2010) showed that congenitally blind people were better able to discriminate emotions using affective prosody information in pseudowords. Dietrich, Hertrich, and Ackermann (2011, 2013) showed that blind participants could comprehend accelerated speech at rates up to 22 syllables per second, whereas the limit for sighted participants was approximately 8 syllables per second.

Bull, Rathborn, and Clifford (1983) reported that blind participants were more accurate than sighted controls in identifying previously heard speakers. Föcker, Best, Hölig, and Röder (2012) showed that, compared to a sighted group, a congenitally blind group learned to associate names and voices more quickly, were more accurate when identifying the speaker using novel voice samples, and displayed enhanced verbal memory (Amedi, Raz, Pianka, Malach, & Zohary, 2003).

Feng et al. (2019) used the mismatch negativity (MMN) evoked potential to investigate Mandarin lexical tone and vowel and consonant processing at the pre-attentive stage in early-onset blind and sighted participants, using a passive oddball paradigm.

Compared to the sighted control group, the blind group had a shorter MMN peak latency for lexical tones in the right hemisphere, possibly suggesting more rapid pre-attentive processing. For consonants and/or vowels the blind group had a larger MMN amplitude in both hemispheres, but a longer peak latency, the latter possibly indicating slower processing. In a behavioural discrimination task, the blind group showed better performance than the control group for lexical tones, vowels, and consonants.

Overall, these results are consistent with P1 (complexity), P2 (discrimination), P3 (detection), and the perceptual enhancement hypothesis.

Auditory non-spatial attention

Several studies have shown that blind participants have faster reaction times than sighted controls when performing sustained non-spatial auditory attention tasks, suggesting more efficient processing of auditory stimuli by the blind. Liotti, Ryder, and Woldorff (1998) investigated auditory attention to level deviants for congenitally blind and sighted groups. Sequences of tones (ñstandardò tones) were presented to each ear, with occasional deviant (ñtargetò) tones of lower level. Participants were asked to attend to the stimuli in one ear while ignoring the stimuli in the other ear, and to press a button when a target was presented. The standard/target level difference was adjusted so that target detectability was 70%. Although discrimination accuracy and standard/target level differences were similar between groups, reaction times were significantly shorter for the blind than for the sighted participants.

Röder, Rösler, and Neville (1999) asked sighted and congenitally blind participants to attend to sequences of standard tones at 1500 Hz presented to the right, left, or both ears, with occasional 1000-Hz target tones presented. Participants were asked to press a button as fast as possible in response to a target, regardless of its ear of presentation. Blind participants showed faster reaction times than controls.

Hugdahl, et al. (2004) tested early blind and sighted participants in a dichotic-listening procedure. Two simultaneous consonant-vowel syllables were presented, one to each ear. Participants were asked to report what syllable they heard, either without specific instructions about which ear to attend to, or with instructions to focus attention on the left ear or the right ear. For the condition without specific instructions, both groups showed a right-ear advantage, a strong tendency to report the syllable presented to the right ear. The blind participants performed better overall. When participants were focussing on the left ear, the sighted group showed only a small left-ear advantage, while the blind group showed a substantial left-ear advantage, indicating that the latter were better able to use attention to overcome the ñnormalò laterality effect.

Overall, these results are consistent with P1 (complexity), P2 (discrimination), P3 (detection), and the perceptual enhancement hypothesis.

Temporal resolution

Several studies have addressed the issue of whether blindness is associated with enhanced auditory temporal processing. Muchnik, et al. (1991) measured thresholds for detection of a temporal gap in noise bursts for early-blind participants and sighted controls. Thresholds were lower (better) for early-blind and late-onset blind participants (10 in each group) than for sighted controls. Bross and Borenstein (1982) showed no difference between five late-blind participants (becoming blind after the age of 7 years) and a sighted group in auditory temporal acuity assessed using a flutter-fusion task. Van der Lubbe, Van Mierlo, and Postma (2010) showed that discrimination of the duration of bursts of noise was better for 12 early-blind participants than for 12 sighted controls. Stevens and Weaver (2005) showed that 15 early-blind participants had lower thresholds than 29 sighted controls in an auditory temporal order judgment task and an auditory backward masking task. They suggested that the superior performance of the blind participants reflected more rapid and precise perceptual consolidation of stimulus properties into working memory. Overall, the results support the idea that blindness enhances at least some aspects of auditory temporal processing for early-blind participants, consistent with P1 (complexity), P2 (discrimination), P3 (detection), and the perceptual enhancement hypothesis.

Auditory memory

Röder and Rösler (2003) investigated the effectiveness of different encoding strategies (semantic or acoustical) for auditory recognition memory in groups of congenital and late onset blind participants, and sighted controls. Initially, participants listened to environmental sounds; half were required to name the sounds, promoting semantic encoding, and half were required to rate the sounds on a scale from harsh to soft, promoting encoding of acoustic properties. After a distraction task to prevent short-term memory affecting recognition performance, participants were presented with a set of sounds, and had to report whether an identical sound had been presented in the initial phase. False memory rates were lower for the congenitally blind group than for the sighted group following acoustical encoding but not following semantic encoding. A late-onset blind group tested using the same paradigm and matched in age to the other groups also showed enhanced performance compared to the sighted group, and similar performance to the congenitally blind group. Similar findings were reported by Röder, Rösler, and Neville (2001), who found that congenitally blind people showed better memory for auditory verbal material compared to sighted controls.

Overall, these results are consistent with P1 (complexity), and the perceptual enhancement hypothesis.

Do blind people have a better musical sense? Pitch, timbre, melody perception, rhythm and beat

The appreciation of music requires the ability to perceive changes in several acoustic variables, including fundamental frequency, temporal pattern and rhythm, and spectral shape. The temporal organization of a musical sequence into sounds interspersed with silences is referred to as rhythm, and salient periodicity of the rhythm marking equal spacing in time is referred to as the beat (see Lerens, Araneda, Renier, & De Volder, 2014). As reviewed below, the majority of studies, but not all, show that blind people have a better musical sense than their sighted counterparts.

Gougoux, et al. (2004) investigated frequency-change perception for early-onset, late-onset, and normally sighted participants. On each trial, participants were presented with two successive pure tones with different frequencies and were required to judge whether the pitch rose or fell. Early-blind participants showed significantly better performance than late-onset blind or normally sighted participants. Rokem and Ahissar (2009) also reported that frequency-discrimination thresholds were lower for congenitally blind participants than for sighted controls. In addition, the prevalence of absolute pitch is markedly higher among blind than sighted musicians (Hamilton, Pascual-Leone, & Schlaug, 2004).

Wan, Wood, Reutens, and Wilson (2010) compared sighted controls with blind participants matched in age and musical ability for three auditory tasks: frequency discrimination, categorization of fundamental frequency and spectral shape (corresponding to the percepts of pitch and timbre, respectively), and working memory for frequency. The authors tested three groups of blind participants: congenitally blind, early-onset blind who lost their sight between the ages of 1.4 and 13 years, and a late-onset blind group who lost their sight after 14 years. Note that these definitions of early and late onset loss are different to those used in Table 1 (early-onset before 5 years of age, late onset after 5 years of age). For the frequency-discrimination task, congenitally and early-onset blind participants performed better than sighted controls, and congenitally blind participants outperformed the sighted group to a greater extent than early-onset blind participants. For the pitch-timbre categorization task, both the congenital and early-onset blind participants showed significantly better performance than the sighted control group. Blind and sighted performance was similar for working memory for frequency. For all tasks, no significant differences in performance were observed between late-onset blind participants and sighted controls.

Voss and Zatorre (2011) tested early-onset blind, late-onset blind and sighted controls using frequency discrimination, intensity discrimination, simple melody discrimination, transposed melody discrimination, and phoneme discrimination tasks. Early-onset blind participants showed significantly better performance than sighted controls for frequency discrimination and the transposed melody discrimination tasks only. Additional analyses showed that this advantage was not due to differences in musical training between the groups. Simple melody discrimination was similar for the early blind and sighted groups, a finding replicated by Zhang, Jiang, Shu, and Zhang (2019).

Arnaud, Gracco, and Ménard (2018) measured thresholds for identifying the direction of fundamental frequency changes for a congenitally blind group and sighted controls who were matched for musical training. The stimuli were native or non-native vowels, musical instrument tones and pure tones. Thresholds were lower, indicating better performance, for the blind group for all stimuli except non-native vowels.

Zhang, et al. (2019) showed that a congenitally blind group performed better than a sighted group in a rhythm-discrimination task. As this task has a strong temporal component, this finding is in line with work showing enhanced temporal sensitivity in blind individuals, as reviewed earlier (Muchnik, et al., 1991). Similarly, enhanced beat asynchrony detection for an early-blind group was reported by Lerens, et al. (2014).

Carrara-Augustenborg and Schultz (2019) assessed the ability of early-blind and sighted participants to learn rhythms that were metrical (rhythms that imply a beat) or non-metrical (rhythms that do not imply a beat). The blind group were better than the sighted group at learning non-metrical auditory rhythms, but were worse when learning metrical rhythms, providing evidence for more accurate formation of temporal expectancies in the blind group but only for the learning of non-metrical auditory rhythms. Only the blind group showed conscious knowledge of the rhythm that they had learned in the non-metrical condition. Based on this, the authors suggested that the blind group only show enhanced learning of rhythm when auditory information reaches consciousness, or learning occurs following explicitly given instructions.

Overall, these results are consistent with P1 (complexity), P2 (discrimination), P9 (age of onset), and the perceptual enhancement hypothesis.

Summary of auditory non-spatial abilities in the blind

Table 2 summarises the auditory non-spatial abilities investigated for the blind population, including many abilities related to music, voice recognition, auditory attention, temporal abilities, verbal memory, and perceptual consolidation. A number of non-spatial abilities have been reported to be enhanced following blindness and only a few have been reported to be degraded, suggesting a general overarching principle that auditory abilities that are not involved in spatial processing are likely to become enhanced following blindness, consistent with P1 (complexity), P2 (discrimination), P3 (detection), P9 (age of onset), and the perceptual enhancement hypothesis.

Auditory ability	Studies	Effect of blindness	Early or late-onset, or a mix
Pitch perception P1-2, 9	Witkin et al. (1968) C	Enhanced	Early
	Gougoux et al. (2004) C	Enhanced	Early
	Rokem & Ahissar (2009) C	Enhanced	Early
	Chen et al. (2006) I	Degraded (slower)	Early
	Wan et al. (2010) C	Enhanced	Early(<13yrs)
	Voss and Zatorre (2011) C	Enhanced	Early
	Arnaud et al. (2018) C	Enhanced	Early
Pitch-timbre categorization P1-2, 9	Wan et al. (2010) C	Enhanced	Early(<13yrs)
Transposed melody discrimination P1-2, 9	Voss and Zatorre (2011) C	Enhanced	Early
Speech perception P1-3	Niemeyer & Starlinger (1981) C	Enhanced	Early
	Lucas (1984) C	Enhanced	Early
	Muchnik, et al. (1991) C	Enhanced	Early
	Röder et al. (2003) C	Enhanced	Early
	Hugdahl et al. (2004) C	Enhanced	Early
	Rokem & Ahissar (2009) C	Enhanced	Early
	Ménard et al. (2009) C	Enhanced	Early
	Klinge et al. (2010) C	Enhanced	Early
	Dietrich et al. (2011; 2013) C	Enhanced	Mix; Mix
	Föcker et al. (2012) C	Enhanced	Early
Lexical tone, vowel, and consonant discrimination P1-3	Feng et al. (2019) C	Enhanced	Early
Temporal resolution P1-3	Muchnik et al. (1991) C	Enhanced	Early
Rhythm discrimination P1-2	Zhang et al., (2019) C	Enhanced	Early
Learning non-metrical rhythms P1-2	Carrara-Augustenborg & Schultz (2019) C	Enhanced	Early
Learning metrical rhythms P1-2	Carrara-Augustenborg & Schultz (2019) I	Degraded	Early

Beat asynchrony detection P1-2	Lerens et al. (2014) C	Enhanced	Early
Voice recognition P1-3	Bull et al. (1983) C	Enhanced	Mix
Auditory attention P1-3	Liotti et al. (1998) C	Enhanced	Early
Bimodal divided attention P1-2	Collignon et al. (2006) C	Enhanced	Early
	Kujala et al. (1997) C	Enhanced	Early
Auditory memory P1	Röder & Rösler (2003) C	Enhanced	Early and late
Verbal memory P1	Röder et al. (2001) C	Enhanced	Early
	Amedi et al. (2003) C	Enhanced	Early
Temporal order judgments P1-3	Stevens & Weaver (2005) C	Enhanced	Early
Duration discrimination P1-3	Van der Lubbe et al. (2010) C	Enhanced	Early
Backward masking P1-3	Stevens & Weaver (2005) C	Enhanced	Early

Table 2: As for Table 1, but for non-spatial auditory abilities affected by blindness.

The effects of partial visual loss on auditory abilities

Research on the effects of visual loss on hearing has primarily focused on the effect of full blindness. However, several studies have shown that partial visual loss can also enhance or degrade certain auditory spatial and non-spatial abilities, as summarized below.

Blindness in one eye only was shown to result in improved accuracy relative to sighted controls for monaural localization of the azimuth of sounds and for binaural localization in azimuth for sounds from frontal regions of space (Hoover, Harris, & Steeves, 2012). Enhanced azimuth localization abilities have also been reported for myopic (short-sighted) participants compared to sighted controls (Després, Candas, & Dufour, 2005b; Dufour & Gérard, 2000). Participants with a range of causes of partial visual loss self-reported that their auditory abilities were enhanced compared to sighted controls in a number of situations, including locating the position of a talker, following speech that switched between one person and another, separating speech from music, being able to hear music clearly, and understanding speech in a car (Kolarik et al., 2017b).

Després, Candas, and Dufour (2005c) showed that near-sighted and amblyopic participants performed better in a self-positioning task than normally sighted controls. Kolarik et al. (2020) investigated the effect of severity of visual loss on auditory distance judgments using stimuli with simulated distances from 1.2 to 13.8 m. Sighted controls and participants with a range of visual losses (groups with mild, mid-range, and severe loss) were tested in simulated anechoic and reverberant environments using speech, music and noise stimuli. Greater severity of visual loss was associated with larger estimates of auditory distance for all stimuli and both acoustic environments, leading to increased absolute errors for closer sounds and decreased errors for farther sounds. Note, however, that the outcomes primarily reflect the magnitude of systematic biases in the relationship between judged and simulated distance. The distance of farther sounds was under-estimated for all groups, but the group with severe visual loss showed the least under-estimation. Calculations of the correlations between judged distances and simulated distances for each group showed that, apart from the anechoic music condition where correlations were similar across groups, correlations decreased as the severity of visual loss increased (correlations across conditions ranged from 0.58 to 0.66 for sighted controls, and 0.43 to 0.56 for the group with severe visual loss). This shows that as severity of visual loss increased the consistency of auditory distance judgments decreased.

Ahmad et al. (2019) studied changes in auditory spatial representations of azimuth and elevation brought on by macular degeneration (MD), which results in central visual losses. White noises were produced from one randomly selected loudspeaker within a 5 × 5 matrix of 25 loudspeakers. Participants were required to touch the position corresponding to the perceived location of the sound. Participants with MD judged off-center sounds to be shifted towards the centre of the loudspeaker matrix, corresponding to the position of the central scotoma. No such bias toward any particular area was found for the sighted controls. The older the participant was at the onset of visual loss, the greater was the magnitude of the bias towards the center.

Lessard, et al. (1998, described above) assessed the accuracy of localization in azimuth for sighted controls, a group with early-onset visual loss who were totally blind, and a group with early-onset central visual loss with residual peripheral vision. Poorest performance was observed for the group with residual vision. In contrast, as noted above, Hoover, et al. (2012) reported that blindness in one eye only resulted in enhanced localization in azimuth. A plausible explanation for the discrepancy is that the normal eye of the participants of Hoover et al. (2012) would have provided high resolution foveal spatial information that could be used to calibrate auditory spatial information. In contrast, the participants in the studies of Ahmad, et al. (2019) and Lessard, et al. (1998) had central visual field losses, so that foveal information was lost and only low resolution peripheral information was available.

Finally, not all studies have shown effects of partial visual loss on auditory abilities. Kolarik, et al. (2013b) reported no difference in distance discrimination between partially sighted participants with a range of causes of visual loss and sighted controls.

In summary, the current evidence shows that partial visual loss does affect a number of auditory spatial abilities (Table 3). Both azimuth and elevation localization show biases (Ahmad, et al., 2019), while locating the position of a talker, following speech switching between people, separating speech from music, hearing music clearly, and ease of understanding speech in a car are self-reported to be enhanced (Kolarik, et al., 2017b). For localization in azimuth, blindness in one eye is associated with enhancement (Hoover, et al., 2012), while central visual loss in both eyes is associated with degradation (Lessard, et al., 1998). Severe visual loss is associated with reduced accuracy in judging the distance of closer sounds and increased accuracy for farther sounds, reflecting systematic changes in the mapping between simulated and perceived distance (Kolarik, et al., 2020). Further studies are needed to clarify the effects of the type of visual loss on hearing, such as monocular blindness with one unimpaired eye or central or peripheral visual loss.

In summary, the literature on partial visual loss shows similar results to that for full visual loss, in that spatial abilities become either enhanced, consistent with the perceptual enhancement hypothesis, or degraded consistent with the perceptual deficiency hypothesis, whereas non-spatial abilities are generally only enhanced, consistent with the perceptual enhancement hypothesis and with the nine principles. However, the results of Lessard, et al. (1998) and Ahmad, et al. (2019) are of particular interest as they are the only studies to date to show that partial visual loss can have the opposite effect (of degrading azimuth localization) to that of full blindness (which usually enhances localization in azimuth). Lessard, et al. (1998) suggested several possible explanations for the degraded performance of participants with partial visual loss, including: (1) abnormal orienting behaviours; (2) conflicts or confusions between auditory spatial maps derived from peripheral and central vision; (3) lack of recruitment of deafferented brain areas. More studies are needed to test these explanations, and to assess the effects of partial visual loss on other auditory abilities.

Auditory ability **Spatial**	**Studies**	**Effect of loss**
Localization in azimuth P1-2, P4-5		
[Monaural and binaural]	Hoover et al. (2012) C	Enhanced for participants with one blind eye
[Binaural; Binaural]	Després et al. (2005b); Dufour & Gérard, (2000) C	Enhanced for myopic participants

[Monaural and binaural]	Lessard et al. (1998) D	Degraded with central loss in both eyes
Self-localization P8	Després, et al. (2005b) C	Enhanced for amblyopic and near-sighted
Absolute distance judgment P6	Kolarik et al. (2020) C	Less consistent judgments
Azimuth P1-2, 4-5, 9 and elevation P6	Ahmad et al. (2019) D	Biased
Locating the position of a talker P1-2, 4-5	Kolarik et al. (2017b) C	Enhanced by self-report
Following speech switching between people P1-5	Kolarik et al. (2017b) C	Enhanced by self-report
Non-spatial		
Separating speech from music P1-2	Kolarik et al. (2017b) C	Enhanced by self-report
Hearing music clearly P1-3	Kolarik et al. (2017b) C	Enhanced by self-report
Ease of understanding speech in a car P1-2	Kolarik et al. (2017b) C	Enhanced by self-report

Table 3: As for Tables 1 and 2, but for auditory abilities enhanced or degraded by partial visual loss. D stands for dependant; the outcome would depend on whether or not the relationship between acoustic cues and the variable that has to be judged has been learned with sufficient accuracy (P5).

Developmental findings regarding the effects of full and partial visual loss on auditory abilities

Studies of the effects of visual loss on hearing for children and adolescents provide information regarding the role of vision in shaping internal representations of auditory space in the early years of life and the development of spatial and non-spatial cognition. Witkin, Birnbaum, Lomonaco, Lehr, and Herman (1968) tested congenitally blind and sighted adolescents aged 12-20 years in an auditory embedded-figures test. A tune of 3-5 notes was followed by a longer and more complex tune, that either did or did not contain the first tune. The participant had to report whether the complex tune contained the first tune. The blind participants performed better than the sighted controls. Enhanced performance in the blind group persisted when musical experience was controlled for. The authors interpreted the results as evidence of greater capacity for sustained auditory attention in the blind, although the results may also be interpreted as evidence for enhanced fundamental-frequency processing or better auditory memory in blind adolescents (Collignon, et al., 2006). These results are consistent with P1 (complexity), P2 (discrimination), P3 (detection), and the perceptual enhancement hypothesis.

As described earlier, early-onset blind adults show very poor spatial-bisection thresholds but normal MAA thresholds. Following on from this, Vercillo, et al. (2016) measured spatial-bisection and MAA thresholds for blind and sighted children with a mean age of 11 yrs. They also measured temporal-bisection thresholds. The blind children displayed degraded performance for the MAA and spatial-bisection tasks but no deficit for the temporal-bisection task. The degraded performance for the MAA task contrasts with the results for blind adults and suggests that lack of visual experience can disrupt the way that ITD and ILD cues are mapped to perceived location. This disruption is overcome with extensive experience, leading to normal MAA performance for blind adults. The degraded performance for the spatial-bisection task is consistent with the results for blind adults and with P6 (calibration requiring visual cues).

Cappagli and Gori (2016) investigated the effect of visual loss on sound localization in azimuth for children aged 7-17 years and for adults. On each trial a 500-Hz tone was delivered from one of a horizontal array of loudspeakers. The participant used a cane to point to the location of the tone. Early- and late-onset blind adults performed similarly to sighted adults. However, blind children and those with low vision performed significantly more poorly than age-matched sighted children. The authors interpreted the developmental delay associated with visual loss as supporting the idea that vision provides the most reliable information for calibrating auditory spatial representations (Alais, Newell, & Mamassian, 2010). However, their data also suggest that non-visual spatial cues (tactile and sensorimotor) provide information that improves auditory spatial representations in later adulthood (Fiehler, Reuschel, & Rösler, 2009).

The findings of Cappagli and Gori (2016) and Vercillo, et al. (2016) are contrary to those of Ashmead, et al. (1998), who assessed spatial cognition for a range of tasks for blind and sighted children aged 6-20 years and reported enhanced localization in azimuth for the blind group. This study involved a horizontal MAA task using pairs of Gaussian noise bursts; participants reported if the second sound was to the left or right of the first (reference) sound, which was presented at 0° azimuth. MAAs were smaller for blind than for sighted children. However, when the reference sounds were presented at –45° or +45°, there was no difference in performance between groups. The authors noted that the task was conceptually difficult with the reference at –45° or +45°, as the left-right judgment did not correspond to the participantôs left and right. This conceptual difficulty may have led to the lack of difference across groups in this condition.

The studies described earlier for adults support the idea that blindness leads to a deficit in localization in elevation (Lewald, 2002b; Zwiers, et al., 2001). However, Ashmead, et al. (1998) showed that blind children had significantly smaller vertical MAAs for Gaussian noise-burst signals than sighted children and sighted adults. Ashmead, et al. (1998) also reported that blind children showed more accurate distance judgments when reaching out and putting their finger on the perceived location of a previously presented sound source. Regarding the difference between the findings of Cappagli and Gori (2016) and Vercillo, et al. (2016) and those of Ashmead, et al. (1998), Vercillo, et al. (2016) noted that the blind children tested by Ashmead, et al. (1998) had a relatively large age range (6-20 years) and included some children who lost their sight later in life and who had light perception or pattern vision, whereas Vercillo, et al. (2016) tested only congenitally blind children with a narrow age range (mean = 11 years, SD = 0.8 years).

Cappagli, Finocchietti, Cocchi, and Gori (2017) compared performance for static and dynamic auditory spatial tasks for sighted, partially sighted and blind children. The mean age of the groups ranged from 3.5 to 4.4 years. In the static task, participants were presented with a ñmeowò sound from one of 25 loudspeakers arranged in an array on a vertical surface measuring 50 x 50 cm, with tactile sensors placed 40 cm away. The participant had to touch the perceived location of the sound source. The dynamic task utilized the same stimulus and array of loudspeakers to present a sound that moved across 5 loudspeakers either horizontally or vertically. The participant had to touch the perceived endpoint of the sound. The partially sighted children showed better performance than the sighted controls for the dynamic task, but for the static task there was no difference between these two groups. For the static task, the blind children performed more poorly than the sighted group and similarly to the low-vision group. For the dynamic task the blind children performed more poorly than the other groups. A positive correlation was found between visual acuity and performance in the dynamic task for all participants, showing that better dynamic spatial performance was associated with more residual vision. The results suggest that blindness from birth degrades static and dynamic sound localization. However, partial visual function allows compensatory mechanisms to operate, leading to accurate static and dynamic sound localization. This highlights the importance of visual information for calibrating auditory space in the early years of life. The results are consistent with a study of Cappagli, Cocchi, and Gori (2015), who reported a deficit in auditory distance discrimination for early-blind children aged between 9 and 17 years.

Yabe and Kaga (2005) showed that ITD discrimination thresholds for adolescents aged between 13 and 15 years were smaller (better) for blind groups who were congenitally blind or who had acquired blindness (age of onset was not reported, assumed here to be late-onset blind) than for sighted controls or a partially sighted group.

In summary, the evidence regarding the effects of visual loss on auditory abilities for children and adolescents is mixed, some studies showing enhancement consistent with the perceptual enhancement hypothesis and others showing degraded performance consistent with the perceptual deficiency hypothesis, even for the same ability, such as localization in azimuth (Table 4). Further work is needed to clarify the ages at which visual loss leads to significant differences in auditory abilities. In addition, with the exception of Witkin, et al. (1968), the studies to date have focussed on auditory spatial abilities; the developmental time course of non-spatial auditory abilities in the blind is currently under researched.

Auditory ability	Studies	Effect of loss	Age range (yrs)
Auditory attention/frequency processing P1-3	Witkin, et al. (1968) C	Enhanced	12-20
Localization in azimuth P1-2, 4-5	Ashmead, et al. (1998) C	Enhanced	6-20
Localization in azimuth P1-2, 4-5	Cappagli and Gori (2016) I	Degraded	7-17
ITD discrimination P1-3, 9	Yabe and Kaga (2005) C	Enhanced	Mean ages 13-15
Absolute distance judgement P6	Ashmead, et al. (1998) D	Enhanced	6-20
Relative distance judgements P1-2, 4	Cappagli, et al. (2015) I	Degraded	9-17
Vertical Minimum Audible Angle P5	Ashmead, et al. (1998) D	Enhanced	6-20
Bisection P6 and Minimum Audible Angle P5	Vercillo, et al. (2016) C for bisection, D for MAA	Degraded	Mean age 10.9±0.8
3D static and dynamic localization P5-6	Cappagli, et al. (2017) C	Degraded for blind	Mean age 3.5-3.6

Table 4. A summary of auditory abilities or children and young adults with visual loss, the studies that investigated these abilities, the effect of visual loss on these abilities, and the age range of the participants. Participants had either full or partial visual loss (see text for details). D stands for dependant; the outcome would depend on whether or not the relationship

between acoustic cues and the variable that has to be judged has been learned with sufficient accuracy (P5-6).

Individual differences and their relationship to the degree and timing of visual loss

Individual differences in auditory abilities within the visually impaired population can be substantial. For example, echolocation abilities vary widely among blind people (Kolarik, et al., 2014a; Schenkman & Nilsson, 2011). Such differences may be caused by several factors, including the magnitude, age of onset, duration and aetiology of visual loss, and a trade-off in skills for vertical and horizontal localization (Voss, et al., 2015, described in more detail below). Social, personality, and cognitive factors may also play a role (Voss & Zatorre, 2012). Inconsistent findings regarding the way that visual loss affects auditory abilities may in part be due to the criteria used for selecting the participants (Röder & Rösler, 2003), to the use of tasks that are not identical for blind and sighted controls, and to different experiences for blind and sighted controls prior to testing (see Thinus-Blanc & Gaunet, 1997).

As described above, differences in auditory spatial performance between groups with full blindness and partial visual loss were reported by Lessard, et al. (1998). Earlier age of onset or longer overall duration of visual loss are often associated with better abilities, consistent with P8-9. Echolocation studies, albeit testing relatively few participants, have shown that early-onset blindness is associated with enhanced acuity for detecting sound echoes (Teng, et al., 2012) and determining the shape, movement, and surface location of objects using echoes (Thaler, Arnott, & Goodale, 2011) compared to late-onset blindness.

Putzar, Goerendt, Lange, Rösler, and Röder (2007) studied the role of early visual experience in shaping audio-visual interactions. They tested sighted controls and a group of participants with congenital binocular cataracts resulting in deprivation of pattern vision for at least the first five months of life, who recovered their sight following treatment. The cataract group showed superior performance in a task requiring reporting the colour of a target flash while ignoring a task-irrelevant auditory distractor tone, indicating less audio-visual interference. The cataract group showed poorer performance in an audio-visual speech fusion task, indicating less audio-visual facilitation or less reliance on visual information. These results suggest that vision early in life is important for audio-visual perception to mature.

Voss and Zatorre (2012) highlighted the possible role of social and personality factors in the development of cortical reorganization that leads to enhanced auditory abilities. Such factors might affect the extent to which the individual takes part in activities that might promote cortical reorganization, such as exploration of the environment. This has not been the focus of systematic study, and needs further exploration.

In some of the studies investigating monaural horizontal localization that were described above, there were marked individual differences among early-onset blind participants, some showing greater accuracy than sighted controls and some showing similar accuracy to sighted controls (Doucet, et al., 2005; Gougoux, et al., 2005; Lessard, et al., 1998). To account for why a subset of blind participants showed superior performance, Voss, et al. (2015) proposed that variations in performance across blind participants may be due to a trade-off in skills for vertical and horizontal localization. They showed that blind participants with the poorest accuracy in vertical localization had the highest accuracy in monaural horizontal localization. These results suggest that enhancement of one auditory ability may come at the cost of worse performance for another auditory ability.

The studies reviewed above are largely consistent with principles P1-P9, although the predictions based on P5 and P6 are sometimes uncertain, because they depend on the extent to which the participant has learned the relationship between auditory cues and the variable that has to be judged, and this is often unknown in advance.

The beneficial effects of cortical reorganization and the neural bases of changes in auditory abilities following blindness

In this section we consider in more detail the neural bases of the changes that underlie the enhanced abilities for some tasks that are associated with blindness, as characterized by P1-P3. Many studies have focused on the link between cross-modal plasticity and enhanced perceptual abilities. The degree of cross-modal plasticity is strongly affected by the age of onset of blindness (for reviews, see Bell et al., 2019; Collignon, et al., 2009; Dormal, Lepore, & Collignon, 2012; Kupers & Ptito, 2014; Occelli, Spence, & Zampini, 2013; Pasqualotto & Proulx, 2012; Voss, 2019; Voss, Collignon, Lassonde, & Lepore, 2010), consistent with P9. There is also evidence that without visual input, neural auditory maps of space become distorted or degraded, as described in the next section.

Following blindness, occipital brain regions, which normally respond primarily to visual stimuli, may be recruited to process auditory signals (Voss & Zatorre, 2012). For example, Gougoux, et al. (2005) and Voss, et al. (2011) presented data suggesting that processing in the occipital cortex was the basis for the enhanced ability of blind people to utilize monaural spatial cues to judge azimuth. There is also evidence for functional plasticity in the temporal cortex, a brain area responsible for auditory spatial processing. van der Heijden et al. (2019) showed that activation patterns for binaural spatial processing were different for sighted and early-onset blind participants in planum temporale within the temporal lobe. They proposed that some blind people have an increased reliance on spectral cues for localization in the horizontal plane or that blind people become adept at using a richer set of cues for horizontal localization, including both binaural (ITD and ILD) and spectral cues. However, blindness does not result in recruitment of occipital brain regions and improved performance for all auditory spatial tasks. For example, congenitally blind participants showed poorer performance of a spatial-bisection task than sighted participants and the blind participants did not show recruitment of the occipital cortex during performance of this task (Campus, et al., 2019). Instead, early contralateral occipital activation in response to sound was strong for sighted participants and substantially lower for blind participants.

Non-spatial and spatial information is segregated in the brain into pathways for identifying objects (the ñwhatò pathway, or ventral stream) and localizing them (the ñwhereò pathway, or dorsal stream). The ñwhereò pathway appears to be highly plastic in early life, and becomes resistant to the effects of experience later in life (Dormal, et al., 2012). Chen, Zhang, and Zhou (2006) presented evidence suggesting that auditory brain plasticity in the blind may occur in the ñwhereò pathway but not the ñwhatò pathway. For tones presented in the periphery, congenitally blind participants showed enhanced localization, but for a non-spatial task (discriminating frequency) blind participants were significantly slower than sighted controls. This finding is surprising, given that other studies have reported that blindness is associated with improved frequency discrimination abilities (Arnaud, et al., 2018; Rokem & Ahissar, 2009; Wan, et al., 2010), and it is unclear why blindness should lead to a decrease in processing speed for this task.

Studies using animals have also suggested that improved auditory abilities following blindness may at least in part be related to functional enhancement in auditory cortical areas. Blindness was found to result in enhanced response specificity of neurons in the auditory cortex (Korte & Rauschecker, 1993) and improved frequency selectivity and stronger responses to changes in frequency and intensity (Petrus et al., 2014). However, there is evidence that blindness disrupts the development of auditory spatial maps. Vision plays a major role in the maturation of the auditory spatial response properties of neurons in the superior colliculus (SC) in the midbrain, where auditory, visual, and tactile inputs are organized into topographically aligned spatial maps (for a review, see King, 2009). An electrophysiological study of the representation of auditory space in the SC of ferrets reared without vision showed that their auditory spatial maps had abnormal topography and precision of their spatial representations (King & Carlile, 1993). Neural auditory maps of space were reported to be degraded in the optic tectum of blind-reared barn owls, an area of the brain containing neurons tuned for sound source location and organized according to their spatial tuning (Knudsen, 1988). As well as a distorted topography of spatial maps, blind-reared owls also showed significantly less precise sound localization behaviour (Knudsen, Esterly, & du Lac, 1991). These findings show that an auditory spatial map can be generated by the brain in the absence of vision, but that the precision and topography are degraded or distorted compared to when vision is present during development.

In summary, there is now an abundance of research demonstrating that that both cross-modal cortical reorganization and reorganization within primarily auditory regions of the brain may underlie the enhanced performance of blind people for some spatial tasks, consistent with the perceptual enhancement hypothesis. However, blind people show deficits in performance compared to sighted controls for auditory spatial tasks that may be performed using internal maps of space (Tables 1-3), consistent with the perceptual deficiency hypothesis. The role that vision plays in calibrating auditory space is the focus of the next section.

How and when vision is used for calibrating auditory space and guiding action

As described earlier, the performance of some auditory spatial tasks requires the auditory system to map the available spatial cues to an internal representation of space (Aggius-Vella, Campus, Kolarik, & Gori, 2019; Kolarik, Pardhan, Cirstea, & Moore, 2013d); this is encapsulated by P6 (calibration requiring visual cues). The auditory system can potentially use vision or sensorimotor contingencies to learn this mapping (O'Regan & Noë, 2001). Auditory calibration by vision is likely to be most precise for frontal space, where visual information is most accurate, and less precise for peripheral space, where alternative feedback signals, such as proprioception, motor feedback, or touch may provide more useful information (Théoret, et al., 2004; Zwiers, et al., 2001).

Calibration of auditory space could arise using experience of how auditory spatial cues change with self-motion, for example when walking or turning the head (Ashmead, et al., 1998), and by using tactile-motor feedback when touching a sound source. Lewald (2002a) proposed that if such cues are used instead of vision to calibrate spatial hearing in blind humans, compensatory plasticity may take the form of enhanced use of sensory mechanisms that relate auditory azimuth cues to body position through the processing of proprioceptive and vestibular cues, rather than via sharpened hearing and enhanced abilities to discriminate between auditory spatial cues.

The representation or model-based control approach to navigation (Frenz & Lappe, 2005; Turano, Yu, Hao, & Hicks, 2005) proposes that to enable safe navigation through the environment, actions have to be based on accurate internal representations of external space. An alternative account, information-based control (Fajen & Warren, 2003; Gibson, 1958; Warren, 1998) proposes that on-going sensory information, such as that obtained using hearing, can direct locomotion without the need for an internal representation. In the absence of vision, auditory information can be used to guide locomotion using an external sound source (Loomis, Klatzky, Philbeck, & Golledge, 1998; Russell & Schneider, 2006), self-generated echolocation clicks (Kolarik, Scarfe, Moore, & Pardhan, 2016b; Kolarik, et al., 2017c; Thaler, et al., 2020), or a device that generates sounds indicating the distance of objects in the environment (Kolarik, Scarfe, Moore, & Pardhan, 2016c; Kolarik, Timmis, Cirstea, & Pardhan, 2014b). These abilities might be based on an internal representation of space, but they might also be accounted for using an information-based control account (see Kolarik, et al., 2016b; Kolarik, et al., 2017c for further discussion). However, more complex tasks involving inferential navigation and planning a safe path probably do require a well-calibrated auditory spatial map. The poorer performance of blind than of sighted participants in performing these tasks (see Table 1), consistent with the perceptual deficiency hypothesis, suggests that lack of visual information to calibrate such a map may adversely affect navigation abilities, consistent with P6 (calibration requiring visual cues).

The crossmodal calibration hypothesis (Gori, et al., 2010) extends the perceptual deficiency hypothesis, proposing that visual information is necessary during development to calibrate the other senses to accurately process spatial information, as vision is the sense that provides the most accurate information regarding the spatial properties of the environment and it provides immediate, simultaneous perception of multiple objects that are present within the visual field (Thinus-Blanc & Gaunet, 1997). Blindness during the early stages of development prevents visual information from being used for calibration of the spatial processing mechanisms of the other senses, which presumably usually occurs during a critical or sensitive developmental period (Thinus-Blanc & Gaunet, 1997). This leads to prolonged negative effects and degraded auditory performance for certain tasks, consistent with P9 (age of onset). The crossmodal calibration hypothesis and the perceptual deficiency hypothesis have been supported by experimental data showing that early visual loss leads to degraded performance in auditory distance discrimination abilities of early blind children (Cappagli, et al., 2015), poorer abilities to judge sound motion by blind adults (Finocchietti, et al., 2015a), and poorer distance bisection and minimum audible angle task performance for blind children (Vercillo, et al., 2016). However, both the crossmodal calibration hypothesis and the perceptual deficiency hypothesis only apply to a specific subset of tasks, and they do not account for why lack of visual calibration information degrades certain abilities such as auditory bisection or encoding of sound motion, whereas other spatial auditory abilities such as distance or motion discrimination are enhanced in adulthood.

Is it possible to improve auditory abilities for individuals with visual loss, and reduce auditory spatial deficits?

Hearing abilities are affected by the level of familiarity and expertise in using auditory information for making spatial and non-spatial judgments, for performing actions, and for locomotion (e.g. Velten, Ugrinowitsch, Portes, Hermann, & Bläsing, 2016). Earlier age of onset of visual loss, longer duration of visual loss, greater experience with spatial tasks, and high mobility, are associated with enhanced auditory abilities (Thaler, et al., 2020; Voss, et al., 2010) (P1-5, 7-9). For example, as described above, using echolocation regularly in day-to-day life improves spatial abilities, such as sensory-motor coordination during walking for blind individuals (Thaler, et al., 2020) (P8). The auditory expertise of blind people can be enhanced by training, practise, and experience (e.g. Hojan et al., 2012) (P8). Ideally, the duration of the training should be short and the training effects persistent over time. However, long periods of training are sometimes necessary to produce measurable benefits (e.g. Skrodzka, Furmann, Bogusz-Witczak, & Hojan, 2015). For a discussion of how visual deprivation and extensive training may interact to produce improved sensory abilities, see Voss (2011).

An understanding of auditory spatial abilities at early ages is necessary in order to develop appropriate intervention programs for restoration or rehabilitation of degraded auditory abilities caused by loss of vision (Cappagli, et al., 2017). Recent years have seen a rise in technical aids for people with visual loss, but the complexity of such aids, especially for blind children, limits the potential benefits and has led to low user acceptance (for a review, see Cuturi, Aggius-Vella, Campus, Parmiggiani, & Gori, 2016). Nevertheless, virtual reality platforms can be developed to train blind people, for example by reproducing a training environment for orientation and mobility (Seki & Sato, 2010). Other means for improving the accuracy and precision of internal spatial representations, such as echolocation or sensory substitution devices (SSDs), have also been shown to overcome spatial deficits brought on by blindness. Evidence for this is discussed next.

Auditory training

Skrodzka, et al. (2015) compared the effects of auditory training and passive music listening on the performance of several auditory tasks for 7ï 12 year old children and 13ï 19 year old adolescent groups of blind and visually impaired participants and age-matched sighted controls. Auditory training involved performance of a range of psychoacoustic tasks including frequency discrimination and memory for frequency, intensity discrimination, lateralization of stationary and moving sounds, spectral shape discrimination, simultaneous categorization of fundamental frequency and spectral shape, and signal in-noise detection. Music listening involved passive listening to music by Mozart, with alternating presentation of the music with ampliýcation of either the low or high frequencies. Auditory training and music listening occurred in sessions over a period of 4-5 weeks. The auditory training was associated with improved lateralization of two moving car sounds for the blind and visually impaired adolescents only. Auditory training did not result in improvement in performance for any other task. Passive music listening did not result in improved performance for any task for any group.

The accuracy and precision of estimates of the distance of objects using echolocation by blindfolded sighted people have been shown to improve with training (Maezawa & Kawahara, 2019; Tonelli, Brayda, & Gori, 2016). The improved performance was attributed to the development of better hearing abilities or to more accurate calibration of auditory space associated with practice and feedback about the location of spatial references (Maezawa & Kawahara, 2019) (P5-6).

Kolarik, et al. (2014a) suggested that echolocation could be used to generate and maintain accurate representations of auditory space, thereby reducing deficits associated with visual loss in judgments of sound elevation (Lewald, 2002b; Zwiers, et al., 2001) and auditory bisection in azimuth (Gori, et al., 2014; Vercillo, et al., 2016; Vercillo, et al., 2015; Wersenyi, 2012). This was confirmed by Vercillo, et al. (2015), who showed that early blind expert echolocators performed bisection in azimuth with similar precision to a sighted control group, whereas early-blind non-echolocators performed significantly more poorly than sighted controls. In view of this, it seems plausible that spatial information derived from alternative sources, such as from SSDs, may also serve to calibrate auditory space in the absence of visual information. SSDs are electronic travel aids designed to help blind people to detect silent objects by providing auditory or tactile information regarding the distance to the object. SSDs can accurately guide locomotion when they are based on echoes (usually for ultrasound) (Hughes, 2001; Kolarik, et al., 2016c; Kolarik, et al., 2017c; Kolarik, et al., 2014b) or on visual pattern information converted to sound, such as the prosthesis substituting vision with audition (PSVA, Renier et al., 2005) and the vOICe (the middle three letters stand for ñoh I see," Meijer, 1992). The use of an echolocation-based SSD improved the accuracy of judgments of the direction and distance of landmarks located along a previously explored route for early-onset blind participants, probably reflecting better accuracy of the internal representation of space (Veraart & Wanet-Defalque, 1987). It is not yet known whether the regular use of SSDs can lead to a reduction in the spatial deficits that are usually associated with visual loss, such as poor spatial bisection. Although SSDs are an example of technology designed to assist blind people in perceiving the spatial layout of the local environment, establishing the scope of their rehabilitative benefits requires further research. Cuturi, et al. (2016) distinguished between ñrehabilitative technologyò that promotes brain plasticity and allows the device to be removed following rehabilitation and ñassistive technologyò such as the white cane, which does not promote neural plasticity and has to be used on an on-going basis. Most technology currently available for the blind is assistive. There is a need to keep rehabilitation at the forefront of training, interventions or technology for the blind, especially from a young age, as this is key to overcoming spatial deficits (Cuturi, et al., 2016).

<u>Audiomotor, orientation and mobility training</u>

Blind football is a sport requiring well-trained audiomotor skills, where players need to be able to accurately localize the position of the ball, opposing players, and teammates while moving. Recent work has shown that blind footballers were faster than groups of sighted controls (who were either matched in athletic ability or were non-athletes) in identifying the direction of 1-kHz tones positioned frontï left, frontï right, backï left, and backï right relative to the participant (Mieda, Kokubu, & Saito, 2019). Blind footballers were also shown to make fewer frontï back confusions than the other groups, a finding previously shown for blind footballers compared to groups of blind or sighted non-athletes (Velten, et al., 2016). Blind footballers are also better than blind or sighted non-athletes in localizing finger-snap sounds

(Velten, Bläsing, Portes, Hermann, & Schack, 2014; Velten, et al., 2016). The enhanced performance of blind footballers can be attributed to improvements in the processing of auditory information and in motor control following long-term training in blind football, rather than being solely due to cross-modal plasticity (Mieda, et al., 2019), consistent with P8 (experience and practise).

Audiomotor training has been shown to improve auditory spatial abilities in blind participants (Cuppone, Cappagli, & Gori, 2019; Finocchietti, Cappagli, & Gori, 2017; Finocchietti et al., 2015b). Training based on audio-motor contingencies may be less demanding than the training needed to master the use of SSDs, as the former involves a natural association between sounds and motor information, rather than the learning of an artificial set of rules governing the relationship between object orientation and distance and the cues provided by the SSD (Cuppone, et al., 2019). Based on the idea that hearing can be used to provide spatial information about the movement of the individualôs body in space, Finocchietti, et al. (2017) assessed the ability of blind participants and sighted controls to localize the end point of a moving sound source before and after a 2-minute audiomotor training session, or without training. Training consisted of participants holding the sound source, and freely moving it with their hand to explore the surrounding space. The training resulted in a marked improvement in localization for the blind group. The authors suggested that ñaudio-motor feedback can substitute the visuo-motor feedback and recalibrate specific spatial abilitiesò.

There is currently a lack of gold standard methods to assess the development of spatial cognition in individuals with visual losses (Finocchietti, Cappagli, Giammari, Cocchi, & Gori, 2019). To help address this, Finocchietti, et al. (2019) developed the Blind Spatial Perception test (BSP) to enable spatial cognition deficits to be identified and measured for visually impaired children. The BSP involves a battery of tests assessing auditory localization, auditory bisection, auditory distance judgments, auditory reaching, proprioceptive reaching, and general mobility. The use of such tests could help evaluate the effectiveness of rehabilitation procedures for the visually impaired. The interaction between age of onset of blindness, experience, and practice requires further investigation (Teng, et al., 2012).

Conclusions

The current paper proposes a framework involving nine principles that can be used to predict whether visual loss leads to enhancement or degradation of specific auditory abilities. The validity of the proposed principles has been demonstrated by showing that the principles broadly predict the findings for both spatial and non-spatial auditory abilities for a wide range of empirical data involving full blindness, partial visual loss, developmental findings, and the effects of early- and late-onset visual loss. However, there are some inconsistences (see Tables 1-4). These may in part be due to issues such as the heterogeneity of the blind participants tested, or indicative of developmental delay associated with lack of visual information that is later improved through the use of non-visual spatial cues. The predictions based on P5 and P6 are sometimes uncertain because they depend on the extent to which the participant has learned the relationship between auditory cues and the variable that has to be judged, and this is often unknown in advance. Future studies of the effects of visual loss on auditory abilities that have not yet been tested can be predicted using the framework. For example it is predicted that early-onset blindness would result in an enhanced ability to judge another person's mood from the sound of their voice (P1-3).

As mentioned in the Introduction, a comprehensive framework is required to account for why some auditory abilities are enhanced and others are degraded. The main elements that the framework needs to capture are the changes in auditory abilities (both better and worse), cortical reorganization, and changes in the way that auditory cues are calibrated, mapped and interpreted following vision loss. As neither the perceptual deficiency hypothesis nor the perceptual enhancement hypothesis manage to capture all of these elements, a novel hypothesis is needed. Grounded within the framework based on P1-9, we propose a new hypothesis, the Perceptual Restructuring Hypothesis, that attempts to bring the enhancement and deficiency hypotheses together. The Perceptual Restructuring Hypothesis is based on the idea that perceptual systems are configured to provide accurate information about the outside world with low variability, within the limits of the available processing resources. Vision provides substantial information that is used by the auditory system, such as for spatial calibration, but it also uses valuable processing resources. In the event of visual loss, the auditory system is restructured so as to make it provide the most accurate information possible utilizing the available cortical resources. This restructuring results in cortical reorganization, crossmodal recruitment, and changes in internal auditory spatial maps. The restructuring of the way that auditory cues are calibrated, mapped and interpreted leads to changes in auditory abilities, where some become better and some become worse according to the nine principles. This restructuring is also associated with developmental delay due to lack of visual information, which is later improved through the use of non-visual spatial cues.

The proposed hypothesis and framework has practical implications for the rehabilitation of blind people, as it is important to identify auditory abilities that are degraded following vision loss in order to improve these abilities through training or technology, such as through the use of SSDs. Similarly, it is important to identify auditory abilities that are significantly enhanced in blind individuals so that these can be utilized maximally in daily life, such as enhanced echo processing abilities that can be used to obtain spatial information and explore the world using echolocation, linking laboratory research to real-life applications.

The proposed principles will likely be refined as further research brings new results to light and it is probable that further principles may be developed. This may especially be the case in areas that have received less attention than the effects of full blindness, such as the effects of partial visual loss or the effects of the developmental time course of visual loss on audition. For example, Kolarik, et al. (2020) reported that greater severity of visual loss was associated with larger estimates of auditory distance. Should further work show similar findings for other auditory abilities, this might lead to a new general principle that ñgreater severity of visual loss is associated with larger changes in auditory abilities.ò

The framework proposed in the current paper was developed to account for the effects of visual loss on auditory abilities. However, the principles proposed might be adapted to apply to other crossmodal configurations, such as the effects of deafness on visual abilities, or the effects of blindness on tactile abilities. Some of the crossmodal effects in the literature are consistent with the (generalized) principles of the current framework. For example, deaf participants are more accurate than normally hearing participants in judging the direction of motion in the visual periphery (P2 and P3) (Neville & Lawson, 1987), while there are no significant differences in visual acuity between deaf and normally hearing participants (P1) (Codina et al., 2011). The finding that blind participants showed enhanced performance compared with sighted controls in a haptic angle discrimination task is consistent with P2 and P3. Further work is needed to investigate the generalizability of the current framework across different crossmodal configurations.

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