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4 **A summary of research investigating echolocation**

5 **abilities of blind and sighted humans**

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20 **Abbreviations**

21	BOLD	Blood oxygen-level dependent
22	D/R	Direct-to-reverberant ratio
23	ILD	Interaural level difference
24	JND	Just-noticeable difference
25	KEMAR	Knowles electronics manikin for acoustics research
26	MRI	Magnetic resonance imaging
27	PET	Positron emission tomography
28	SSD	Sensory substitution device

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45 Abstract

46 There is currently considerable interest in the consequences of loss in one sensory modality
47 on the remaining senses. Much of this work has focused on the development of enhanced
48 auditory abilities among blind individuals, who are often able to use sound to navigate
49 through space. It has now been established that many blind individuals produce sound
50 emissions and use the returning echoes to provide them with information about objects in
51 their surroundings, in a similar manner to bats navigating in the dark. In this review, we
52 summarize current knowledge regarding human echolocation. Some blind individuals develop
53 remarkable echolocation abilities, and are able to assess the position, size, distance, shape,
54 and material of objects using reflected sound waves. After training, normally sighted people
55 are also able to use echolocation to perceive objects, and can develop abilities comparable to,
56 but typically somewhat poorer than, those of blind people. The underlying cues and
57 mechanisms, operable range, spatial acuity and neurological underpinnings of echolocation
58 are described. Echolocation can result in functional real life benefits. It is possible that these
59 benefits can be optimized via suitable training, especially among those with recently acquired
60 blindness, but this requires further study. Areas for further research are identified.

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62 Keywords

63 Echolocation. Spatial hearing. Blindness. Compensatory plasticity.

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65 **1. Introduction and background**

66 Adaptation to sensory loss has been the focus of considerable interest in psychology
67 and neuroscience. Visual loss is often, although not uniformly, associated with enhanced
68 auditory abilities, and these may be partly a consequence of cortical reorganization and
69 recruitment of visual areas for auditory processing (Collignon et al., 2009; Voss et al., 2004;
70 Voss et al., 2010). Many studies have examined the role that echolocation can play in
71 improving spatial awareness for those who have lost their sight. For blind individuals,
72 audition provides the sole source of information about sound-producing objects in far space,
73 and even silent objects can be located using reflections of self-generated sounds (Boehm,
74 1986; Rowan et al., 2013; Supa et al., 1944; Wallmeier et al., 2013; Welch, 1964). Some blind
75 individuals develop echolocation skills to a high standard, and display remarkable spatial
76 abilities. Thaler et al. (2011, described below) tested two blind participants who used
77 echolocation in their daily lives when exploring cities and during hiking, mountain biking and
78 playing basketball. McCarty and Worchel (1954) reported that a blind boy was able to avoid
79 obstacles while riding a bicycle by making clicking sounds with his mouth and listening to the
80 returning echoes. Echolocation may have functional benefits for blind individuals (Thaler,
81 2013), and the ability to echolocate can be improved by suitable training for people with
82 normal hearing (Teng and Whitney, 2011).

83 Echolocation has also formed the basis of sensory substitution devices (SSDs). These
84 devices use an acoustic (ultrasound) or optic source that emits a signal together with a
85 receiver to detect reflections of the signal. The received signal is used to calculate the distance
86 between the source and reflecting object using the time taken for the reflections to return to
87 the source. The distance information is then converted into an auditory (or haptic) signal
88 (Hughes, 2001; Kellogg, 1962). This assistive technology has been used to help increase the

89 spatial awareness and independent mobility of blind people (for reviews, see Roentgen et al.,
90 2008; 2009).

91 In this review, we summarize current knowledge regarding the acoustic cues used for
92 echolocation, work concerning the range of distances over which echolocation is effective
93 (referred to as the operable range), the types of features of objects that can be discriminated
94 using echolocation, and the underlying mechanisms. We describe research that has
95 investigated whether some acoustic cues are used more effectively by the blind than by the
96 sighted, and argue that evidence for enhanced echolocation skills in blind listeners is
97 reasonably strong, although there can be considerable overlap between the echolocation skills
98 of blind and sighted people, following suitable training. Neural underpinnings of echolocation
99 and areas for further research are discussed.

100

101 *1.1. Early research investigating human echolocation abilities*

102 The term echolocation was first used by Griffin (1944) to describe the outstanding
103 ability of bats flying in the dark to navigate and to locate prey using sound. Echolocation has
104 since been identified and extensively studied for other animals, including dolphins and
105 toothed whales (Jones, 2005). In 1749, Diderot described a blind acquaintance who was able
106 to locate silent objects and estimate their distance (see Jourdain, 1916), although at that time it
107 was not known that sound was involved. Diderot believed that the proximity of objects caused
108 pressure changes on the skin, and this led to the concept of ‘facial vision’ the objects were
109 said to be felt on the face. Further cases were identified of blind individuals who had this
110 ability, and numerous theories were put forward about the mechanisms underlying the
111 phenomenon. The blind individuals themselves were unable to account for their abilities, and
112 none of the many theories provided a satisfactory explanation. Hayes (1941) described

113 fourteen competing theories that attempted to explain facial vision in perceptual, sensory, or
114 occult terms.

115 Soon after, a series of pioneering studies carried out in the Cornell Psychological
116 Laboratory established that facial vision was actually an auditory ability (Supa et al., 1944;
117 Worchel and Dallenbach, 1947; Cotzin and Dallenbach, 1950). In the first of these studies,
118 Supa et al. (1944) asked blind and sighted blindfolded participants to approach an obstacle,
119 report as soon as they were able to detect it, and stop as close as possible to the obstacle.
120 When the ears were occluded, the ability to detect the obstacle and to judge its distance
121 disappeared. Worchel and Dallenbach (1947) and Cotzin and Dallenbach (1950) further
122 demonstrated that acoustic stimulation was necessary to perceive the obstacle, and a later
123 study showed that anesthetizing the facial skin had no effect on the perception of obstacles
124 (Köhler, 1964). Further studies confirmed that both blind and sighted participants were able to
125 echolocate (Ammons et al., 1953; Rice, 1967; Worchel and Mauney, 1951; Worchel et al.,
126 1950), and the notion of facial vision was replaced by that of echolocation.

127 Sound echoes may provide the listener with substantial information regarding the
128 properties of distal objects, including the distance to the object, the shape, and the object's
129 size (Passini et al., 1986; Stoffregen and Pittenger, 1995). This is discussed in more detail
130 later in this review.

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132 **2. Acoustic cues, underlying mechanisms, and the operable range of echolocation**

133 *2.1. Characteristics of echolocation signals used by humans*

134 Bats echolocate using biosonar: the emitted signals are mainly in the ultrasonic range,
135 beyond the upper frequency limit of human hearing (approximately 20,000 Hz). This can
136 provide the bat with a rich source of information about very small objects, such as insects,
137 including size, position, and direction of movement. Many blind individuals also use self-

138 generated sounds to echolocate, such as clicks produced by rapidly moving the tongue in the
139 palatal area behind the teeth (Rojas et al., 2009), or sounds produced by mechanical means
140 such as tapping a cane against the floor (Burton, 2000). The sounds produced by humans are,
141 naturally, at least partly within the audible frequency range for humans, but usually contain
142 strong frequency components in the upper part of this range (Schörnich et al., 2012; Rowan et
143 al., 2013). Also, there is evidence that high-frequency components are useful for at least some
144 aspects of echolocation (Cotzin and Dallenbach, 1950; Rowan et al., 2013).

145 Echolocation involves three successive types of sound at the listener's ears (Rowan et
146 al., 2013): (i) the emission (self-generated sound) only, (ii) the emission and echo
147 superimposed, or, for short emissions and distant objects, a brief silent gap, and (iii) the echo
148 only. This is illustrated in the left panel of Fig. 1, which shows responses to clicks measured
149 in the ear of an acoustic manikin by Rowan et al. (2013). Click spectra are shown in the right
150 panel. Clicks produced by the echolocator are often of short duration, approximately 10 ms,
151 and have a broad spectrum (Schörnich et al., 2012; Thaler et al., 2011). Sound levels range
152 from 60-108 dB SPL, with maximum energy in the frequency range 6-8 kHz (Schörnich et al.,
153 2012). For analyses of the physical properties of self-generated sounds used for human
154 echolocation, see Rojas et al. (2009; 2010). They suggested that short sounds generated at the
155 palate are the most effective for echolocation. However, this requires experimental testing.
156 Findings from other studies have suggested that longer duration sounds are most effective.
157 Rowan et al. (2013) found that the ability of normally sighted participants to identify the
158 lateral position of a board using echoes improved as duration increased from 10 to 400 ms for
159 an object distance of 0.9 m. Schenkman and Nilsson (2010) reported that echolocation
160 detection performance increased as signal duration increased from 5 to 500 ms for normally
161 sighted participants, and that blind participants could detect objects at farther distances than
162 sighted participants when using longer duration signals.

163 FIGURE 1

164

165 *2.2. Cues used for echolocation, and operable range.*

166 In this section we describe the currently known acoustic cues used for echolocation.

167 Putative acoustic cues for echolocation as an active mode of perception include:

168 (1) Energy: the returning echo increases the overall energy at the listener's ears, if the sound
169 intensity is integrated over a few tens of ms. This cue is sometimes referred to in the literature
170 in terms of the subjective quality of loudness. The level of the echo relative to that of the
171 emission may also provide a cue.

172 (2) The time delay between the emitted sound and the echo. This may be perceived as such
173 if the delay is relatively long (a few tens of ms) or it may be perceived as a time separation
174 pitch or repetition pitch (Bilsen, 1966) when the delay is in the range 1 to 30 ms; the
175 perceived pitch is inversely related to the delay.

176 (3) Changes in spectrum of the sound resulting from the addition of the echo to the emission.
177 Constructive and destructive interference lead to a ripple in the spectrum, the spacing between
178 spectral peaks being inversely related to the time delay of the echo relative to the emission.
179 This cue may be heard as a change in timbre or pitch and it is the frequency-domain
180 equivalent of cue (2). In many cases it is not clear whether analysis in the temporal domain or
181 the spectral domain is critical.

182 (4) Differences in the sound reaching the two ears, especially at high frequencies. These can
183 provide information about the orientation of objects. For example, when a flat board faces the
184 listener, the signals are similar at the two ears, as illustrated in Figure 1. If the board is at an
185 oblique angle relative to the listener, the sound differs at the two ears, particularly at high
186 frequencies.

187 (5) Differences in the reverberation pattern within a reverberant room. An obstacle within a

188 reverberant environment will alter the pattern of reverberation, and lead to reflections with
189 shorter delays.

190 The above list of cues is not necessarily exhaustive, as some cues that have been
191 proposed for echolocation have not yet been demonstrated to be useful for humans. One such
192 cue is echoic tau, which is a derived quantity that may be used to predict time to contact when
193 the echolocator is approaching an object. It refers to the ratio (distance between the
194 echolocator and the object)/(speed of approach). It is monotonically related to time to contact.
195 The speed of approach may be estimated from kinesthetic and motor information about the
196 speed of walking, while the distance may be estimated from one or more of cues 1-5. Echoic
197 tau may provide an additional source of information to support echolocation; for example, if
198 an echolocator moves so as to keep echoic tau constant, they will halt just as the object is
199 reached (Stoffregen and Pittenger, 1995). Rosenblum et al. (2000) conducted a study with
200 blindfolded sighted participants, who were required to use echolocation to detect a wall while
201 either approaching the wall or standing still. The wall was then removed, and participants
202 were asked to walk to the prior location of the wall. Accuracy in judging the distance of the
203 wall was slightly higher for moving than for stationary echolocation for some wall distances,
204 possibly due to use of time-to-arrival information based upon echoic tau. The use of echoic
205 time-to-arrival information for controlling approach when moving was discussed by
206 Stoffregen and Pittenger (1995), following evidence that echoic tau is used by echolocating
207 bats (Lee et al., 1992). However, it has not been clearly demonstrated that echoic tau is used
208 by humans.

209 Although this review focuses on active echolocation, we note that the term
210 echolocation is sometimes used to describe navigation behaviors that rely on passive cues,
211 which are not discussed in detail here. These include changes in the ambient sound field due
212 to the buildup of sound pressure approximately a meter in front of a wall, which result in a

213 shift in spectral balance towards lower frequencies. This shift may provide a cue that enables
214 blind individuals to maintain a constant distance from a wall for safe travel (Ashmead and
215 Wall, 1999).

216 Cotzin and Dallenbach (1950) investigated the role of pitch and loudness in
217 echolocation. Steel wires were used to suspend a carriage with a loudspeaker and microphone
218 that was moved toward an obstacle from various starting points using a soundproofed motor.
219 The speed of approach was controlled by the participant. The stimuli were thermal noise
220 (similar to white noise) or pure tones with frequencies ranging from 0.125 to 10 kHz. The
221 sounds were picked up by the microphone and delivered to the participant's ears using
222 headphones. The task was to stop the approach and report when the obstacle was first
223 perceived, and then to move the carriage as close as possible to the obstacle without collision.
224 All participants (sighted and blind) reported a rise in pitch of the thermal noise as the obstacle
225 was approached that enabled them to perform the task. Performance was poor for pure tones
226 with frequencies up to 8 kHz, but performance improved for the 10-kHz tone. For the thermal
227 noise stimulus only, Cotzin and Dallenbach also tested whether perceived loudness increased
228 when the carriage was nearer to an obstacle, and reported this not to be the case. They
229 concluded that changes in pitch but not loudness for sounds containing high frequencies were
230 necessary and sufficient for blind individuals to perceive obstacles. However, changes in pitch
231 cannot account for the above-chance performance obtained with the 10-kHz tone.
232 Presumably, performance in that case depended on constructive and destructive interference
233 between the direct sound and the reflection, which led to marked fluctuations in level,
234 especially an increase in level when the loudspeaker was very close to the obstacle. One
235 participant reported "The tone becomes more piercing and shrill when it nears the obstacle"
236 and another reported "The tone suddenly gets louder . . . it screams when near the obstacle."

237 Arias and Ramos (1997) investigated the role of repetition pitch detection and

238 discrimination in an echolocation paradigm. They used stimuli composed of a direct signal
239 (a click or burst of noise recorded at the output of a loudspeaker), presented either alone or
240 together with a reflected signal or echo. The latter was either a real echo produced by a
241 reflecting disc or was a delayed copy of the direct sound attenuated by 3.5 dB. Baseline
242 delays of 2 ms and 5 ms between the direct and reflected signal were used. For such delays,
243 strong repetition pitches are heard (Bilsen, 1966; Yost and Hill, 1978). The tasks included
244 detecting the object (discriminating sounds with and without echoes), and discriminating
245 changes in the distance between the sound source and the object, produced by varying the
246 delay between the direct sound and echo from the baseline value. For the discrimination task,
247 because repetition pitch varies inversely with distance, the presence of an obstacle closer to or
248 farther from a reference position (corresponding to the baseline delay) would result in a
249 higher or lower pitch being perceived, respectively, allowing participants to use repetition
250 pitch as a cue. Participants were well able to perform both tasks. Note that in the condition
251 with the original sound plus a delayed copy of the sound attenuated by 3.5 dB, the overall
252 level and the relative level of the echo did not change when the distance (delay) was changed,
253 but performance was good, suggesting that the absolute or relative level of the echo is not a
254 critical cue for distance discrimination. Arias and Ramos (1997) suggested that repetition
255 pitch was a good cue for detecting objects and discriminating their distance via echolocation.

256 Schenkman and Nilsson (2011) investigated whether level information (described by
257 them as loudness) or some other form of information (described by them as pitch) was
258 used in echolocation. Blind and sighted participants were asked to indicate which of two
259 recordings of a noise burst (recorded using an acoustic manikin) was made in the presence of
260 a reflecting disc. The recordings were presented in three conditions: (1) in their original form
261 (all cues available); (2) with the level of the two recorded signals equated, so that the level
262 cue was removed, but all other cues remained; (3) when both of the two signals presented in a

263 trial were recorded in the absence of a reflecting disc, but one of the sounds was increased in
264 level so as to simulate the level cue only. Their results when the distance to the disc was 2 m
265 are shown in Fig. 2. The performance of both blind and sighted participants was worse when
266 only the level cue was available than when the level cue was removed but other cues
267 remained. The results suggest that the level cue plays a small role, but that other spectral
268 and/or temporal cues are more important. The performance of blind participants was close to
269 chance for objects at 3 m. The individual differences are discussed later.

270

271

FIGURE 2

272

273 The accuracy of echolocation by humans can depend upon object distance (Kellogg,
274 1962; Rice et al., 1965; Rowan et al., 2013). Kellogg (1962) tested two blind individuals in an
275 echolocation size discrimination task. One was able to perform well for object distances of 12
276 inches, and performance fell as the distance of the object was increased to 24 inches.
277 However, no effect of distance was observed for the second blind individual tested. Rice et al.
278 (1965) found that thresholds for detecting metal discs using echoes remained constant with
279 distance. Rowan et al. (2013) found that accuracy in judging the lateral position of a board
280 based on echolocation decreased with increasing distance, and for distances of 2 m and above
281 the performance of both blind and blindfolded sighted participants was at chance. The lateral
282 position of the board was more likely to be correctly identified in the ‘angled’ condition of
283 Rowan et al. (2013), where the flat face of the board was positioned so as to reflect sounds
284 directly toward the participant, in which case specular (mirror-like) reflection paths to both
285 ears were present. Performance was lower in the ‘flat’ condition, in which the board’s flat
286 face was positioned so that specular reflections did not reach both ears of the participant. In
287 this case, binaural cues were weaker and more complex for the majority of distances tested

288 (Papadopoulos et al., 2011). Based on these results, Rowan et al. suggested that judgments of
289 lateral position were dependent upon high-frequency binaural cues such as interaural level
290 difference, or ILD (Papadopoulos et al., 2011), although the possibility that participants used
291 monaural changes in level at the ears was not ruled out.

292 Changes in the pattern of reverberation in a room caused by a reflecting object may
293 also act as a cue to echolocation, as the presence of an object will result in reflections with
294 shorter delays. Schenkman and Nilsson (2010) found that the largest distance at which
295 echolocation could be used was greater in a reverberant conference room than in an anechoic
296 room. However the use of cues related to the pattern of reverberation may only be possible in
297 rooms with relatively short reverberation times (see section 5 for further discussion of this
298 point).

299

300 *2.3. The information provided by echolocation regarding the position, size, material and* 301 *shape of an object*

302 Echolocation can be used to judge and discriminate both the lateral position and
303 distance of objects. Teng et al. (2012) measured echolocation acuity for discriminating the
304 relative lateral position of two reflecting discs, using an auditory analogue of the visual
305 Vernier task, which involves judging the relative position of two objects (Kniestedt and
306 Stamper, 2003). Teng et al. found that blind expert echolocators showed acuities of
307 approximately 1.2° of azimuth, approaching the resolution of spatial hearing in the
308 frontomedial plane. This low threshold reflects best performance among experts for this task,
309 and may not be typical of acuity among the general population. For young, sighted, normally
310 hearing participants, Schörnich et al. (2012) showed that echolocation just-noticeable-
311 differences (JNDs) for distance were in general below 1 m. For a reference distance of 1.7 m,
312 JNDs were generally less than 0.5 m.

313 Echolocation can also be used to judge the relative sizes of objects. Rice and Feinstein
314 (1965) found that blind participants were able to use echoes to discriminate object size, and
315 that their best-performing participants were able to discriminate objects with area ratios as
316 low as 1.07:1. Since large objects reflect more acoustic energy than small objects, two cues
317 that might be used for discrimination of size are overall sound level and sound level of the
318 echo relative to that of the emission. However, level differences between the echoes produced
319 by reflections from objects can occur not only as a result of differences in size, but also as a
320 result of differences in the material from which the object is composed, distance between the
321 echolocator and the object, and the shape of the facing surface (e.g. a flat vs. a concave
322 surface). Stoffregen and Pittenger (1995) suggested that size information may be obtained by
323 combining information about delay, spectrum and level. The delay between the emission and
324 echo can be used to determine the expected level difference between the emission and echo
325 due to distance. Differences in spectrum between the emission and echo are determined by the
326 type of material from which the object is composed (see below for details) and can be allowed
327 for if the type of material is fixed over trials or is known in advance. Given this information,
328 any remaining differences in level or spectrum between the emission and echo can be used to
329 estimate the size of the object.

330 Objects made of different materials can be identified and discriminated using echoic
331 information (DeLong et al., 2007; Hausfeld et al., 1982). Following training, blindfolded
332 sighted participants were able to use echoes to distinguish objects made from fabric,
333 plexiglass, wood, or carpet (Hausfeld et al., 1982). Participants reported using pitch and
334 timbre changes to perform the task (DeLong et al., 2007; Hausfeld et al., 1982).

335 Materials differ in their absorption characteristics. For example, soft materials such as
336 carpet tend to strongly absorb high frequencies, whereas rigid materials such as plexiglass
337 reflect higher as well as lower frequencies. Hence, if the spectrum of the echo contains

338 relatively less high-frequency energy than the emission, it can be inferred that the material is
339 soft, whereas if the spectra of the echo and emission are similar, it can be inferred that the
340 material is hard. Stoffregen and Pittenger (1995) proposed that object material may be
341 identified using the relative frequency spectra of the emission and the echo, and it has been
342 suggested that sound echoes contain sufficient acoustical cues in the frequency range below
343 3000 Hz to distinguish between several different wood surfaces (Rojas et al., 2012). However,
344 it has not yet been demonstrated that these cues can be used.

345 While there is good evidence that echoes can be used to discriminate objects made of
346 different materials, evidence for the identification of objects in isolation on the basis of
347 echoes is weak. In studies that have investigated echo-based perception of materials,
348 participants usually had to distinguish echoic information from successively presented
349 materials or to identify the materials from a small possible pool of choices (e.g. Hausfeld et
350 al., 1982). Further research is needed to investigate how many different types of materials can
351 be distinguished, to assess the magnitude of the difference between materials needed to
352 support accurate discrimination, and to determine whether echoic information can be used to
353 identify objects in isolation.

354 Objects of different shapes that are matched in area and distance can also be
355 distinguished using echoic information. Following training, blindfolded sighted participants
356 were able to use echoes to discriminate the shapes of various objects, including circle,
357 triangle, square, or no target (DeLong et al., 2007; Hausfeld et al., 1982; Rice, 1967). The
358 cues underlying this ability remain somewhat unclear. Rice (1967) investigated the ability to
359 detect (not discriminate) flat aluminium objects of different shape but identical surface area
360 (31 cm^2) at a distance of 122 cm from the participant. Performance was best for a square and
361 circle, lower for an oblong shape (4:1), and lower still for a longer oblong (16:1). The
362 orientation of the oblong did not affect performance. Rice hypothesized that the decrease in

363 performance as the target became longer and thinner was caused by a reduction of echo
364 intensity, due to the specular reflection of energy away from the ears with increasing angle at
365 which the signal struck the target. Hence, echo intensity provides a possible cue for
366 discrimination of target shape, although presumably this cue would not be effective for
367 absolute identification of target shape.

368 Rice observed that bending an oblong target, thus focusing echoes back toward the
369 ear, increased the number of detections of the longer of the two oblong targets. Similarly, the
370 concavity of a bowl will amplify returning echoes relative to those for objects with flat
371 surfaces (Arnott et al., 2013). Hence, echo intensity also provides a potential cue for
372 discriminating surfaces of the same shape and area, but different concavity. For objects that
373 vary in concavity, the emission-to-echo delay will differ for parts of objects nearer to and
374 farther from the participant, so changes in concavity will lead to changes in overall delay and
375 spectrum of the echo. The extent to which these cues support concavity discrimination
376 remains somewhat unclear.

377

378 **3. Do blind individuals develop enhanced echolocation abilities?**

379 *3.1. A summary of research comparing echolocation performance of blind and sighted* 380 *participants*

381 Echoic information provides useful information regarding the surrounding
382 environment (Kolarik et al., 2013c; Mershon et al., 1989), and blind individuals rely heavily
383 upon this information for perceiving the spatial layout of their surroundings. In this section,
384 we address the issue of whether blind people have superior echolocation abilities to sighted
385 people. Various factors may contribute to the development of superior echolocation abilities
386 in blind people, such as reliance on and extensive experience in using echoic information (i.e.

387 increased practice), and crossmodal takeover of visual cortex following visual loss, leading
388 to increased cortical resources for auditory processing (see Section 4 for more details).

389 Some studies have demonstrated that blind people have higher sensitivity to non-self-
390 generated echoic information than sighted controls (Dufour et al., 2005; Kolarik et al., 2013a).
391 Dufour et al. (2005) showed that blind participants were more accurate than sighted controls
392 in localizing an object using echoic information from sound generated by a loudspeaker, and
393 were more sensitive to task-irrelevant echoes from a nearby lateral wall when localizing
394 sounds in azimuth. Kolarik et al. (2013) reported that blind participants were better able than
395 sighted participants to perform a distance-discrimination task when only direct-to-reverberant
396 ratio cues were available. However, not all studies reveal superior abilities of blind listeners in
397 using non-self-generated sounds. Burton (2000) studied the use of cane tapping to determine
398 whether a gap in a walkway could be crossed with a normal step while walking. In a condition
399 designated "sound only" the experimenter tapped the cane on the vertical faces on either side
400 of the gap. Burton found no difference between blind and sighted participants for this
401 condition. Several studies have reported that blind participants have echolocation abilities
402 superior to those of sighted participants when using self-generated sounds (Clarke et al.,
403 1975; Juurmaa and Suonio, 1975; Kellogg, 1962; Neuhoff, 2004; Rice, 1969; Schenkman and
404 Nilsson, 2010; 2011). However, echolocation abilities within both the blind and sighted
405 populations show considerable individual variability (Teng and Whitney, 2011; Teng et al.,
406 2012; Rowan et al., 2013). Some sighted individuals, following training, achieved
407 echolocation abilities similar to those of a blind expert (Teng and Whitney, 2011).
408 Furthermore, echolocation abilities are very likely to be task dependent, and further research
409 is needed to compare performance across blind and sighted groups for different echolocation
410 tasks.

411 Schenkman and Nilsson (2010) measured accuracy in judging which of two
412 recordings of a noise burst was made in the presence of a reflecting disc. On average, blind
413 participants performed better than sighted participants, a finding replicated in a second study
414 (Schenkman and Nilsson, 2011, as described in section 2.2) and supporting previous work by
415 Kellogg (1962). The superior performance of the blind participants was most apparent when
416 the reflective disc was positioned between 2 and 5 m from the participant; all participants
417 performed well for distances less than 2 m. As shown in Fig. 2, on average, the blind
418 participants in Schenkman and Nilsson's (2011) study performed better than the sighted
419 participants in all conditions. Scores varied widely across participants within each group,
420 especially when not all cues were present. However, when all cues were available, the blind
421 participants all achieved relatively high scores (84% correct or better), while some sighted
422 participants scored close to chance (50% correct). Also, three blind participants made no
423 errors when all cues were present, while none of the sighted participants achieved this. The
424 scores for blind and sighted participants overlapped much more in the condition where only
425 the level cue was available.

426 Since most studies comparing the echolocation abilities of blind and sighted
427 participants have not reported audiometric thresholds, it is possible that some of the
428 differences across groups were related to differences in audiometric thresholds. However,
429 since the groups were usually reasonably well matched in terms of age, there is no obvious
430 reason why audiometric thresholds should have differed across blind and sighted participants.
431 Carlson-Smith and Weiner (1996) found no statistically significant correlation between high-
432 frequency hearing sensitivity (measured by pure-tone thresholds at 8, 10, and 12 kHz) and
433 echolocation performance (the detection of obstacles and doorways), although echolocation
434 performance was related to the ability to detect changes in frequency and amplitude of low-

435 frequency sounds. However, it may have been the case that all participants had sufficiently
436 good hearing at high frequencies to make use of echoic information at those frequencies.

437 More generally, it has been suggested that enhanced auditory abilities in blind
438 individuals may be due to an increased ability to discern pertinent acoustic cues (Voss et al.,
439 2004). The greater reliance of blind people on acoustic cues in everyday life may improve the
440 ability to use subtle cues, such as small differences in spectral envelope, and this may lead to
441 more effective processing of acoustic spatial information (Voss et al., 2004), including
442 information for echolocation. Spectral envelope variations lead to changes in perceived timbre
443 that can be utilized to recognize objects or extract information regarding the environment
444 (Ashmead and Wall., 1999; Au and Martin, 1989; Schenkman, 1986). Doucet et al. (2005)
445 showed that blind participants were better able to localize sounds monaurally, presumably
446 based on spectral cues resulting from reflections of sound from the pinna, suggesting superior
447 abilities of the blind in processing spectral information. Enhanced spectral processing may
448 extend to enhanced echolocation abilities among the blind.

449 In summary, the weight of evidence supports the idea that, on average, blind people
450 are better echolocators than sighted people. It has been argued that while normally sighted
451 individuals do echolocate, this is not necessarily a conscious process, and it occurs to a much
452 lesser degree than for blind echolocators (Stoffregen and Pittenger, 1995; Schwitzgebel and
453 Gordon, 2000). It remains somewhat unclear whether the best blind echolocators have
454 superior skills to those of the best trained sighted echolocators. The extent to which takeover
455 of the visual cortex for auditory processing contributes to the echolocation skills of blind
456 people also remains uncertain; see below for further discussion of this point.

457

458

459

460 3.2. *The effect of training on echolocation abilities*

461 Although many blind people develop echolocation skills that they use to aid in
462 navigation and object location, these skills vary substantially across individuals, and not all
463 blind people can echolocate. Sighted people do not generally display echolocation abilities
464 without training, probably because visual signals provide substantially more accurate spatial
465 information. Congenitally blind children are often able to use ambient auditory information to
466 detect an obstacle, suggesting that no formal training is necessary to use sound to perceive
467 objects if blindness occurs early in life (Ashmead et al., 1989). For blind participants, Teng et
468 al. (2012) observed a strong correlation between age of onset of blindness and echolocation
469 ability, consistent with improvements in performance produced by practice and/or by brain
470 plasticity.

471 An important issue for future research is to establish whether systematic training can
472 lead to the acquisition of echolocation skills among blind adults who have failed to develop
473 such skills, and also to establish whether training can enhance the acquisition of echolocation
474 abilities among those who have newly lost their vision (Schenkman and Nilsson, 2010).

475

476 **4. Neuronal bases of echolocation**

477 Little is currently known regarding the neural basis of echolocation, and whether the
478 mechanisms subserving echolocation differ between sighted and blind individuals. In addition
479 to the evidence for enhanced echolocation by blind people (Kellogg, 1962; Rice, 1969;
480 Schenkman and Nilsson, 2010; Schenkman and Nilsson, 2011), as described above, there is
481 evidence that blind people display enhanced abilities for auditory tasks such as sound
482 localization (Lessard et al., 1998; Voss et al., 2004) and distance discrimination (Kolarik et
483 al., 2013a; Voss et al., 2004). It has been proposed that functional recruitment of visually
484 deafferented regions of the occipital cortex, an area that processes visual information for

485 normally sighted individuals, may underlie these abilities (see Voss and Zatorre, 2012 for a
486 review). If the echo-processing abilities of blind people partly reflect the recruitment of visual
487 (occipital) areas of the brain, those areas should be activated during an echolocation task.

488 De Volder et al. (1999) used positron emission tomography (PET) to compare brain
489 activity for early-blind and sighted participants who were trained to use an ultrasonic SSD to
490 detect and evaluate the distance of an object. Activity in the occipital cortex was found to be
491 higher for the blind than for the sighted participants. Higher activation was found in
492 Brodmann areas 17, 18 and 19 for the blind but not for the sighted participants when the SSD
493 was used to localize the object. Thaler et al. (2011) showed that functional magnetic
494 resonance imaging (MRI) activity increased in the visual cortex of one early-onset and one
495 late-onset blind participant (both experienced echolocators) when listening to sounds
496 containing clicks and returning echoes, compared to the situation where sounds with no
497 returning echoes were present (see Fig. 3). This activation was not observed for normally
498 sighted, non-echolocating controls, even though they had received training listening to these
499 sounds. No differences in activity in the auditory cortex were observed.

500 In a follow-up study, Arnott et al. (2013) investigated activation in the occipital cortex
501 in response to shape-specific echo processing. Echolocation audio was recorded in an
502 anechoic chamber or hallway using tongue-clicks in the presence of a concave or flat object
503 that was covered either in aluminum foil or a cotton towel. For an early blind participant with
504 extensive echolocation experience, blood oxygen-level dependent (BOLD) activity in
505 ventrolateral occipital areas and the bilateral occipital pole was greater when the participant
506 attended to shape than when they attended to the material or location of the object.
507 Furthermore, feature specific echo-derived object representations were organized
508 topographically in the calcarine cortex. A congenitally blind participant who began using
509 echolocation comparatively later in life and a late-onset blind participant did not show the

510 same type of activation, suggesting that extensive echolocation training at an early or critical
511 age establishes echo-processing mechanisms in these brain areas.

512 Thaler et al. (in press) conducted an MRI study where BOLD activity was recorded
513 while blind echolocation experts and normally sighted echolocation novices listened to
514 binaural recordings of sounds. For one class of ‘echolocation’ sounds, the recordings
515 contained both self-generated mouth clicks and echoes of the clicks reflected from an object.
516 For the other class of ‘source’ sounds, the object emitted the sound and no echo was involved.
517 The object was positioned either to the left or right of the participant and was either moving
518 or stationary. Thaler et al. reported that temporal-occipital cortex visual cortical areas were
519 recruited for echo-motion processing for blind but not for sighted participants. They
520 suggested that ‘echo-motion response in blind experts may represent a reorganization rather
521 than exaggeration of response observed in sighted novices’ and that ‘There is the possibility
522 that this reorganization involves the recruitment of ‘visual’ cortical areas.’

523 Overall, these results support the idea that visual cortical areas are recruited for
524 auditory processing, including echolocation, in blind people. The extent to which such
525 recruitment contributes to the echolocation abilities of the blind remains unclear. Normally
526 sighted individuals can also echolocate, despite the absence of visual cortex recruitment for
527 this group. It is not yet known whether brain areas that process echoic information for other
528 auditory tasks, such as perceiving the distance of a sound source, are also activated during
529 echolocation tasks. Sound echoes provide listeners with a primary cue to sound source
530 distance (direct-to-reverberant ratio or D/R, Zahorik et al., 2005; Kolarik et al., 2013a;
531 2013b). A recent study in near space showed that neural populations in the planum temporale
532 and posterior superior temporal gyrus were sensitive to acoustic distance cues including D/R,
533 independent of level (Kopčo et al., 2012). It is possible that these areas are also activated

534 during echolocation tasks for both normally sighted and blind individuals. However, this
535 requires further study.

536

537 FIGURE 3 6 INTENDED FOR COLOR REPRODUCTION ON THE WEB AND IN PRINT

538

539 **5. Concluding remarks and suggestions for further research**

540 The studies described in this review have provided numerous insights into
541 echolocation in humans. However, many aspects of echolocation are not yet understood, and
542 the reasons for individual differences in echolocation ability have not been determined.
543 Further work is needed to clarify what cues are used in the various aspects of echolocation, to
544 establish the functional benefits of echolocation, to investigate the accuracy of locomotive
545 guidance using echolocation, and to establish how the acoustic characteristics of the
546 environment, such as background noise and reverberant energy, affect echolocation abilities.
547 The effects of age of onset of blindness on echolocation abilities have only recently begun to
548 be investigated in depth and the effects of hearing loss on echolocation have not been studied.
549 These areas are discussed in the following paragraphs.

550 The acoustic characteristics of the environment, particularly background noise and
551 reverberant energy present during sound emission, may affect echolocation performance.
552 Background noise may make it difficult to perceive an object based on echoic information and
553 to distinguish it from other objects, in a similar way that background noise can make it
554 difficult to separate sounds based on their location (Moore, 2012). In reverberant rooms, room
555 reflections may interfere with reflections from the target object (Schörnich et al., 2012).
556 Background reverberation distorts the monaural spectrum, as well as the interaural level
557 differences and interaural phase differences of sounds reaching the listener's ears (Shinn-
558 Cunningham et al., 2005). Spectral distortions may particularly affect blind listeners, as

559 spectral cues appear to play an important role in their ability to echolocate (Doucet et al.,
560 2005).

561 Surprisingly, as mentioned in section 2.2, Schenkman and Nilsson (2010) reported that
562 echolocation was possible for objects at greater distances in a reverberant conference room
563 than in an anechoic room, suggesting that a reverberant environment can actually enhance
564 performance. The presence of a reflecting object will change the pattern of reverberation, and
565 introduce shorter delays to the reflections, thus providing a potential cue. However, the
566 reverberation time in the study of Schenkman and Nilsson (2010) was rather low ($T_{60} = 0.4$ s),
567 and it is possible that longer reverberation times would lead to impaired rather than improved
568 performance. Although the usefulness of some acoustic spatial cues, such as direct-to-
569 reverberant ratio for distance discrimination, has been shown to depend upon reverberation
570 time (Kolarik et al., 2013b), the effects of reverberation time on echolocation performance
571 have yet to be quantified.

572 Echolocation abilities are often useful in navigating through outdoor environments
573 (McCarty and Worchel, 1954), where the environmental conditions and absorption
574 characteristics of the various obstacles encountered vary considerably. For example, snow
575 absorbs sound, with the degree of absorption varying depending upon whether the snow is
576 wet or dry (Albert, 2001). Thus, one might expect that echolocation would be generally less
577 effective under snowy conditions. The effectiveness of echolocation in rainy or snowy
578 conditions requires further investigation, in order to examine the conditions in which
579 echolocation provides real benefits for navigation.

580 There has been little investigation of the accuracy with which echolocation
581 information can be used to form internal representations for navigating safely through the
582 individual's surrounding environment. As described above, echoic information can allow
583 obstacles to be located at least crudely. However, precise motor responses must be made in

584 order to avoid collisions, by walking around obstacles or across gaps, or safely moving
585 through apertures. Hughes (2001) showed that echoic information from an SSD could provide
586 sighted blindfolded participants with spatial layout information regarding the width of various
587 apertures. In a study of Kolarik et al. (in press), blindfolded sighted participants were required
588 to use echoic information from SSDs to rotate their shoulders and pass through apertures of
589 various widths. Their results showed that the participants could indeed adjust their shoulder
590 rotations depending on the width of the aperture. However, human echolocation signals
591 provide less precise spatial information than SSDs, and human echolocation requires a
592 comparison between self-generated sound and the echoes (Thaler et al., 2011). Further work
593 is needed to investigate how useful human echolocation signals are for tailoring locomotor
594 adjustments, such as shoulder rotations when passing through apertures and walking around
595 obstacles during navigation.

596 Relatively few studies have investigated the effects of early versus late-onset visual
597 loss on echolocation abilities (Thaler et al., 2011). However, the results suggest that early
598 visual loss results in better echolocation. As noted above, Teng et al. (2012) found that age of
599 onset of visual loss was strongly correlated with echolocation acuity in a group of expert
600 echolocators. The study of Thaler et al. (2011), described above, showed that click-echo
601 processing recruited visual brain areas in both early- and late-blind echolocation experts. The
602 authors suggested that further work is needed to determine whether such recruitment occurs
603 for normally sighted individuals who are trained to echolocate, and for blind individuals with
604 \neq regular sensitivity to echoes who do not echolocate (blind novices). Whether individuals
605 with partial non-correctable visual losses develop enhanced echolocation abilities remains to
606 be tested. Evidence for sensory compensation in this group is mixed, with some studies
607 showing improvement (Hoover et al., 2012), and others showing no improvement (Kolarik et
608 al., 2013a; Lessard et al., 1998). There is some evidence that individuals who have partial

609 correctable visual losses develop enhanced echolocation skills and a higher sensitivity to echo
610 cues than normal-sighted controls (Després et al., 2005).

611 The consequences of hearing loss for echolocation abilities are currently unknown.
612 This issue is especially important for older blind echolocators, who are at risk of hearing
613 impairment. Rowan et al. (2013) reported that judgments of the lateral position of an object
614 using echolocation were primarily based on information from frequency components above 2
615 kHz. Other studies suggest that useful cues for echolocation lie above 5 kHz (Cotzin and
616 Dallenbach, 1950). Since hearing loss is typically greater at high than at low frequencies
617 (Moore, 2007), echolocation abilities may be degraded as a consequence of hearing
618 impairment. Carlson-Smith and Wiener (1996) reported that echolocation performance was
619 not correlated with audiometric thresholds at high frequencies, which at first sight seems
620 inconsistent with this idea. However, their subjects all had normal hearing. Although
621 hearing aids partially compensate for loss of audibility at high frequencies, they do not
622 necessarily restore the ability to discriminate high-frequency sounds. For example, they do
623 not compensate for the effects of reduced frequency selectivity. Also, most hearing aids do
624 not produce useful gain for frequencies above about 5 kHz. The effects of hearing impairment
625 and hearing aid processing on echolocation remain to be explored.

626 Recent studies have investigated how auditory space emerges for blind individuals,
627 and how this space is maintained in the absence of visual calibration cues (Lewald, 2002;
628 2013). Accurate spatial representations of auditory space are maintained among blind
629 individuals, at least in the horizontal dimension, (Lessard et al., 1998; Voss et al., 2004). This
630 has been attributed to calibration based upon audiomotor feedback, which refers to the
631 relationship between self-motion and systematic changes in auditory stimuli (Lewald, 2002;
632 2013), e.g. angle of head rotation and changes in interaural time difference and ILD cues for
633 azimuthal localization. To our knowledge, echolocation has not yet been considered within

634 this context. However, it seems plausible that echoic information may aid in the calibration of
635 auditory space and especially of distance. This remains to be confirmed.

636

637

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643

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818

819 **Figure captions**

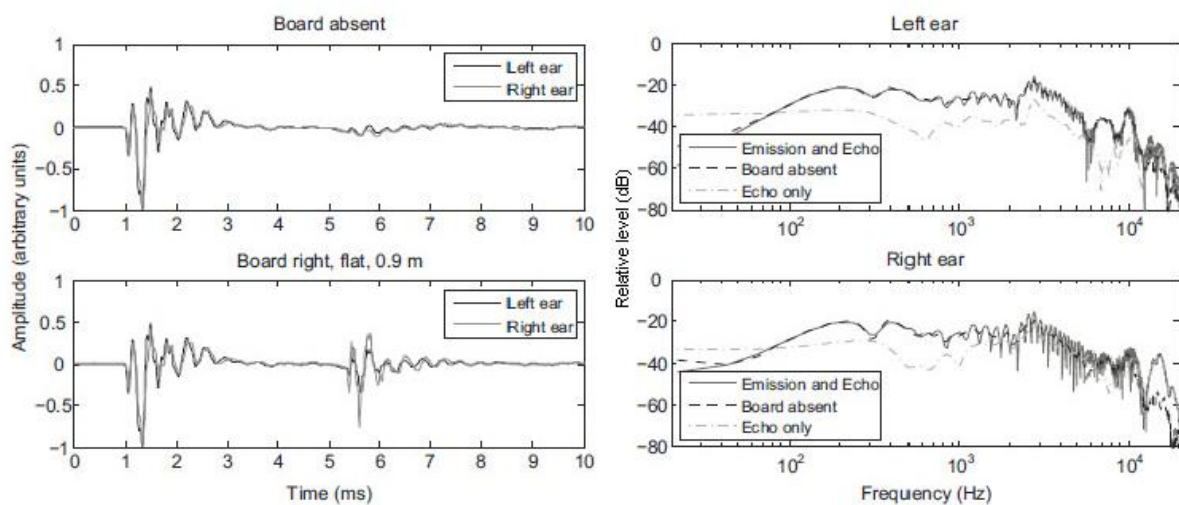
820 **Fig. 1.** Recordings of responses to clicks obtained using a KEMAR manikin, taken from the
821 study of Rowan et al. (2013), their Fig. 2. The left panel shows waveforms, and the right
822 panel shows their spectra, recorded in the presence or absence of a reflective board 0.9 m
823 away, oriented so that its flat surface faced the manikin. The waveform of the emission is
824 shown in the top-left panel; this is small after 4 ms. The bottom left-panel shows the emission,
825 gap, and response associated with the echo from the board, which occurs just after 5 ms. Used
826 with permission from Rowan et al. (2013).

827 **Fig. 2.** Scores from the study of Schenkman and Nilsson (2011), showing the proportion of
 828 correct responses in judging whether a disc was present, based on echolocation. The distance
 829 to the disc was 2 m. The left and right panels show the mean and individual results,
 830 respectively. The conditions were: all cues, level cue removed, and level cue only. Redrawn
 831 from Figure 6 of Schenkman and Nilsson (2011).

832 **Fig. 3.** Blood oxygen-level dependent (BOLD) activity projected on the cortical surface of
 833 participants from the study of Thaler et al. (2011), their Fig. 2. Concavities are colored dark
 834 and convexities are colored light. CS: central sulcus, CaS: calcarine sulcus, LS: lateral sulcus,
 835 MFS: middle frontal sulcus. The upper panel shows BOLD activity for blind participants EB
 836 and LB listening to recordings of their own echolocation sounds. The lower panel shows
 837 BOLD activity for sighted controls C1 and C2, listening to EB and LB's echolocation sounds,
 838 with which they had received prior training. There was clear BOLD activity in the calcarine
 839 sulcus, an area associated with visual processing, for the blind but not for the sighted
 840 participants. Used with permission from Thaler et al. (2011).

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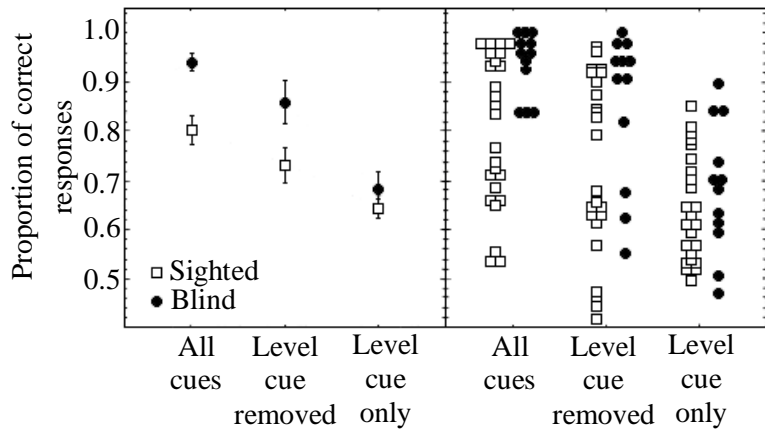
842 FIGURE 1



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844 FIGURE 2

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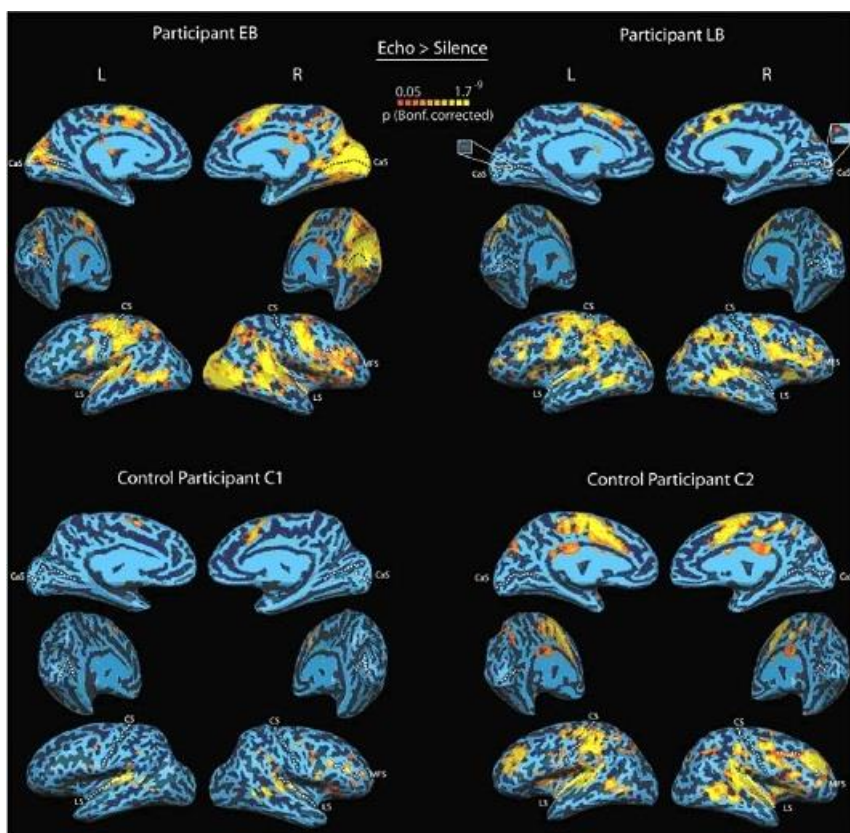


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849 FIGURE 3



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