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

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20 **Abstract**

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

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

**41 Introduction**

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

58         Auditory abilities, which are the focus of the current paper, are especially important to  
59 people with full and severe visual loss, who rely heavily on sound for navigating and  
60 exploring new environments and communicating and interacting with others. In the absence  
61 of vision, auditory cues provide spatial information about sound sources and sound-reflecting  
62 objects in extrapersonal space, the region beyond reaching distance. Visual loss does not seem  
63 to affect auditory performance for very basic detection or discrimination tasks, such as the  
64 detection of pure tones in quiet (Yabe & Kaga, 2005) or the detection of changes in intensity  
65 (Voss & Zatorre, 2011). However, blindness can have substantial effects on the accuracy of

66 judgments of the azimuth, distance and elevation of sound sources, and the impact of  
67 blindness on auditory spatial abilities in particular has been the focus of considerable research  
68 (for reviews, see Hotting & Roder, 2009; Kolarik, Moore, Zahorik, Cirstea, & Pardhan,  
69 2016a; Théoret, Merabet, & Pascual-Leone, 2004; Voss, 2016).

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### 71 The perceptual deficiency hypothesis and the perceptual enhancement hypothesis

72 Two primary hypotheses have been put forward to account for how and why auditory  
73 abilities are either degraded or enhanced. These are the perceptual deficiency hypothesis and  
74 the perceptual enhancement hypothesis, respectively. First proposed around sixty years ago,  
75 these hypotheses have continued to shape modern interpretations of the effects of visual loss  
76 on hearing. The perceptual deficiency hypothesis (Axelrod, 1959; Jones, 1975) is specific to  
77 spatial processing, and posits that without an intact visual signal to accurately calibrate  
78 auditory information, performance for auditory spatial tasks will be poorer than normal. This  
79 hypothesis has been supported by studies showing that blind people show deficits in the  
80 construction of internal auditory spatial maps (Gori, et al., 2014; Lewald, 2002b; Zwiers, Van  
81 Opstal, & Cruysberg, 2001); these studies are described in more detail later in this paper. The  
82 perceptual deficiency hypothesis has been used to explain the poorer auditory performance of  
83 visually impaired people in judging elevation (Lewald, 2002b; Zwiers, et al., 2001) and  
84 absolute distance (Kolarik, Pardhan, Cirstea, & Moore, 2017a), and in a spatial bisection task,  
85 which involves presentation of three successive sounds in different locations, the participant  
86 being asked to judge whether the second sound is closer to the first or the third (Gori, et al.,  
87 2014). In contrast, the compensation or perceptual enhancement hypothesis (Rice, 1970)  
88 suggests that loss of or reduced visual input leads to greater reliance on and experience with  
89 the use of auditory information compared to fully sighted people, and this, combined with  
90 compensatory processes such as recruitment of visual areas of the brain for the processing of

91 auditory information, leads to enhanced performance (Collignon, Voss, Lassonde, & Lepore,  
92 2009; Dormal, Rezk, Yakobov, Lepore, & Collignon, 2016; Voss, 2016; Voss & Zatorre,  
93 2012). The perceptual enhancement hypothesis has been used to explain results showing  
94 enhanced auditory performance following blindness for judgments of sound source azimuth  
95 (Lessard, Pare, Lepore, & Lassonde, 1998), frequency discrimination (Gougoux et al., 2004),  
96 distance discrimination (Kolarik, Cirstea, & Pardhan, 2013b; Voss et al., 2004) and detection  
97 of motion (Lewald, 2013).

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

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

127

128 Proposed principles determining whether enhancement or degradation occurs following  
129 blindness

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

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

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

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

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

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

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

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

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

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

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

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

#### 156 Relative auditory distance perception

157 A number of studies have shown that blindness results in an enhanced ability to judge the  
158 relative distance of sounds, e.g. to judge which of two successive sounds is closer. Ashmead  
159 et al. (1998) assessed distance discrimination for pairs of Gaussian noise bursts presented at

160 distances between 1.55 and 1.95 m in a reverberant environment. Blind children (a mixture of  
161 early and late-onset) were significantly better able to discriminate distance than groups of  
162 sighted children or sighted adults. Voss, et al. (2004) reported that early- and late- onset blind  
163 groups were able to discriminate the distances of pairs of broadband noises presented in a  
164 reverberant environment between 3 and 4 m from the participant, whereas sighted controls  
165 were unable to discriminate the distances of the noise bursts. Kolarik, et al. (2013b) assessed  
166 distance discrimination for pairs of broadband noise bursts presented between 1 and 8 m away  
167 in virtual anechoic and reverberant environments. The blind participants were better than  
168 sighted or partially sighted groups at using two the two main auditory distance cues, level and  
169 direct-to-reverberant energy ratio (DRR)(Kolarik, Cirstea, & Pardhan, 2013a; Kolarik, et al.,  
170 2016a; Zahorik, Brungart, & Bronkhorst, 2005), to discriminate distance. These findings are  
171 consistent with P1 (complexity), P2 (discrimination), and P4 (identifying the direction of  
172 monotonic change). Overall, the findings for relative auditory distance perception are  
173 consistent with the perceptual enhancement hypothesis. They are not consistent with the  
174 perceptual deficiency hypothesis.

175

### 176 Echolocation

177 Human echolocation is the ability to emit sounds and utilize the returning echoes to obtain  
178 information regarding silent objects in the vicinity, in a similar manner to bats and dolphins  
179 (for reviews, see Kolarik, et al., 2014a; Stoffregen & Pittenger, 1995; Thaler & Goodale,  
180 2016). Within the blind population, those who echolocate often have real-life advantages,  
181 including higher salary and higher mobility in unfamiliar places, than those who are not  
182 echolocators (Thaler, 2013). Successful echolocation depends on the ability to produce  
183 appropriate signals, such as tongue clicks, and to detect and discriminate the sound reflections  
184 (Tirado, Lundén, & Nilsson, 2019). Although both sighted and blind people are able to

185 echolocate, blind people display enhanced skills for several aspects of echolocation, including  
186 object detection (Kolarik, Scarfe, Moore, & Pardhan, 2017c; Rice, 1969) and localization  
187 (Rice, 1969; Schenkman & Nilsson, 2010, 2011), discrimination of the spatial positions of  
188 two disks (Teng & Whitney, 2011), discrimination of object material or texture (but not  
189 density, Hausfeld, Power, Gorta, & Harris, 1982; Kellogg, 1962), judgment of size and  
190 distance (Kellogg, 1962), and shape (Hausfeld, et al., 1982), and when using sound to  
191 navigate around obstacles (Kolarik, et al., 2017c) or to walk in a straight line parallel to a  
192 wall (Strelow & Brabyn, 1982). Blind people are also more sensitive than sighted controls to  
193 non-self-generated sound echoes (Dufour, Després, & Candas, 2005; Kolarik, et al., 2013b).

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

203 Schenkman and Nilsson (2010) played recorded bursts of noise to blind (a mix of  
204 early and late-onset) and sighted participants with an aluminum disk present at distances  
205 between 0.5-5 m, or with the disk absent. Blind participants were better able to detect the  
206 presence of the disk than sighted participants. Possible cues were: (1) the overall level was  
207 higher when the disk was present; (2) the interaction of the direct sound and the reflected  
208 sound from the disk produced spectral and temporal cues that evoked a pitch percept. In a  
209 follow-up study Schenkman and Nilsson (2011) showed that a mix of early and late-onset

210 blind participants performed better than sighted participants when only the pitch cue was  
211 present but not when only the level cue was present, suggesting the importance of spectral and  
212 temporal information for blind people when detecting objects using echolocation.

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

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

227 Kolarik, et al. (2017c) investigated the kinematics of obstacle circumvention for an  
228 early-onset blind echolocation expert, an early-onset blind group untrained in echolocation,  
229 and a sighted control group. Participants were blindfolded and had to detect and navigate  
230 around an obstacle using echolocation clicks. The obstacle was placed in a random location at  
231 the midline of the participant or to the left or right, at a distance of 1.5 or 2 m, or was absent.  
232 Blind non-echolocators navigated significantly more effectively than blindfolded sighted  
233 controls, as shown by a greater obstacle detection range, fewer collisions, lower movement  
234 times, and fewer velocity corrections (number of stops and starts, a measure of how fluid the

235 movement is). The blind expert echolocator showed performance similar to or better than for  
236 the other groups, although the differences were not significant. The results suggest that blind  
237 people develop enhanced abilities to process sound echoes and these can be used to enhance  
238 locomotor performance, resulting in more accurate, faster and more fluid navigation using  
239 echolocation, even without extensive training or experience.

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

259 (Arnott, Thaler, Milne, Kish, & Goodale, 2013; Milne, Arnott, Kish, Goodale, & Thaler,  
260 2015; Teng, Puri, & Whitney, 2012; Teng & Whitney, 2011; Thaler, et al., 2020).

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

263

#### 264 Sound localization in azimuth

265 Auditory cues to azimuth can in principle be calibrated without visual information. For  
266 example, a blind person may be able to feel the position of a nearby sound source such as a  
267 radio. Also, for a sound source that is fixed in azimuth, the person can rotate their head to  
268 sample how the cues change with azimuth. Under these conditions, blindness may lead to  
269 enhanced performance (P5), but only if accurate calibration has been achieved. Several  
270 studies have shown that judgments of sound azimuth are indeed enhanced as a result of  
271 blindness (Després, Boudard, Candas, & Dufour, 2005a; Muchnik, Efrati, Nemeth, Malin, &  
272 Hildesheimer, 1991; Rice, 1969). This enhancement is often evident only in specific  
273 conditions, such as when listening monaurally (Doucet et al., 2005; Gougoux, Zatorre,  
274 Lassonde, Voss, & Lepore, 2005; Lessard, et al., 1998; Voss, Lepore, Gougoux, & Zatorre,  
275 2011; Voss, Tabry, & Zatorre, 2015) or towards the side (Fieger, Röder, Teder-Sälejärvi,  
276 Hillyard, & Neville, 2006; Röder et al., 1999; Voss, et al., 2004) or back (Després, et al.,  
277 2005a). Several studies showed enhanced performance for approximately half of their blind  
278 participants only. A possible explanation for this was investigated by Voss, et al. (2015) and  
279 is discussed in more detail later in this paper.

280 Lessard, et al. (1998) asked participants to judge the location of broad-band noise  
281 bursts presented binaurally or monaurally (by plugging one ear) at azimuths between 0° and  
282 ±78° to sighted participants and participants with congenital visual loss who either had  
283 residual vision or were totally blind. In the monaural condition, half of the totally blind group

284 showed highly accurate performance and localized the stimuli on the appropriate side of the  
285 head, suggesting a good ability to use monaural spectral cues for judgments of azimuth.  
286 Sighted controls, blind participants with residual vision, and half of the totally blind group  
287 showed poor performance and a bias to localize the stimuli on the side of the non-plugged ear.  
288 There were no significant differences in localization between sighted and totally blind groups  
289 under binaural conditions.

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

302 Similar findings were reported by Voss, et al. (2011) for a spectral discrimination task.  
303 They presented participants with broadband noise bursts filtered using monaural head-related  
304 transfer functions measured using a KEMAR manikin so as to simulate sounds with azimuths  
305 between  $0^\circ$  and  $\pm 60^\circ$ . The sounds were presented via a single loudspeaker at  $0^\circ$  azimuth, so  
306 only spectral cues for azimuth were available. Approximately half of the early-onset blind  
307 group showed markedly better performance than the other half of that group, a late-onset  
308 blind group, and sighted controls. Overall, the results of these studies support the proposal

309 that more efficient use of spectral information underlies the superior performance of some  
310 blind participants for the monaural localization of sounds in azimuth.

311 Voss, et al. (2004) measured binaural localization in azimuth for sighted, early-onset,  
312 and late-onset blind groups using a minimum audible angle (MAA) task, in which two  
313 successive sounds, a reference and a target, were presented at different spatial locations. The  
314 participant was asked to report whether the second sound was located to the left or right of the  
315 first sound (or more to the front or to the back). Voss et al. used reference stimuli presented at  
316  $0^\circ$  (using test sounds to the left or the right of  $0^\circ$ ) or  $90^\circ$  azimuth (using test sounds in front of  
317 or behind  $90^\circ$ ). The sound sources were beyond reaching and touching distance and  
318 background noise was present. For the  $90^\circ$  reference azimuth and for the rear hemifield only,  
319 the early- and late-onset blind groups performed better than sighted controls. For the  $0^\circ$   
320 reference azimuth, there were no significant differences between the groups, which was  
321 attributed to ceiling effects.

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

327 Feierabend, Karnath, and Lewald (2019) reported that blind participants (a mixture of  
328 early and late onset) performed more poorly than sighted participants when localizing sounds  
329 at azimuths between  $-45^\circ$  and  $+45^\circ$ . This is the only study that we are aware of showing an  
330 effect in this direction for judgments of azimuth. In this study, the participant adjusted a  
331 swivel pointer to indicate the perceived direction of the source. Possibly, the blind  
332 participants were relatively poor in judging the direction of the pointer, rather than being poor

333 in judging the locations of the sounds themselves. However, that study also differed from  
334 other studies in other ways, for example in the use of environmental sounds (a cuckoo clock,  
335 laughing man, crying baby, barking dog, or ringing telephone) as stimuli, whereas previous  
336 studies generally presented noise bursts. Also, the heterogeneity of the blind participants in  
337 severity of visual loss, age of blindness onset, and duration of blindness, may have influenced  
338 the results.

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

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

353         The results are in line with the perceptual enhancement hypothesis. The enhanced  
354 performance in the use of monaural spectral cues and binaural cues (in peripheral space) for  
355 localization in azimuth is consistent with P1 (complexity), P2 (discrimination), P4  
356 (identifying the direction of monotonic change), P5 (identifying the direction of non-

357 monotonic change) and P7 (calibration using non-visual cues), if it is assumed that blind  
358 participants have learned the relationship between the complex spectral cues produced by the  
359 pinna and sound source azimuth. The spectral cues may be calibrated via the ITD and ILD  
360 cues that usually accompany them or by monitoring how the spectral cues associated with a  
361 fixed sound source change when the person moves around a room or moves their head in the  
362 left-right direction.

363

#### 364 Auditory motion perception

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

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

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

388

### 389 Self-localization using sound

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

397

### 398 Auditory spatial attention

399 Kujala, Lehtokoski, Alho, Kekoni, and Näätänen (1997) compared performance for early-  
400 blind and sighted participants in a bimodal divided spatial attention task. Intermixed auditory  
401 tones (delivered via headphones with an ITD of 0.5 ms and heard on the right) and tactile  
402 pulses (applied to the left index finger) were presented in a sequence together with occasional  
403 target stimuli that differed in location from the other stimuli (0 ms ITD for the auditory

404 stimuli and left middle finger for the tactile stimuli). Participants were required to press a key  
405 as quickly as they could in response to each auditory and tactile target. Blind participants had  
406 faster reaction times for auditory targets. Similar results were found in another study  
407 investigating auditory-tactile divided spatial attention (Collignon, Renier, Bruyer, Tranduy, &  
408 Veraart, 2006): blind participants had faster reaction times than sighted participants for the  
409 auditory component of the task. Collignon, et al. (2006) suggested that a previous failure to  
410 find differences between blind and sighted participants in an auditory spatial selective  
411 attention task (Kujala et al., 1995) may have been due to attentional disengagement stemming  
412 from the ease of the task. Overall, the results are consistent with P1 (complexity) and P2  
413 (discrimination), and the perceptual enhancement hypothesis.

414

#### 415 **Summary of results on enhanced auditory spatial abilities in the blind**

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

428

429 **Auditory spatial abilities that are degraded as a result of full blindness**430 Tasks involving spatial metrics: Spatial bisection, and auditory encoding and movement  
431 reproduction

432 The ability to judge the position of a sound source relative to the positions of other sound  
433 sources has been explored using a spatial-bisection task (Campus, Sandini, Amadeo, & Gori,  
434 2019; Gori, et al., 2014; Vercillo, et al., 2016; Vercillo, et al., 2015). As mentioned earlier,  
435 this involves listening to three successive sounds with different spatial locations. The  
436 participant is asked to report whether the second sound is closer to the first or the last sound.  
437 It has been argued that this task requires that auditory cues for location are used to create an  
438 internal map of the positions of objects in space; the task is then performed by comparing  
439 distances in the internal map (Finocchietti, et al., 2015a; Gori, et al., 2014). Performance for  
440 this bisection task has often been compared with that for an MAA task. The MAA task has  
441 been argued to involve simple discrimination of two sound positions based on cues such as  
442 changes in ITD or ILD; a map of space is not required (Aggius-Vella et al., 2020;  
443 Finocchietti, et al., 2015a; Gori, et al., 2014).

444 Several studies have shown that blindness results in poorer spatial bisection in azimuth  
445 than for sighted controls under binaural listening conditions (Campus, et al., 2019; Gori, et al.,  
446 2014; Vercillo, et al., 2016; Vercillo, et al., 2015). In contrast, blind and sighted groups show  
447 similar performance for a MAA task (Gori, et al., 2014; Vercillo, et al., 2016; Vercillo, et al.,  
448 2015; Wersenyi, 2012) or a temporal bisection task (Campus, et al., 2019). These results are  
449 consistent with P1 (complexity) and P6 (calibration requiring visual cues).

450 Another relatively difficult task that has been argued to require a spatial metric was  
451 used by Finocchietti, et al. (2015a). The task involved listening to a sound source that was

452 moving in two-dimensional space and then reproducing the pattern of movement on a vertical  
453 panel located in front of the participant. Performance was compared for early- and late-onset  
454 blind and sighted participants. The early-onset blind group were less accurate than the other  
455 groups in determining the end-point sound position, and showed a bias for targets presented in  
456 the lower area of the vertical plane, located below the nose of the participant, to be perceived  
457 in space located above the nose. These results are consistent with P1 (complexity), P5  
458 (identifying the direction of non-monotonic change), P6 (calibration requiring visual cues),  
459 and P9 (age of onset). The results are consistent with the perceptual deficiency hypothesis, but  
460 not with the perceptual enhancement hypothesis.

461

#### 462 Sound localization in elevation

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

472 Lewald (2002b) measured the ability of early-blind and sighted groups to judge the  
473 location of high-frequency band-pass-filtered “frozen” noises (the same noise waveform on  
474 each trial) presented at elevations ranging from  $-30^\circ$  to  $+30^\circ$ . The groups showed similar

475 performance in judging the relative positions of the sound sources. However, the blind group  
476 showed a deficit in judging the absolute vertical positions of the sound sources.

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

495

#### 496 Absolute distance judgments

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

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

506         Wanet and Veraart (1985) assessed the ability to judge the direction and distance of  
507 800-Hz tones in near space, between 18 and 62 cm from the participant, for early- and late-  
508 onset blind groups, and sighted controls. Distance judgments were less accurate for the early-  
509 blind group than for the other groups, although the differences would have been non-  
510 significant if the authors had adjusted their significance levels to allow for multiple  
511 comparisons. Macé, Dramas, and Jouffrais (2012) showed that early-onset blind participants  
512 were less accurate than sighted participants at reaching towards white-noise sounds presented  
513 in peripersonal space. Lai and Chen (2006) obtained absolute distance judgments of blind  
514 (age of onset not reported) and sighted participants for a musical tone or telephone sound  
515 presented at 3 m distance. The sighted group on average made lower errors than the blind  
516 group, although the difference was not significant.

517         Kolarik, Cirstea, Pardhan, and Moore (2013c) obtained absolute distance judgments  
518 for speech sounds heard at virtual distances between 1.2 and 13.8 m. Normally sighted  
519 participants judged the distances of closer sounds accurately, but underestimated the distance  
520 to far sounds, as found in previous studies (for reviews, see Kolarik, et al., 2016a; Zahorik, et  
521 al., 2005). Early-blind participants underestimated the absolute distance of far sound sources,  
522 and overestimated the absolute distance of closer sound sources. This deficit was found to

523 generalize across reverberant and anechoic environments and speech, music and noise stimuli  
524 in extrapersonal space (Kolarik, et al., 2017a).

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

531

### 532 Inferential navigation and road crossing decisions using sound

533 Visual loss adversely affects navigation, impairing the ability to move safely through the  
534 environment and maintain orientation towards a destination (Veraart & Wanet-Defalque,  
535 1987). Gait is also affected; relative to sighted people, early and late-onset blind people have  
536 a slower walking speed, shorter stride length, and longer time spent in the stance phase of  
537 gait, during which the foot remains in contact with the ground. This enables blind people to  
538 move safely and to maintain a posture with greater stability (Nakamura, 1997).

539 Inferential navigation requires participants to derive novel relationships between  
540 themselves and objects in the environment based on prior experience, such as completing a  
541 triangular route (Seemungal, Glasauer, Gresty, & Bronstein, 2007; Thinus-Blanc & Gaunet,  
542 1997). Several studies have shown that blindness results in poorer inferential navigation  
543 (Gori, Cappagli, Baud-Bovy, & Finocchietti, 2017; Herman, Chatman, & Roth, 1983; Rieser,  
544 Guth, & Hill, 1986; Seemungal, et al., 2007; Thinus-Blanc & Gaunet, 1997; Veraart &  
545 Wanet-Defalque, 1987). Veraart and Wanet-Defalque (1987) tested early-onset blind, late-  
546 onset blind, and blindfolded sighted controls in a task designed to assess the accuracy of  
547 internal representations of space. Participants were guided along a route in which landmarks

548 were indicated both with and without the use of an ultrasonic echolocation device that  
549 allowed object localization (the device was not used with the sighted controls). Participants  
550 then inferred the distance between their position and each landmark, and indicated the  
551 directions of the landmarks. Without the device, early-onset blind participants performed  
552 more poorly than the other groups for both distance and direction, indicating that early-onset  
553 blindness resulted in impaired internal representations of space, consistent with P1, 6 and 9.  
554 With the device, both blind groups improved. The results obtained without the device are  
555 consistent with a study of Rieser, et al. (1986), who reported that early-onset blindness  
556 resulted in lower sensitivity to changes in perspective structure (changes in direction and  
557 distance to stationary objects) when moving through the environment. However, this result  
558 was not replicated by Loomis et al. (1993), who suggested that mobility skills may have  
559 affected performance, and that blind participants who travel independently are likely to  
560 develop better locomotor abilities. Overall, the majority of studies support the view that early-  
561 onset blindness results in poorer performance for inferential navigation tasks using sound,  
562 consistent with P5 (identifying the direction of non-monotonic change), P6 (calibration  
563 requiring visual cues), and P9 (age of onset).

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

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

573 (2012). Pedestrian safety when crossing a road relies substantially on accurate judgments of  
574 the time required to cross the road and the time before the next vehicle arrives (Hassan, 2012).  
575 Guth, et al. (2013) investigated road crossing judgments of a mix of early and late-onset blind  
576 and sighted controls at a roundabout. The blind group made riskier judgments, especially  
577 when traffic volume was high and the participant was positioned near the roundabout. The  
578 blind group also accepted fewer safe opportunities for crossing and were slower to make  
579 crossing judgments. Hassan (2012) assessed road-crossing decisions for sighted controls,  
580 participants with partial visual loss, and a totally blind group (age of onset not reported).  
581 When crossing decisions were based on auditory information only, the blind group made  
582 significantly less accurate decisions than the other groups. Overall, these results are consistent  
583 with P5 (identifying the direction of non-monotonic change), and P6 (calibration requiring  
584 visual cues).

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

595

596

597 **Summary of enhanced and degraded auditory spatial abilities in the blind**

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

602

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 Voss et al. (2004) C	Enhanced Enhanced	Mix Early (<11 yrs) and Late (>16 yrs)
Motion discrimination P1-3, 9	Kolarik, et al. (2013a) C Schiff & Oldak (1990) C Lewald (2013) C, I Jiang et al. (2014) C Jiang et al. (2016) C	Enhanced Enhanced Enhanced Enhanced Enhanced	Mix Early Early and Late Early 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

603

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

612

### 613 **The effect of visual loss on non-spatial auditory abilities**

#### 614 Speech perception

615 Several studies have shown enhanced speech perception in quiet and noisy environments for  
616 blind people (Hugdahl et al., 2004; Lucas, 1984; Muchnik, et al., 1991; Niemeyer &  
617 Starlinger, 1981; Röder, Demuth, Streb, & Rösler, 2003; Rokem & Ahissar, 2009). Niemeyer

618 and Starlinger (1981) reported better discrimination by early-onset blind than by sighted  
619 participants for speech in quiet or in background noise at 50 dB SPL. Muchnik, et al. (1991)  
620 reported better speech discrimination by early blind than by sighted controls for speech in  
621 noise presented at 40 dB above the speech reception threshold, but similar performance  
622 between groups in quiet. Rokem and Ahissar (2009) showed that speech reception thresholds  
623 were lower (better) for congenitally blind than for sighted controls for speech in quiet and in  
624 background noise at 60 dB SPL. Compared to sighted controls, early blind participants  
625 showed earlier evoked potentials when deciding whether or not a sentence was meaningful  
626 (Röder, Rösler, & Neville, 2000), were faster when performing a lexical decision task (Röder,  
627 et al., 2003), had better vowel discrimination (Ménard, Dupont, Baum, & Aubin, 2009), and  
628 had better discrimination of syllables (Hugdahl, et al., 2004). Klinge, Röder, and Büchel  
629 (2010) showed that congenitally blind people were better able to discriminate emotions using  
630 affective prosody information in pseudowords. Dietrich, Hertrich, and Ackermann (2011,  
631 2013) showed that blind participants could comprehend accelerated speech at rates up to 22  
632 syllables per second, whereas the limit for sighted participants was approximately 8 syllables  
633 per second.

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

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

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

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

651

#### 652 Auditory non-spatial attention

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

663 Röder, Rösler, and Neville (1999) asked sighted and congenitally blind participants to  
664 attend to sequences of standard tones at 1500 Hz presented to the right, left, or both ears, with  
665 occasional 1000-Hz target tones presented. Participants were asked to press a button as fast as

666 possible in response to a target, regardless of its ear of presentation. Blind participants showed  
667 faster reaction times than controls.

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

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

680

### 681 Temporal resolution

682 Several studies have addressed the issue of whether blindness is associated with enhanced  
683 auditory temporal processing. Muchnik, et al. (1991) measured thresholds for detection of a  
684 temporal gap in noise bursts for early-blind participants and sighted controls. Thresholds were  
685 lower (better) for early-blind and late-onset blind participants (10 in each group) than for  
686 sighted controls. Bross and Borenstein (1982) showed no difference between five late-blind  
687 participants (becoming blind after the age of 7 years) and a sighted group in auditory temporal  
688 acuity assessed using a flutter-fusion task. Van der Lubbe, Van Mierlo, and Postma (2010)  
689 showed that discrimination of the duration of bursts of noise was better for 12 early-blind

690 participants than for 12 sighted controls. Stevens and Weaver (2005) showed that 15 early-  
691 blind participants had lower thresholds than 29 sighted controls in an auditory temporal order  
692 judgment task and an auditory backward masking task. They suggested that the superior  
693 performance of the blind participants reflected more rapid and precise perceptual  
694 consolidation of stimulus properties into working memory. Overall, the results support the  
695 idea that blindness enhances at least some aspects of auditory temporal processing for early-  
696 blind participants, consistent with P1 (complexity), P2 (discrimination), P3 (detection), and  
697 the perceptual enhancement hypothesis.

698

#### 699 Auditory memory

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

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

716

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

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

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

734 Wan, Wood, Reutens, and Wilson (2010) compared sighted controls with blind  
735 participants matched in age and musical ability for three auditory tasks: frequency  
736 discrimination, categorization of fundamental frequency and spectral shape (corresponding to  
737 the percepts of pitch and timbre, respectively), and working memory for frequency. The

738 authors tested three groups of blind participants: congenitally blind, early-onset blind who lost  
739 their sight between the ages of 1.4 and 13 years, and a late-onset blind group who lost their  
740 sight after 14 years. Note that these definitions of early and late onset loss are different to  
741 those used in Table 1 (early-onset before 5 years of age, late onset after 5 years of age). For  
742 the frequency-discrimination task, congenitally and early-onset blind participants performed  
743 better than sighted controls, and congenitally blind participants outperformed the sighted  
744 group to a greater extent than early-onset blind participants. For the pitch-timbre  
745 categorization task, both the congenital and early-onset blind participants showed  
746 significantly better performance than the sighted control group. Blind and sighted  
747 performance was similar for working memory for frequency. For all tasks, no significant  
748 differences in performance were observed between late-onset blind participants and sighted  
749 controls.

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

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

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

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

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

780

### 781 **Summary of auditory non-spatial abilities in the blind**

782 Table 2 summarises the auditory non-spatial abilities investigated for the blind population,  
783 including many abilities related to music, voice recognition, auditory attention, temporal  
784 abilities, verbal memory, and perceptual consolidation. A number of non-spatial abilities have  
785 been reported to be enhanced following blindness and only a few have been reported to be  
786 degraded, suggesting a general overarching principle that auditory abilities that are not

787 involved in spatial processing are likely to become enhanced following blindness, consistent  
 788 with P1 (complexity), P2 (discrimination), P3 (detection), P9 (age of onset), and the  
 789 perceptual enhancement hypothesis.

790

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-Augustenberg & Schultz (2019) C	Enhanced	Early
Learning metrical rhythms P1-2	Carrara-Augustenberg & 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 Kujala et al. (1997) C	Enhanced Enhanced	Early Early
Auditory memory P1	Röder & Rösler (2003) C	Enhanced	Early and late
Verbal memory P1	Röder et al. (2001) C Amedi et al. (2003) C	Enhanced Enhanced	Early 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

---

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

792

793 **The effects of partial visual loss on auditory abilities**

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

797       Blindness in one eye only was shown to result in improved accuracy relative to  
 798 sighted controls for monaural localization of the azimuth of sounds and for binaural  
 799 localization in azimuth for sounds from frontal regions of space (Hoover, Harris, & Steeves,  
 800 2012). Enhanced azimuth localization abilities have also been reported for myopic (short-  
 801 sighted) participants compared to sighted controls (Després, Candas, & Dufour, 2005b;  
 802 Dufour & Gérard, 2000). Participants with a range of causes of partial visual loss self-  
 803 reported that their auditory abilities were enhanced compared to sighted controls in a number  
 804 of situations, including locating the position of a talker, following speech that switched

805 between one person and another, separating speech from music, being able to hear music  
806 clearly, and understanding speech in a car (Kolarik et al., 2017b).

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

824 Ahmad et al. (2019) studied changes in auditory spatial representations of azimuth and  
825 elevation brought on by macular degeneration (MD), which results in central visual losses.  
826 White noises were produced from one randomly selected loudspeaker within a  $5 \times 5$  matrix of  
827 25 loudspeakers. Participants were required to touch the position corresponding to the  
828 perceived location of the sound. Participants with MD judged off-center sounds to be shifted  
829 towards the centre of the loudspeaker matrix, corresponding to the position of the central

830 scotoma. No such bias toward any particular area was found for the sighted controls. The  
831 older the participant was at the onset of visual loss, the greater was the magnitude of the bias  
832 towards the center.

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

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

847 In summary, the current evidence shows that partial visual loss does affect a number  
848 of auditory spatial abilities (Table 3). Both azimuth and elevation localization show biases  
849 (Ahmad, et al., 2019), while locating the position of a talker, following speech switching  
850 between people, separating speech from music, hearing music clearly, and ease of  
851 understanding speech in a car are self-reported to be enhanced (Kolarik, et al., 2017b). For  
852 localization in azimuth, blindness in one eye is associated with enhancement (Hoover, et al.,  
853 2012), while central visual loss in both eyes is associated with degradation (Lessard, et al.,

854 1998). Severe visual loss is associated with reduced accuracy in judging the distance of closer  
 855 sounds and increased accuracy for farther sounds, reflecting systematic changes in the  
 856 mapping between simulated and perceived distance (Kolarik, et al., 2020). Further studies are  
 857 needed to clarify the effects of the type of visual loss on hearing, such as monocular blindness  
 858 with one unimpaired eye or central or peripheral visual loss.

859 In summary, the literature on partial visual loss shows similar results to that for full  
 860 visual loss, in that spatial abilities become either enhanced, consistent with the perceptual  
 861 enhancement hypothesis, or degraded consistent with the perceptual deficiency hypothesis,  
 862 whereas non-spatial abilities are generally only enhanced, consistent with the perceptual  
 863 enhancement hypothesis and with the nine principles. However, the results of Lessard, et al.  
 864 (1998) and Ahmad, et al. (2019) are of particular interest as they are the only studies to date to  
 865 show that partial visual loss can have the opposite effect (of degrading azimuth localization)  
 866 to that of full blindness (which usually enhances localization in azimuth). Lessard, et al.  
 867 (1998) suggested several possible explanations for the degraded performance of participants  
 868 with partial visual loss, including: (1) abnormal orienting behaviours; (2) conflicts or  
 869 confusions between auditory spatial maps derived from peripheral and central vision; (3) lack  
 870 of recruitment of deafferented brain areas. More studies are needed to test these explanations,  
 871 and to assess the effects of partial visual loss on other auditory abilities.

872

<b>Auditory ability</b>	<b>Studies</b>	<b>Effect of loss</b>
<b>Spatial</b>		
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 Less consistent judgments
Absolute distance judgment P6	Kolarik et al. (2020) C	Biased
Azimuth P1-2, 4-5, 9 and elevation P6	Ahmad et al. (2019) D	Enhanced by self-report
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
<b>Non-spatial</b>		
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

873

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

878

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

881 Studies of the effects of visual loss on hearing for children and adolescents provide  
882 information regarding the role of vision in shaping internal representations of auditory space  
883 in the early years of life and the development of spatial and non-spatial cognition. Witkin,  
884 Birnbaum, Lomonaco, Lehr, and Herman (1968) tested congenitally blind and sighted  
885 adolescents aged 12-20 years in an auditory embedded-figures test. A tune of 3-5 notes was  
886 followed by a longer and more complex tune, that either did or did not contain the first tune.  
887 The participant had to report whether the complex tune contained the first tune. The blind  
888 participants performed better than the sighted controls. Enhanced performance in the blind  
889 group persisted when musical experience was controlled for. The authors interpreted the  
890 results as evidence of greater capacity for sustained auditory attention in the blind, although  
891 the results may also be interpreted as evidence for enhanced fundamental-frequency

892 processing or better auditory memory in blind adolescents (Collignon, et al., 2006). These  
893 results are consistent with P1 (complexity), P2 (discrimination), P3 (detection), and the  
894 perceptual enhancement hypothesis.

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

906 Cappagli and Gori (2016) investigated the effect of visual loss on sound localization in  
907 azimuth for children aged 7-17 years and for adults. On each trial a 500-Hz tone was  
908 delivered from one of a horizontal array of loudspeakers. The participant used a cane to point  
909 to the location of the tone. Early- and late-onset blind adults performed similarly to sighted  
910 adults. However, blind children and those with low vision performed significantly more  
911 poorly than age-matched sighted children. The authors interpreted the developmental delay  
912 associated with visual loss as supporting the idea that vision provides the most reliable  
913 information for calibrating auditory spatial representations (Alais, Newell, & Mamassian,  
914 2010). However, their data also suggest that non-visual spatial cues (tactile and sensorimotor)  
915 provide information that improves auditory spatial representations in later adulthood (Fiehler,  
916 Reuschel, & Rösler, 2009).

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

928           The studies described earlier for adults support the idea that blindness leads to a deficit  
929 in localization in elevation (Lewald, 2002b; Zwiers, et al., 2001). However, Ashmead, et al.  
930 (1998) showed that blind children had significantly smaller vertical MAAs for Gaussian  
931 noise-burst signals than sighted children and sighted adults. Ashmead, et al. (1998) also  
932 reported that blind children showed more accurate distance judgments when reaching out and  
933 putting their finger on the perceived location of a previously presented sound source.  
934 Regarding the difference between the findings of Cappagli and Gori (2016) and Vercillo, et  
935 al. (2016) and those of Ashmead, et al. (1998), Vercillo, et al. (2016) noted that the blind  
936 children tested by Ashmead, et al. (1998) had a relatively large age range (6-20 years) and  
937 included some children who lost their sight later in life and who had light perception or  
938 pattern vision, whereas Vercillo, et al. (2016) tested only congenitally blind children with a  
939 narrow age range (mean = 11 years, SD = 0.8 years).

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

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

965 In summary, the evidence regarding the effects of visual loss on auditory abilities for  
 966 children and adolescents is mixed, some studies showing enhancement consistent with the  
 967 perceptual enhancement hypothesis and others showing degraded performance consistent with  
 968 the perceptual deficiency hypothesis, even for the same ability, such as localization in  
 969 azimuth (Table 4). Further work is needed to clarify the ages at which visual loss leads to  
 970 significant differences in auditory abilities. In addition, with the exception of Witkin, et al.  
 971 (1968), the studies to date have focussed on auditory spatial abilities; the developmental time  
 972 course of non-spatial auditory abilities in the blind is currently under researched.

973

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 Degraded for blind	Mean age 10.9±0.8
3D static and dynamic localization P5-6	Cappagli, et al. (2017) C		Mean age 3.5-3.6

974

975 Table 4. A summary of auditory abilities or children and young adults with visual loss, the  
 976 studies that investigated these abilities, the effect of visual loss on these abilities, and the age  
 977 range of the participants. Participants had either full or partial visual loss (see text for details).  
 978 D stands for dependant; the outcome would depend on whether or not the relationship  
 979 between acoustic cues and the variable that has to be judged has been learned with sufficient  
 980 accuracy (P5-6).

981

**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

1007 task, indicating less audio-visual facilitation or less reliance on visual information. These  
1008 results suggest that vision early in life is important for audio-visual perception to mature.

1009 Voss and Zatorre (2012) highlighted the possible role of social and personality factors  
1010 in the development of cortical reorganization that leads to enhanced auditory abilities. Such  
1011 factors might affect the extent to which the individual takes part in activities that might  
1012 promote cortical reorganization, such as exploration of the environment. This has not been the  
1013 focus of systematic study, and needs further exploration.

1014 In some of the studies investigating monaural horizontal localization that were  
1015 described above, there were marked individual differences among early-onset blind  
1016 participants, some showing greater accuracy than sighted controls and some showing similar  
1017 accuracy to sighted controls (Doucet, et al., 2005; Gougoux, et al., 2005; Lessard, et al.,  
1018 1998). To account for why a subset of blind participants showed superior performance, Voss,  
1019 et al. (2015) proposed that variations in performance across blind participants may be due to a  
1020 trade-off in skills for vertical and horizontal localization. They showed that blind participants  
1021 with the poorest accuracy in vertical localization had the highest accuracy in monaural  
1022 horizontal localization. These results suggest that enhancement of one auditory ability may  
1023 come at the cost of worse performance for another auditory ability.

1024 The studies reviewed above are largely consistent with principles P1-P9, although the  
1025 predictions based on P5 and P6 are sometimes uncertain, because they depend on the extent to  
1026 which the participant has learned the relationship between auditory cues and the variable that  
1027 has to be judged, and this is often unknown in advance.

1028

1029 **The beneficial effects of cortical reorganization and the neural bases of changes in**  
1030 **auditory abilities following blindness**

1031 In this section we consider in more detail the neural bases of the changes that underlie the  
1032 enhanced abilities for some tasks that are associated with blindness, as characterized by P1-  
1033 P3. Many studies have focused on the link between cross-modal plasticity and enhanced  
1034 perceptual abilities. The degree of cross-modal plasticity is strongly affected by the age of  
1035 onset of blindness (for reviews, see Bell et al., 2019; Collignon, et al., 2009; Dormal, Lepore,  
1036 & Collignon, 2012; Kupers & Ptito, 2014; Occelli, Spence, & Zampini, 2013; Pasqualotto &  
1037 Proulx, 2012; Voss, 2019; Voss, Collignon, Lassonde, & Lepore, 2010), consistent with P9.  
1038 There is also evidence that without visual input, neural auditory maps of space become  
1039 distorted or degraded, as described in the next section.

1040 Following blindness, occipital brain regions, which normally respond primarily to  
1041 visual stimuli, may be recruited to process auditory signals (Voss & Zatorre, 2012). For  
1042 example, Gougoux, et al. (2005) and Voss, et al. (2011) presented data suggesting that  
1043 processing in the occipital cortex was the basis for the enhanced ability of blind people to  
1044 utilize monaural spatial cues to judge azimuth. There is also evidence for functional plasticity  
1045 in the temporal cortex, a brain area responsible for auditory spatial processing. van der  
1046 Heijden et al. (2019) showed that activation patterns for binaural spatial processing were  
1047 different for sighted and early-onset blind participants in planum temporale within the  
1048 temporal lobe. They proposed that some blind people have an increased reliance on spectral  
1049 cues for localization in the horizontal plane or that blind people become adept at using a  
1050 richer set of cues for horizontal localization, including both binaural (ITD and ILD) and  
1051 spectral cues. However, blindness does not result in recruitment of occipital brain regions and  
1052 improved performance for all auditory spatial tasks. For example, congenitally blind  
1053 participants showed poorer performance of a spatial-bisection task than sighted participants

1054 and the blind participants did not show recruitment of the occipital cortex during performance  
1055 of this task (Campus, et al., 2019). Instead, early contralateral occipital activation in response  
1056 to sound was strong for sighted participants and substantially lower for blind participants.

1057         Non-spatial and spatial information is segregated in the brain into pathways for  
1058 identifying objects (the “what” pathway, or ventral stream) and localizing them (the “where”  
1059 pathway, or dorsal stream). The “where” pathway appears to be highly plastic in early life,  
1060 and becomes resistant to the effects of experience later in life (Dormal, et al., 2012). Chen,  
1061 Zhang, and Zhou (2006) presented evidence suggesting that auditory brain plasticity in the  
1062 blind may occur in the “where” pathway but not the “what” pathway. For tones presented in  
1063 the periphery, congenitally blind participants showed enhanced localization, but for a non-  
1064 spatial task (discriminating frequency) blind participants were significantly slower than  
1065 sighted controls. This finding is surprising, given that other studies have reported that  
1066 blindness is associated with improved frequency discrimination abilities (Arnaud, et al., 2018;  
1067 Rokem & Ahissar, 2009; Wan, et al., 2010), and it is unclear why blindness should lead to a  
1068 decrease in processing speed for this task.

1069         Studies using animals have also suggested that improved auditory abilities following  
1070 blindness may at least in part be related to functional enhancement in auditory cortical areas.  
1071 Blindness was found to result in enhanced response specificity of neurons in the auditory  
1072 cortex (Korte & Rauschecker, 1993) and improved frequency selectivity and stronger  
1073 responses to changes in frequency and intensity (Petrus et al., 2014). However, there is  
1074 evidence that blindness disrupts the development of auditory spatial maps. Vision plays a  
1075 major role in the maturation of the auditory spatial response properties of neurons in the  
1076 superior colliculus (SC) in the midbrain, where auditory, visual, and tactile inputs are  
1077 organized into topographically aligned spatial maps (for a review, see King, 2009). An  
1078 electrophysiological study of the representation of auditory space in the SC of ferrets reared

1079 without vision showed that their auditory spatial maps had abnormal topography and  
1080 precision of their spatial representations (King & Carlile, 1993). Neural auditory maps of  
1081 space were reported to be degraded in the optic tectum of blind-reared barn owls, an area of  
1082 the brain containing neurons tuned for sound source location and organized according to their  
1083 spatial tuning (Knudsen, 1988). As well as a distorted topography of spatial maps, blind-  
1084 reared owls also showed significantly less precise sound localization behaviour (Knudsen,  
1085 Esterly, & du Lac, 1991). These findings show that an auditory spatial map can be generated  
1086 by the brain in the absence of vision, but that the precision and topography are degraded or  
1087 distorted compared to when vision is present during development.

1088         In summary, there is now an abundance of research demonstrating that that both cross-  
1089 modal cortical reorganization and reorganization within primarily auditory regions of the  
1090 brain may underlie the enhanced performance of blind people for some spatial tasks,  
1091 consistent with the perceptual enhancement hypothesis. However, blind people show deficits  
1092 in performance compared to sighted controls for auditory spatial tasks that may be performed  
1093 using internal maps of space (Tables 1-3), consistent with the perceptual deficiency  
1094 hypothesis. The role that vision plays in calibrating auditory space is the focus of the next  
1095 section.

1096

1097

1098

### 1099 **How and when vision is used for calibrating auditory space and guiding action**

1100 As described earlier, the performance of some auditory spatial tasks requires the auditory  
1101 system to map the available spatial cues to an internal representation of space (Aggius-Vella,

1102 Campus, Kolarik, & Gori, 2019; Kolarik, Pardhan, Cirstea, & Moore, 2013d); this is  
1103 encapsulated by P6 (calibration requiring visual cues). The auditory system can potentially  
1104 use vision or sensorimotor contingencies to learn this mapping (O'Regan & Noë, 2001).  
1105 Auditory calibration by vision is likely to be most precise for frontal space, where visual  
1106 information is most accurate, and less precise for peripheral space, where alternative feedback  
1107 signals, such as proprioception, motor feedback, or touch may provide more useful  
1108 information (Théoret, et al., 2004; Zwiers, et al., 2001).

1109           Calibration of auditory space could arise using experience of how auditory spatial cues  
1110 change with self-motion, for example when walking or turning the head (Ashmead, et al.,  
1111 1998), and by using tactile-motor feedback when touching a sound source. Lewald (2002a)  
1112 proposed that if such cues are used instead of vision to calibrate spatial hearing in blind  
1113 humans, compensatory plasticity may take the form of enhanced use of sensory mechanisms  
1114 that relate auditory azimuth cues to body position through the processing of proprioceptive  
1115 and vestibular cues, rather than via sharpened hearing and enhanced abilities to discriminate  
1116 between auditory spatial cues.

1117           The representation or model-based control approach to navigation (Frenz & Lappe,  
1118 2005; Turano, Yu, Hao, & Hicks, 2005) proposes that to enable safe navigation through the  
1119 environment, actions have to be based on accurate internal representations of external space.  
1120 An alternative account, information-based control (Fajen & Warren, 2003; Gibson, 1958;  
1121 Warren, 1998) proposes that on-going sensory information, such as that obtained using  
1122 hearing, can direct locomotion without the need for an internal representation. In the absence  
1123 of vision, auditory information can be used to guide locomotion using an external sound  
1124 source (Loomis, Klatzky, Philbeck, & Golledge, 1998; Russell & Schneider, 2006), self-  
1125 generated echolocation clicks (Kolarik, Scarfe, Moore, & Pardhan, 2016b; Kolarik, et al.,  
1126 2017c; Thaler, et al., 2020), or a device that generates sounds indicating the distance of

1127 objects in the environment (Kolarik, Scarfe, Moore, & Pardhan, 2016c; Kolarik, Timmis,  
1128 Cirstea, & Pardhan, 2014b). These abilities might be based on an internal representation of  
1129 space, but they might also be accounted for using an information-based control account (see  
1130 Kolarik, et al., 2016b; Kolarik, et al., 2017c for further discussion). However, more complex  
1131 tasks involving inferential navigation and planning a safe path probably do require a well-  
1132 calibrated auditory spatial map. The poorer performance of blind than of sighted participants  
1133 in performing these tasks (see Table 1), consistent with the perceptual deficiency hypothesis,  
1134 suggests that lack of visual information to calibrate such a map may adversely affect  
1135 navigation abilities, consistent with P6 (calibration requiring visual cues).

1136         The crossmodal calibration hypothesis (Gori, et al., 2010) extends the perceptual  
1137 deficiency hypothesis, proposing that visual information is necessary during development to  
1138 calibrate the other senses to accurately process spatial information, as vision is the sense that  
1139 provides the most accurate information regarding the spatial properties of the environment  
1140 and it provides immediate, simultaneous perception of multiple objects that are present within  
1141 the visual field (Thinus-Blanc & Gaunet, 1997). Blindness during the early stages of  
1142 development prevents visual information from being used for calibration of the spatial  
1143 processing mechanisms of the other senses, which presumably usually occurs during a critical  
1144 or sensitive developmental period (Thinus-Blanc & Gaunet, 1997). This leads to prolonged  
1145 negative effects and degraded auditory performance for certain tasks, consistent with P9 (age  
1146 of onset). The crossmodal calibration hypothesis and the perceptual deficiency hypothesis  
1147 have been supported by experimental data showing that early visual loss leads to degraded  
1148 performance in auditory distance discrimination abilities of early blind children (Cappagli, et  
1149 al., 2015), poorer abilities to judge sound motion by blind adults (Finocchietti, et al., 2015a),  
1150 and poorer distance bisection and minimum audible angle task performance for blind children  
1151 (Vercillo, et al., 2016). However, both the crossmodal calibration hypothesis and the

1152 perceptual deficiency hypothesis only apply to a specific subset of tasks, and they do not  
1153 account for why lack of visual calibration information degrades certain abilities such as  
1154 auditory bisection or encoding of sound motion, whereas other spatial auditory abilities such  
1155 as distance or motion discrimination are enhanced in adulthood.

1156

1157 **Is it possible to improve auditory abilities for individuals with visual loss, and reduce**  
1158 **auditory spatial deficits?**

1159 Hearing abilities are affected by the level of familiarity and expertise in using auditory  
1160 information for making spatial and non-spatial judgments, for performing actions, and for  
1161 locomotion (e.g. Velten, Ugrinowitsch, Portes, Hermann, & Bläsing, 2016). Earlier age of  
1162 onset of visual loss, longer duration of visual loss, greater experience with spatial tasks, and  
1163 high mobility, are associated with enhanced auditory abilities (Thaler, et al., 2020; Voss, et  
1164 al., 2010) (P1-5, 7-9). For example, as described above, using echolocation regularly in day-  
1165 to-day life improves spatial abilities, such as sensory-motor coordination during walking for  
1166 blind individuals (Thaler, et al., 2020) (P8). The auditory expertise of blind people can be  
1167 enhanced by training, practise, and experience (e.g. Hojan et al., 2012) (P8). Ideally, the  
1168 duration of the training should be short and the training effects persistent over time. However,  
1169 long periods of training are sometimes necessary to produce measurable benefits (e.g.  
1170 Skrodzka, Furmann, Bogusz-Witczak, & Hojan, 2015). For a discussion of how visual  
1171 deprivation and extensive training may interact to produce improved sensory abilities, see  
1172 Voss (2011).

1173 An understanding of auditory spatial abilities at early ages is necessary in order to  
1174 develop appropriate intervention programs for restoration or rehabilitation of degraded  
1175 auditory abilities caused by loss of vision (Cappagli, et al., 2017). Recent years have seen a

1176 rise in technical aids for people with visual loss, but the complexity of such aids, especially  
1177 for blind children, limits the potential benefits and has led to low user acceptance (for a  
1178 review, see Cuturi, Aggius-Vella, Campus, Parmiggiani, & Gori, 2016). Nevertheless, virtual  
1179 reality platforms can be developed to train blind people, for example by reproducing a  
1180 training environment for orientation and mobility (Seki & Sato, 2010). Other means for  
1181 improving the accuracy and precision of internal spatial representations, such as echolocation  
1182 or sensory substitution devices (SSDs), have also been shown to overcome spatial deficits  
1183 brought on by blindness. Evidence for this is discussed next.

1184

#### 1185 Auditory training

1186 Skrodzka, et al. (2015) compared the effects of auditory training and passive music listening  
1187 on the performance of several auditory tasks for 7–12 year old children and 13–19 year old  
1188 adolescent groups of blind and visually impaired participants and age-matched sighted  
1189 controls. Auditory training involved performance of a range of psychoacoustic tasks including  
1190 frequency discrimination and memory for frequency, intensity discrimination, lateralization of  
1191 stationary and moving sounds, spectral shape discrimination, simultaneous categorization of  
1192 fundamental frequency and spectral shape, and signal in-noise detection. Music listening  
1193 involved passive listening to music by Mozart, with alternating presentation of the music with  
1194 amplification of either the low or high frequencies. Auditory training and music listening  
1195 occurred in sessions over a period of 4-5 weeks. The auditory training was associated with  
1196 improved lateralization of two moving car sounds for the blind and visually impaired  
1197 adolescents only. Auditory training did not result in improvement in performance for any  
1198 other task. Passive music listening did not result in improved performance for any task for any  
1199 group.

1200           The accuracy and precision of estimates of the distance of objects using echolocation  
1201 by blindfolded sighted people have been shown to improve with training (Maezawa &  
1202 Kawahara, 2019; Tonelli, Brayda, & Gori, 2016). The improved performance was attributed  
1203 to the development of better hearing abilities or to more accurate calibration of auditory space  
1204 associated with practice and feedback about the location of spatial references (Maezawa &  
1205 Kawahara, 2019) (P5-6).

1206           Kolarik, et al. (2014a) suggested that echolocation could be used to generate and  
1207 maintain accurate representations of auditory space, thereby reducing deficits associated with  
1208 visual loss in judgments of sound elevation (Lewald, 2002b; Zwiers, et al., 2001) and auditory  
1209 bisection in azimuth (Gori, et al., 2014; Vercillo, et al., 2016; Vercillo, et al., 2015; Wersenyi,  
1210 2012). This was confirmed by Vercillo, et al. (2015), who showed that early blind expert  
1211 echolocators performed bisection in azimuth with similar precision to a sighted control group,  
1212 whereas early-blind non-echolocators performed significantly more poorly than sighted  
1213 controls. In view of this, it seems plausible that spatial information derived from alternative  
1214 sources, such as from SSDs, may also serve to calibrate auditory space in the absence of  
1215 visual information. SSDs are electronic travel aids designed to help blind people to detect  
1216 silent objects by providing auditory or tactile information regarding the distance to the object.  
1217 SSDs can accurately guide locomotion when they are based on echoes (usually for  
1218 ultrasound) (Hughes, 2001; Kolarik, et al., 2016c; Kolarik, et al., 2017c; Kolarik, et al.,  
1219 2014b) or on visual pattern information converted to sound, such as the prosthesis substituting  
1220 vision with audition (PSVA, Renier et al., 2005) and the vOICe (the middle three letters stand  
1221 for “oh I see,” Meijer, 1992). The use of an echolocation-based SSD improved the accuracy of  
1222 judgments of the direction and distance of landmarks located along a previously explored  
1223 route for early-onset blind participants, probably reflecting better accuracy of the internal  
1224 representation of space (Veraart & Wanet-Defalque, 1987). It is not yet known whether the

1225 regular use of SSDs can lead to a reduction in the spatial deficits that are usually associated  
1226 with visual loss, such as poor spatial bisection. Although SSDs are an example of technology  
1227 designed to assist blind people in perceiving the spatial layout of the local environment,  
1228 establishing the scope of their rehabilitative benefits requires further research. Cuturi, et al.  
1229 (2016) distinguished between “rehabilitative technology” that promotes brain plasticity and  
1230 allows the device to be removed following rehabilitation and “assistive technology” such as  
1231 the white cane, which does not promote neural plasticity and has to be used on an on-going  
1232 basis. Most technology currently available for the blind is assistive. There is a need to keep  
1233 rehabilitation at the forefront of training, interventions or technology for the blind, especially  
1234 from a young age, as this is key to overcoming spatial deficits (Cuturi, et al., 2016).

1235

#### 1236 Audiomotor, orientation and mobility training

1237 Blind football is a sport requiring well-trained audiomotor skills, where players need to be  
1238 able to accurately localize the position of the ball, opposing players, and teammates while  
1239 moving. Recent work has shown that blind footballers were faster than groups of sighted  
1240 controls (who were either matched in athletic ability or were non-athletes) in identifying the  
1241 direction of 1-kHz tones positioned front–left, front–right, back–left, and back–right relative  
1242 to the participant (Mieda, Kokubu, & Saito, 2019). Blind footballers were also shown to make  
1243 fewer front–back confusions than the other groups, a finding previously shown for blind  
1244 footballers compared to groups of blind or sighted non-athletes (Velten, et al., 2016). Blind  
1245 footballers are also better than blind or sighted non-athletes in localizing finger-snap sounds  
1246 (Velten, Bläsing, Portes, Hermann, & Schack, 2014; Velten, et al., 2016). The enhanced  
1247 performance of blind footballers can be attributed to improvements in the processing of  
1248 auditory information and in motor control following long-term training in blind football,

1249 rather than being solely due to cross-modal plasticity (Mieda, et al., 2019), consistent with P8  
1250 (experience and practise).

1251         Audiomotor training has been shown to improve auditory spatial abilities in blind  
1252 participants (Cuppone, Cappagli, & Gori, 2019; Finocchietti, Cappagli, & Gori, 2017;  
1253 Finocchietti et al., 2015b). Training based on audio-motor contingencies may be less  
1254 demanding than the training needed to master the use of SSDs, as the former involves a  
1255 natural association between sounds and motor information, rather than the learning of an  
1256 artificial set of rules governing the relationship between object orientation and distance and  
1257 the cues provided by the SSD (Cuppone, et al., 2019). Based on the idea that hearing can be  
1258 used to provide spatial information about the movement of the individual's body in space,  
1259 Finocchietti, et al. (2017) assessed the ability of blind participants and sighted controls to  
1260 localize the end point of a moving sound source before and after a 2-minute audiomotor  
1261 training session, or without training. Training consisted of participants holding the sound  
1262 source, and freely moving it with their hand to explore the surrounding space. The training  
1263 resulted in a marked improvement in localization for the blind group. The authors suggested  
1264 that "audio-motor feedback can substitute the visuo-motor feedback and recalibrate specific  
1265 spatial abilities".

1266         There is currently a lack of gold standard methods to assess the development of spatial  
1267 cognition in individuals with visual losses (Finocchietti, Cappagli, Giammari, Cocchi, & Gori,  
1268 2019). To help address this, Finocchietti, et al. (2019) developed the Blind Spatial Perception  
1269 test (BSP) to enable spatial cognition deficits to be identified and measured for visually  
1270 impaired children. The BSP involves a battery of tests assessing auditory localization,  
1271 auditory bisection, auditory distance judgments, auditory reaching, proprioceptive reaching,  
1272 and general mobility. The use of such tests could help evaluate the effectiveness of

1273 rehabilitation procedures for the visually impaired. The interaction between age of onset of  
1274 blindness, experience, and practice requires further investigation (Teng, et al., 2012).

1275

## 1276 **Conclusions**

1277 The current paper proposes a framework involving nine principles that can be used to predict  
1278 whether visual loss leads to enhancement or degradation of specific auditory abilities. The  
1279 validity of the proposed principles has been demonstrated by showing that the principles  
1280 broadly predict the findings for both spatial and non-spatial auditory abilities for a wide range  
1281 of empirical data involving full blindness, partial visual loss, developmental findings, and the  
1282 effects of early- and late-onset visual loss. However, there are some inconsistencies (see  
1283 Tables 1-4). These may in part be due to issues such as the heterogeneity of the blind  
1284 participants tested, or indicative of developmental delay associated with lack of visual  
1285 information that is later improved through the use of non-visual spatial cues. The predictions  
1286 based on P5 and P6 are sometimes uncertain because they depend on the extent to which the  
1287 participant has learned the relationship between auditory cues and the variable that has to be  
1288 judged, and this is often unknown in advance. Future studies of the effects of visual loss on  
1289 auditory abilities that have not yet been tested can be predicted using the framework. For  
1290 example it is predicted that early-onset blindness would result in an enhanced ability to judge  
1291 another person's mood from the sound of their voice (P1-3).

1292 As mentioned in the Introduction, a comprehensive framework is required to account  
1293 for why some auditory abilities are enhanced and others are degraded. The main elements that  
1294 the framework needs to capture are the changes in auditory abilities (both better and worse),  
1295 cortical reorganization, and changes in the way that auditory cues are calibrated, mapped and  
1296 interpreted following vision loss. As neither the perceptual deficiency hypothesis nor the

1297 perceptual enhancement hypothesis manage to capture all of these elements, a novel  
1298 hypothesis is needed. Grounded within the framework based on P1-9, we propose a new  
1299 hypothesis, the Perceptual Restructuring Hypothesis, that attempts to bring the enhancement  
1300 and deficiency hypotheses together. The Perceptual Restructuring Hypothesis is based on the  
1301 idea that perceptual systems are configured to provide accurate information about the outside  
1302 world with low variability, within the limits of the available processing resources. Vision  
1303 provides substantial information that is used by the auditory system, such as for spatial  
1304 calibration, but it also uses valuable processing resources. In the event of visual loss, the  
1305 auditory system is restructured so as to make it provide the most accurate information  
1306 possible utilizing the available cortical resources. This restructuring results in cortical  
1307 reorganization, crossmodal recruitment, and changes in internal auditory spatial maps. The  
1308 restructuring of the way that auditory cues are calibrated, mapped and interpreted leads to  
1309 changes in auditory abilities, where some become better and some become worse according to  
1310 the nine principles. This restructuring is also associated with developmental delay due to lack  
1311 of visual information, which is later improved through the use of non-visual spatial cues.

1312         The proposed hypothesis and framework has practical implications for the  
1313 rehabilitation of blind people, as it is important to identify auditory abilities that are degraded  
1314 following vision loss in order to improve these abilities through training or technology, such  
1315 as through the use of SSDs. Similarly, it is important to identify auditory abilities that are  
1316 significantly enhanced in blind individuals so that these can be utilized maximally in daily  
1317 life, such as enhanced echo processing abilities that can be used to obtain spatial information  
1318 and explore the world using echolocation, linking laboratory research to real-life applications.

1319         The proposed principles will likely be refined as further research brings new results to  
1320 light and it is probable that further principles may be developed. This may especially be the  
1321 case in areas that have received less attention than the effects of full blindness, such as the

1322 effects of partial visual loss or the effects of the developmental time course of visual loss on  
1323 audition. For example, Kolarik, et al. (2020) reported that greater severity of visual loss was  
1324 associated with larger estimates of auditory distance. Should further work show similar  
1325 findings for other auditory abilities, this might lead to a new general principle that “greater  
1326 severity of visual loss is associated with larger changes in auditory abilities.”

1327         The framework proposed in the current paper was developed to account for the effects  
1328 of visual loss on auditory abilities. However, the principles proposed might be adapted to  
1329 apply to other crossmodal configurations, such as the effects of deafness on visual abilities, or  
1330 the effects of blindness on tactile abilities. Some of the crossmodal effects in the literature are  
1331 consistent with the (generalized) principles of the current framework. For example, deaf  
1332 participants are more accurate than normally hearing participants in judging the direction of  
1333 motion in the visual periphery (P2 and P3) (Neville & Lawson, 1987), while there are no  
1334 significant differences in visual acuity between deaf and normally hearing participants (P1)  
1335 (Codina et al., 2011). The finding that blind participants showed enhanced performance  
1336 compared with sighted controls in a haptic angle discrimination task is consistent with P2 and  
1337 P3. Further work is needed to investigate the generalizability of the current framework across  
1338 different crossmodal configurations.

1339

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1345

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