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Human exploration of enclosed spaces through echolocation

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28 **Abstract**

29 Some blind humans have developed echolocation, as a method of navigation in space.

30 Echolocation is a truly active sense because subjects analyze echoes of dedicated, self-

31 generated sounds to assess space around them. Using a special virtual space technique we

32 assess how humans perceive enclosed spaces through echolocation, thereby revealing the

33 interplay between sensory and vocal-motor neural activity while humans perform this task.

34 Sighted subjects were trained to detect small changes in virtual room size analyzing real-time

35 generated echoes of their vocalizations. Individual differences in performance were related to

36 the type and number of vocalizations produced. We then asked subjects to estimate virtual-

37 room size with either active or passive sounds, while measuring their brain activity with

38 fMRI. Subjects were better at estimating room size when actively vocalizing. This was

39 reflected in the hemodynamic activity of vocal-motor cortices, even after individual motor

40 and sensory components were removed. Activity in these areas also varied with perceived

41 room size, although the vocal-motor output was unchanged. In addition, thalamic and

42 auditory-midbrain activity was correlated with perceived room size, a likely result of top-

43 down auditory pathways for human echolocation, comparable to those described in

44 echolocating bats. Our data provide evidence that human echolocation is supported by active

45 sensing, both behaviorally and in terms of brain activity. The neural sensory-motor coupling

46 complements the fundamental acoustic motor – sensory coupling via the environment in

47 echolocation.

48

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Significance

Passive listening is the predominant method for examining brain activity during echolocation, the auditory analysis of self-generated sounds. We show that sighted humans perform better when they actively vocalize than during passive listening. Correspondingly, vocal motor and cerebellar activity is greater during active echolocation than vocalization alone. Motor and subcortical auditory brain activity covaries with the auditory percept, although motor output is unchanged. Our results reveal behaviorally relevant neural sensory-motor coupling during echolocation.

Introduction

In the absence of vision, the only source of information for the perception of far space in humans comes from audition. Complementary to the auditory analysis of external sound sources, blind individuals can detect, localize, and discriminate silent objects using the reflections of self-generated sounds (Rice, 1967; Griffin, 1974; Stoffregen and Pittenger, 1995). The sounds are produced either mechanically, e.g. via tapping of a cane (Burton, 2000), or vocally using tongue clicks (Rojas et al., 2009). This type of sonar, or echolocation, departs from classical spatial hearing in that the listener is also the sound source, i.e. he or she must use her own motor commands to ensonify the environment. It is a specialized form of spatial hearing also called echolocation that is known from bats and toothed whales. In these echolocating species, a correct interpretation of echo information involves precise sensory-motor coupling between vocalization and audition (Schuller et al., 1997; Smotherman, 2007). However, the importance of sensory-motor coupling in human echolocation is unknown.

Neuroimaging studies on echolocation have shown that the presentation of spatialized echoes to blind echolocation experts results in strong activations of visual cortical areas (Thaler et al., 2011; Thaler et al., 2014b). In these studies, participants did not vocalize during imaging, an approach we will refer to as 'passive echolocation'. While these studies have resulted in valuable insights into the representations in, and possible reorganizations of sensory cortices, passive echolocation is not suitable to investigate the sensory-motor coupling of echolocation. Sonar object localization may involve the processing of interaural time and level differences of echoes, similar to classical spatial hearing. For other echolocation tasks, however, the relative difference between the emitted vocalisation and the returning echoes provides the essential information about the environment (Kolarik et al., 2014). Sonar object detection is easier in a room with reflective surfaces (Schenkman and Nilsson, 2010), suggesting that reverberant information, such as an echo, provides important and ecologically relevant information for human audition. Reverberant information can be used to evaluate enclosed

84 spaces in passive listening (Seraphim, 1958, 1961), although it is actively suppressed when

85 listening and interpreting speech or music (Blauert, 1997; Litovsky et al., 1999; Watkins,

86 2005; Watkins and Makin, 2007; Nielsen and Dau, 2010). Psychophysical analyses of room-

87 size discrimination based on auditory information alone are scarce (McGrath et al., 1999).

88 How can we quantify the acoustic properties of an enclosed space? The binaural room

89 impulse response (BRIR), a measure from architectural acoustics of the reverberant properties

90 of enclosed spaces (Blauert and Lindemann, 1986; Hidaka and Beranek, 2000), captures the

91 complete spatial and temporal distribution of reflections that a sound undergoes from a

92 specific source to a binaural receiver. In a recent study we introduced a technique allowing

93 subjects to actively produce tongue clicks in the MRI and evaluate real-time generated echoes

94 from a virtual reflector (Wallmeier et al., 2015). Here, we used this same technique but with a

95 virtual echo-acoustic space, defined by its BRIR, to examine the brain regions recruited

96 during human echolocation.

97 In this study, participants vocally excited the virtual space and evaluated the echoes,

98 generated in real-time, in terms of their spatial characteristics. They had full control over

99 timing and frequency content of their vocalizations and could optimize these parameters for

100 the given echolocation task. As such, we consider this active echolocation. First, we

101 quantified room-size discrimination behavior and its relationship to the vocalizations'

102 acoustic characteristics. Then we compared the brain activity and performance between active

103 and passive echolocation to elucidate the importance of active perception. Then the

104 relationship between brain activity and the behavioral output was investigated in a parametric

105 analysis. Finally, we compared the brain activity of a blind echolocation expert during active

106 echolocation to the sighted subjects we measured.

Methods

108 Three experiments on active echolocation in humans were performed. First a psychophysical

109 experiment (see *Room size discrimination*) examined the effect of individual call choice on

110   performance. Second, we examined the difference between active and passive echolocation in

111   terms of behavior and brain activity, as measured with fMRI (see *Active vs. passive*

112   *echolocation*). Finally, we tested the relationship between brain activity and perceived room

113   size in a group of sighted subjects and in a blind echolocation expert (see *Active echolocation*

114   *only* and *Blind echolocation expert*). The acoustic recordings and stimuli were the same for all

115   three experiments and will be explained first. All experiments were approved by the ethics

116   committee of the medical faculty of the LMU (Project Nrs. 359-07 and 109-10). All

117   participants gave their informed consent in accordance with the Declaration of Helsinki and

118   voluntarily participated in the experiment.

119   **Acoustic recordings**

120   To conduct the experiments under realistic conditions, the BRIR of a real building was

121   measured. A small chapel in Gräfelfing, Germany (Old St. Stephanus Fig. 1A) with highly

122   reflective surfaces was chosen because the reverberation time, i.e. the time it takes for

123   reflections of a direct sound to decay by 60 dB, was long enough to not be masked by the

124   direct sound. The floor consisted of stone flaggings, the walls and the ceiling were made of

125   stone with wall plaster and the sparse furnishings were wooden. The chapel had a maximum

126   width of 7.18 m, a maximum length of 17.15 m, and a maximum height of 5.54 m.

127   BRIR recordings were performed with a B&K head-and-Torso Simulator 4128C (*Brüel &*

128   *Kjaer Instruments, Naerum, Denmark*) positioned in the middle of the chapel facing the altar

129   (Fig. 1A). Microphones of the head-and-torso simulator were amplified with a *Brüel & Kjaer*

130   *Nexus* conditioning amplifier. The recording was controlled via a notebook connected to an

131   external soundcard (*Motu Traveler, Cambridge, USA*). The chapel was acoustically excited

132   with a 20 s sine sweep from 200 to 20000 Hz. The sweep was created with Matlab (*The*

133   *MathWorks, Inc., Natick, USA*); playback and recording were implemented with

134   SoundMexPro (*HörTech GmbH., Oldenburg, Germany*). The frequency response of the

135   mouth simulator was digitally equalized. The sweep was amplified (Stereo Amplifier A-109,

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136   *Pioneer Electronics, Willich, Germany*) and transmitted to the inbuilt loudspeaker behind the

137   mouth opening of the head-and-torso simulator. The BRIR was extracted through cross-

138   correlation of the emission and binaural recording (Fig. 1B) and had a reverberation time of

139   approximately 1.8 s. This BRIR recording was used for all of the following experiments.

140   ### *Stimuli*

141   The BRIRs presented were all derived from the BRIR recorded in the chapel (see *Acoustic*

142   *recordings*). The BRIRs were compressed along the time axis, a technique well established

143   for scale models in architectural acoustics (Blauert and Xiang, 1993), resulting in scaled-

144   down versions of the original, measured space. The BRIR recorded in the chapel was

145   compressed by factors 0.2, 0.5, and 0.7; a compression factor of 0.2 produced the smallest

146   room. The reverberation time scales with the same compression factors. From these

147   reverberation times, the volume of a cube that would produce an equal reverberation time can

148   be calculated according to Sabine (1923) (cf, Fig 1C). Note that the spectral center of gravity

149   of the BRIR increases with decreasing compression factor (Fig. 1C). The co-variation of

150   spectral and temporal parameters of the BRIRs is characteristic of the reverberations from

151   different-sized rooms. Also the overall level of the BRIR decreases with temporal

152   compression: specifically, attenuations were -2, -3, and -9 dB for compression factors of 0.7,

153   0.5, and 0.2, respectively.

154   The experimental setup was designed around a real-time convolution kernel (Soundmexpro,

155   Oldenburg, Germany) running on a personal computer (PC with Windows XP) under Matlab.

156   Participants' vocalizations were recorded, convolved with a BRIR and presented over

157   headphones in real time, with the echo-acoustically correct latencies.

158   The direct sound, i.e. the sound path from the mouth directly to the ears, was simulated as a

159   switchable direct input-output connection with programmable gain ('asio direct monitoring')

160   with an acoustic delay of less than 1 ms. The result of the real-time convolution was added

161   with a delay equal to the first reflection at 9.1 ms. The correct reproduction of the chapel

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162 acoustics was verified using the same recording setup and procedure as in the chapel but now

163 the head-and-torso simulator was equipped with the experimental headset microphone and

164 earphones in an anechoic chamber (see *Psychophysical procedure*).

165 *Room size discrimination*

166 Here, we psychophysically quantified the ability of sighted human subjects to detect changes

167 in the size of an enclosed space by listening to echoes of their own vocalizations.

168 *Participants*

169 Eleven healthy subjects with no history of medical or neurological disorder participated in the

170 psychophysical experiment (age 23.4 ± 2.2 yrs (mean $\pm$ SD), 4 female).

171 *Procedure*

172 The psychophysical experiments were conducted in a 1.2 m x 1.2 m x 2.2 m sound-attenuated

173 anechoic chamber (*G+H Schallschutz GmbH, Ludwigshafen, Germany*). Just-noticeable

174 differences (JNDs) in acoustic room size were quantified using an adaptive two-interval, two-

175 alternative, forced-choice paradigm. Each observation interval started with a short tone beep

176 (50 ms, 1000 Hz) followed by a 5 s interval in which both the direct path and the BRIR were

177 switched on. Within this interval, subjects evaluated the virtual echo-acoustic space by

178 emitting calls and listening to the echoes from the virtual space. The calls were typically

179 tongue clicks (see *Results* and Fig. 3). The end of an interval was marked by another tone

180 beep (50 ms, 2000 Hz). The pause between the two intervals of each trial was 1 s. After the

181 end of the second interval, the subjects judged which of the two intervals contained the

182 smaller virtual room (smaller compression factor). To focus the subjects' attention away from

183 overall loudness towards the temporal properties of the reverberation, we roved the amplitude

184 of the BRIR by ± 6 dB across intervals. This rove rendered discrimination based on the sound

185 level of the reverberation difficult, at least for the larger three compression factors (see

186 'Stimuli', above).

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187 Subjects were equipped with a professional headset microphone (*Sennheiser HS2-EW,*

188 *Wedemark, Germany*) and in-ear headphones (*Etymotic Research ER-4S, Grove Village, IL,*

189 *USA*). The headset microphone was positioned at a distance of about 3 cm to the left of the

190 subjects' mouth. Headphones and microphone were connected to an external soundcard (*RME*

191 *Fireface 400, Haimhausen, Germany*), which was connected to the PC. A gamepad (*BigBen*

192 *interactive, Bergheim, Germany*) was used as response device. Auditory feedback was

193 provided with a 250 ms tonal sweep, which was upward modulated for a correct decision and

194 downward modulated for a wrong decision.

195 Compression-factor JNDs were measured following a three-down, one-up rule, i.e. the

196 difference between the two intervals was reduced after three correct decisions and increased

197 after one incorrect decision. An adaptive track was continued until 11 reversals (a wrong

198 response after three consecutive correct trials, or three correct responses after one wrong

199 response) were gathered. The compression-factor difference was 2 for reversals 1-3, 1.2 for

200 reversals 4 and 5, and 1.1 for reversals 6 to 11. The mean compression-factor difference

201 across the last six reversals was taken as the threshold for an experimental run. Data shown

202 are the average of three consecutive runs, once the subjects' performance was stable, i.e., the

203 standard deviation of the thresholds across the last three runs was less than ¼ of the mean

204 threshold. JNDs are specified by the percentage of each side of the virtual room that must be

205 increased such that the BRIR changes perceptibly.

206 The psychophysical procedure challenged the subjects to optimize both their vocal emissions

207 and the auditory analysis of the virtual echoes to extract room-size dependent echo

208 characteristics based on the trial-to-trial feedback. Considering that loudness, spectral, and

209 temporal cues covaried with IR compression, we cannot isolate the perceptual cue or

210 combination of cues that was used. However, listeners were deterred from using loudness

211 cues by the roving-level procedure. Parts of the current psychophysical data were presented at

9

212 the 2012 International Symposium on Hearing and can be found in the corresponding

213 proceedings (Schornich et al., 2013).

214 *Sound analysis*

215 To test for the effects of individual sound vocalizations on psychophysical performance, we

216 analyzed the temporal and spectral properties of the echolocation calls used by each subject.

217 The microphone recording from the second interval of every fifth trial was saved to hard disk

218 for a total number of available recordings per subject of between 300 and 358. The number of

219 calls, RMS sound level, duration and frequency were analyzed from these sound recordings.

220 The number of calls in each recording was determined by counting the number of maxima in

221 the recording's Hilbert envelope that exceeded threshold (mean amplitude of the whole

222 recording plus three times the standard deviation of the amplitude). Clipped calls and calls

223 starting within the last 50 ms of the interval were excluded from further analysis. Each

224 identified call was positioned in a 186 ms rectangular temporal window to determine the RMS

225 sound level. The call duration was determined as the duration containing 90 % of the call

226 energy. The peak frequency of each call was determined from the Fourier transform of the

227 186 ms rectangular window. Correlations between an echolocation-call parameter of a subject

228 and that subjects' JND were quantified using Spearman's Rho.

229 ### *Active vs. passive echolocation*

230 To understand the importance of active sensing for echolocation, we compared active and

231 passive echolocation while measuring brain activity with fMRI. In this experiment,

232 participants judged the size of a virtual room by either actively producing vocalizations, or

233 passively listening to previously produced vocalizations and evaluating the resulting echoes.

234 *Participants*

235 Ten healthy participants with no history of medical or neurological disorder took part in the

236 experiment (age 25.2 ± 3.1 yrs (mean $\pm$ SD), 6 females). Three subjects from the room size

237   discrimination experiment participated in this experiment. All participants were recruited

238   from other behavioral echolocation experiments to ensure that they were highly trained in

239   echolocation at the time of the experiment.

240   ***Setup***

241   During active echolocation, subjects preferred calls were recorded by an MRI compatible

242   optical microphone (*Sennheiser MO 2000, Wedemark, Germany*), amplified (*Sennheiser MO*

243   *2000 CU*), converted (*Motu Traveler, Cambridge, USA*), convolved in real time with one of

244   four BRIRs, converted back to analog (Motu Traveler) and played back over MRI compatible

245   circumaural headphones (*Nordic Neurolabs, Bergen, Norway*). The frequency-response

246   characteristics of this setup were calibrated with the head-and-torso simulator to ensure that

247   the BRIR recorded with the MRI-compatible equipment was identical to the BRIR measured

248   with the same simulator in the real (church) room. The convolution kernel and programming

249   environment were the same as the psychophysics experiment.

250   ***Procedure***

251   The task was to rate the size of the room on a scale from 1 to 10 (magnitude estimation) when

252   presented with one of four BRIR compression factors (see *Stimuli*). Subjects were instructed

253   to close their eyes, to keep their heads still and to use a constant number of calls for each trial.

254   A single trial consisted of a 5 s observation interval, where subjects produce calls and

255   evaluate the virtual echoes, bordered by auditory cues (beeps to delineate the start and end of

256   an observation interval). Passive and active trials were signaled to the subjects with beeps

257   centered at 0.5 and 1 kHz, respectively. The observation interval was temporally jittered

258   within a 10 s window across repetitions (0.4-4.8 s from the start of the window in 0.4 steps)).

259   The 10 s window allowed us to provide a quiesescent period for the task, followed by one

260   MRI acquisition. Jittering was done to improve the fit of the functional imaging data by

261   sampling from different points of the hemodynamic response function and is a way to

262   optimize sampling of the hemodynamic signal.

11

263   The time from the start of the 5-second echolocation interval to the start of fMRI acquisition

264   was therefore between 10.1 and 5.7 seconds. Following the 10 s window, one MR-image (2.5

265   s) was collected framed by two 500 ms breaks after which subjects verbally expressed their

266   rating within a 3 s response interval bordered by 2 kHz tone beeps. The total trial time was

267   16.5 seconds.

268   In half of the trials participants actively vocalized (active echolocation) and in half of the

269   trials calls and echoes were passively presented to the participants (passive echolocation). In

270   the passive trials, vocalizations of a randomly chosen, previously recorded active trial was

271   convolved with a BRIR and presented to participants. Thus, in the passive trials, subjects

272   received the same auditory input as in a previous active trial, but the subject did not vocalize.

273   Three additional null-conditions were introduced; 1) an active-null during which subjects

274   vocalized but neither direct sound nor echoes were played through the headphones, 2) a

275   passive-null in which the previously recorded vocalizations were presented through an

276   anechoic BRIR and 3) silence (complete-null), in which no sound was presented and no

277   vocalizations were made. This resulted in a total of 5 active conditions (four BRIRs and one

278   null), 5 passive conditions (four BRIRs and one null) and a complete-null condition. All null

279   conditions were to be rated with a '0'.

280   In a 40-minute session, subjects were trained on the timing of the procedure and to distinguish

281   between active and passive trials. One MRI session included two runs of fMRI data

282   acquisition. Within one run the 11 pseudo-randomized conditions were repeated five times,

283   for a total of 55 trials in each run. Subjects were scanned in two separate sessions for a total of

284   four runs of fMRI data acquisition.

285   ***Image acquisition***

286   Images were acquired with a 3T MRI Scanner (*Signa HDx, GE Healthcare, Milwaukee, USA*)

287   using a standard 8-channel head coil. 38 contiguous transverse slices (slice thickness 3.5 mm,

288   no gap) were acquired using a gradient echo echo-planar-imaging (EPI) sequence (TR 16.5 s.,

289   TE 40 ms, flip angle 90 deg. Matrix 64 x 64 voxel, FOV 220 mm, interleaved slice

290   acquisition). Image acquisition time was 2.5 s; the remaining 14 s of quiescence minimized

291   acoustical interference during task performance, a methodological procedure known as sparse

292   imaging (Hall et al., 1999; Amaro et al., 2002). A T1-weighted high-resolution structural

293   image of the entire brain (0.8 x 0.8 x 0.8 isotropic voxel size) was also acquired using a fast

294   spoiled gradient recalled sequence.

295   *Analysis*

296   To test for behavioral performance differences between active and passive echolocation, a

297   within-subject 2 x 4 ANOVA with factors active/passive and BRIR compression factor was

298   performed. Two separate within-subject one-way ANOVAs were then used to assess whether

299   loudness and number of clicks differed between BRIR compression factors.

300   Image processing and data analysis were performed using SPM8 (*Wellcome Trust Centre for*

301   *Neuroimaging, UCL, London, UK*) for Matlab. Volumes were corrected for head motion

302   using realignment, and spatially normalized to Montreal Neurological Institute (MNI) space

303   through segmentation of the high-resolution MR-image (Ashburner and Friston, 2005).

304   Images were smoothed with an 8 mm full-width at half maximum isotropic Gaussian kernel to

305   reduce spatial noise.

306   Single-subject effects were tested with the general linear model (GLM). High-pass filtering

307   (cut-off time constant = 500 s) the time series reduced baseline shifts. Each run was modeled

308   separately in one design to correct for within-run effects. The 5 s observation interval for

309   active and passive echolocation trials and their null conditions (active-null, passive-null) were

310   modeled separately as boxcar functions convolved with the hemodynamic response function

311   (HRF). The four BRIRs were combined into a single regressor for either active or passive

312   echolocation. In addition, two regressors corresponding to the mean centered linear

313   parametric modulation of reported room size for active and passive trials separately, modeled

13

314 additional variability in the experimental design. The complete silence null was not explicitly

315 modeled. Head movement parameters were included as regressors of no interest.

316 The behavioral results of the room size rating task showed us that participants could not

317 distinguish between the smallest BRIR compression factor (0.2) and the passive null, without

318 echoes (see *Results*). Therefore in the analyses we did not use the passive null, but compared

319 passive echolocation to the baseline control null. The two contrast images corresponding to

320 the subtractive effects of echolocation compared to null (active echolocation - active null, and

321 passive echolocation - baseline) were used to create a paired t-test at the group level to

322 compare active and passive echolocation. Voxels exceeding an extent threshold of five

323 contiguous voxels and a voxel-level height threshold of $p < 0.05$ corrected for multiple

324 comparisons (false discovery rate (FDR), (Genovese et al., 2002)) were considered significant

325 unless otherwise stated.

326 ### *Active echolocation only*

327 The active vs. passive experiment randomly switched between active production of

328 echolocation calls and passive listening to these calls. This task switching could have lead to

329 additional brain activation patterns that are not directly related to active or passive

330 echolocation. We therefore performed a second experiment, in which participants only

331 performed active echolocation during fMRI data acquisition. Throughout this experiment, all

332 subjects actively produced consistent echolocation calls and were familiar with the vocal

333 excitation and auditory evaluation of BRIRs.

334 *Participants*

335 The same participants that participated in the psychophysical experiment (see *Room size*

336 *discrimination*) were recruited for this experiment.

337 *Setup, imaging parameters and procedure*

338 The setup and the imaging parameters were the same as in the active vs. passive echolocation

339 experiment except that only active echolocation trials were presented. A single trial consisted

14

340   of a 5 s observation interval, where subjects produce calls and evaluate the virtual echoes,

341   bordered by 2 kHz tone beeps. The observation interval was also temporally jittered within a

342   10 s window across repetitions (see *Active vs. passive echolocation*). Each BRIR compression

343   factor was additionally presented at four amplitude levels corresponding to +1, +2, +3 and

344   +4 dB relative to the calibrated level. These small level changes filled the level steps

345   concomitant with the IR compression. The active-null condition, during which neither direct

346   sound nor echoes were played through the headphones, was presented four times for every

347   other combination of BRIR compression factor and amplitude level (16 combinations in

348   total).

349   One scanning session included 2 runs of 3 repetitions, each repetition consisting of 20

350   pseudo-randomized trials (the 16 different reverberation conditions plus the four null

351   conditions) for a total of 60 trials per run, 48 of which were reverberation conditions. Subjects

352   completed four runs in two separate sessions (each session was approximately 45 min).

353   *Analysis*

354   Room size ratings were analyzed using a within-subject 4 x 4 ANOVA with factors BRIR

355   compression factor and amplitude level.

356   FMRI analysis, including preprocessing and significance levels, was the same as in the active

357   vs. passive echolocation experiment. For the single-subject GLMs, a single regressor was

358   used to model all of the 16 conditions with echoes. The null condition was not explicitly

359   modeled. Four additional regressors modeled linear and quadratic parametric modulations of

360   the mean-centered room size rating and BRIR amplitude levels on each trial. Head movement

361   parameters were included as regressors of no interest. Contrasts for echolocation – baseline

362   and for the linear and quadratic modulations with BRIR amplitude levels and room size rating

363   were entered into t-tests at the group level.

364   No voxels were significantly correlated with the quadratic modulations of room size or BRIR

365   amplitude. We therefore only report the linear modulations. We first compared the brain

366   activity during active echolocation in the first experiment (Active vs. passive echolocation) to

367   the activity during active echolocation in this experiment using a two-sample t-test at the

368   group level. We then tested the activation pattern during active echolocation compared to

369   active vocalization without auditory feedback (the active null) using a one-sample t-test.

370   Parametric modulations of brain activity with a stimulus or behavioral parameters (i.e.

371   correlations between the the strength of a stimulus or the response subjects and height of the

372   brain activity) provide strong evidence that brain regions with significant parametric

373   modulation are involved in the given task. Therefore, complementary to the subtractive

374   analysis, we examined parametric modulations of brain activity with room size rating and

375   BRIR amplitude changes using one-sample group-level t-tests.

376   ### *Blind echolocation expert*
377   We also measured brain activity during echolocation of an echolocation expert to examine the

378   brain regions recruited during active echolocation when audition is the primary source of

379   information about far, or extrapersonal space. The male congenitally blind, right-handed

380   subject, aged 44, performed the active only echolocation experiment, with the same imaging

381   parameters, and single-subject data analysis. Additionally, a two-group model tested for

382   significant differences in echolocation – null between the echolocation expert and the healthy

383   subjects.

384   ## Results

385   ### *Room size discrimination*
386   All sighted subjects quickly learned to produce tongue clicks and perceive virtual rooms using

387   echolocation. Subjects could detect changes in the BRIR compression factor independent of

388   the roving BRIR amplitude levels, suggesting that they were able to use properties of the echo

389   other than loudness to solve the task. The JNDs were quite stable within each subject but

390   varied between about 5 and 25 % across subjects. Previous findings on spatial acuity and

391   object localization using echolocation in sighted subjects also found a high degree of

16

392 variability in subjects' performance (Teng and Whitney, 2011). The across-subject mean is on

393 the order of 10 %, i.e. the percent that each side of the virtual room must be increased to

394 perceive a different sized room (Fig 2 bottom). To show what 10% means, we created

395 theoretical rooms. The mean psychophysical performance was such that the grey-filled room

396 could be discriminated from the transparent room surrounding it (cf. Fig. 2 top). These

397 discrimination thresholds were much finer than reported previously (McGrath et al., 1999) but

398 are consistent with passive-acoustic evaluation of reverberation times (Seraphim, 1958).

399 Temporal and spectral call analyses revealed that all subjects produced relatively short,

400 broadband tongue clicks at relative high sound levels to solve the psychophysical task (Fig.

401 3). Our participants, although free to choose their preferred vocalization, all produced clicks

402 with durations that varied between 3 and 37 ms and absolute sound pressure levels that varied

403 between 88 and 108 dB SPL. The peak frequencies of the clicks ranged from 1 to 5 kHz. We

404 then correlated the properties of the tongue-call click with the JND for each subject to see

405 which vocal-motor properties may be related to the psychophysical performance. Significant

406 correlations were found between the click level and JNDs and the number of clicks per trial

407 and JNDs, but there were no significant correlations for click duration and the peak frequency

408 (Fig. 3 bottom). These effects do not survive a correction for multiple comparisons (for four

409 independent tests), however as the trends are in the same direction across all room sizes, this

410 is likely due to the relatively small number of participants. Recruiting was an issue because of

411 the time investment in training sighted subjects. Our results are also supported by previous

412 work on the relationship between acoustic features of echolocation vocalizations and

413 performance for object detection (Thaler and Castillo-Serrano, 2016).

414 In particular, in our study, louder clicks were associated with better JNDs than fainter clicks,

415 presumably because the majority of the power from the echo is still above hearing thresholds;

416 i.e., the virtual room is excited more effectively. A higher number of clicks per trial on the

417 other hand, corresponded to worse JNDs. At first glance this goes against the principle of

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418   "information surplus" (Schenkman and Nilsson, 2010), however, this effect is likely related to

419   masking of the current reverberation by the subsequent click,. Using short clicks or pulses

420   with intermittent periods of silence, adjusted to target range, is also common in echolocating

421   bats and toothed whales, allowing them to produce loud calls that effectively excite space and

422   still analyze the comparatively faint echoes (Thomas et al., 2004). Humans trained to

423   echolocate appear to optimize their vocalizations in a similar way.

Active vs. passive echolocation

425   After characterizing performance psychophysically, we were interested in the brain activity

426   during echolocation. Most of what we know about the neural basis of human echolocation is

427   based on passive listening. Therefore, we first compared brain activation patterns between

428   active-acoustic conditions, where subjects produced clicks in the scanner to passive-acoustic

429   conditions where subjects only listened to clicks and their echoes. Data were collected with

430   intermittent passive- and active-acoustic trials. Participants were asked to rate, on a scale from

431   one to ten, the size of the virtual room, represented as one of four BRIR compression factors.

Behavioral performance

433   Both in the active and the passive-acoustic condition, subjects reliably rated the larger

434   compression factors to correspond to a larger perceived room size (rm-ANOVA,

435   $F_{(4,36)}=102.24$, $p=7.44 \times 10^{-15}$, Fig 4A). Although there was no main effect of echolocation

436   type (active or passive) ($F_{(1,9)}=0.015$, $p=0.91$) there was a significant interaction between

437   room size and echolocation type ($F_{(4,36)}=19.93$, $p=5.11 \times 10^{-7}$). The ratings differed

438   significantly across all active-acoustically presented compression factors but not across all

439   passive-acoustically presented compression factors (Scheffé-Test), and for the largest room,

440   the active rating was significantly higher than the passive rating.

441   Subjects' vocalizations during the active-acoustic condition were also analyzed. Subjects

442   produced between 9 and 10 clicks within each 5 s observation interval. The loudness and the

443   number of clicks per observation interval did not differ significantly across the different

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444   compression factors or the null condition (ANOVA, $F_{(4,36)}=0.41$, p=0.74, and $F_{(4,36)}=1.92$,

445   p=0.15 respectively), confirming that subjects followed the instructions and did not attempt to

446   change their motor strategy to aid in determining the room size.

447   *Brain activity during active vs. passive sensing*

448   Because the number and loudness of clicks did not differ between the echolocation and the

449   active null condition, any differences in brain activity between these two conditions in the

450   motor cortices should be related to the sensory perception of the echoes from the BRIR

451   compression factors and not the motor commands. To test for differences between active and

452   passive echolocation we compared active echolocation with the active null subtracted out, to

453   passive echolocation. Significantly higher activations in the active-acoustic condition were

454   found in the vocal motor centers of the primary motor cortex and in the cerebellum (Fig. 4B,

455   Table 1). This is not surprising because the active acoustic condition includes a motor

456   component, the clicking, which the passive-acoustic condition does not. Note, however, that

457   these activation differences persist although the active null condition was subtracted before

458   the active-minus-passive subtraction. In particular the pre and postcentral gyri were active,

459   with the peak voxel around z = 27 mm, the cerebellar vermis VI was active bilaterally, and

460   smaller activations in the frontal regions, the anterior insula, the thalamus, caudate nucleus

461   and precuneus were found. The reverse comparison showed no significantly stronger

462   activations in the passive-acoustic condition than in the active acoustic condition.

463   **Active echolocation only**

464   The results of the active vs. passive echolocation experiment suggest that active echolocation

465   improves performance and increases brain activity in motor centers although the output

466   related motor components were subtracted from the analysis. However, in that experiment,

467   subjects were required to switch between active call production and passive listening, which

468   may have led to activity more related to task switching than to the actual task (Dove et al.,

469   2000). We therefore performed an additional fMRI experiment where participants only

470   performed active echolocation. In addition to characterizing the activity during active

471   echolocation, we examined the effect of the stimulus factors BRIR compression factor and

472   amplitude changes on performance and on brain activity.

473   ***Behavioral performance***

474   Subjects' performance was similar to the previous experiment (Fig. 5A). The spectral and

475   temporal properties of the clicks produced were consistent across conditions within subjects.

476   Both BRIR compression factor (rm-ANOVA, $F_{(3,30)}$=488.34, p=0) and BRIR amplitude

477   ($F_{(3,30)}$=39.64, p=1.47x10^{-10}) statistically affected room size rating and the two factors showed

478   a significant interaction ($F_{(9,90)}$=2.45, p=0.015). All BRIR compression factors were rated

479   significantly different from one another. To some extent, the subjects' ratings also reflected

480   the small changes in BRIR amplitude. The larger the BRIR compression factor the more

481   different the rating was from the ratings of neighboring BRIR amplitudes. Specifically, when

482   the BRIR was compressed by a factor of 0.2, corresponding to the smallest room, ratings

483   ranged between 1 and 1.6 on the 1-10 scale. For a compression factor of 1, ratings ranged

484   between 7.9 and 8.9.

485   Although we cannot assume a linear relationship between the stimulus parameters and the

486   rating responses, the ratings more accurately reflect changes in BRIR compression than sound

487   level changes induced by compression, independent of the amplitude changes that were

488   introduced. The physical BRIR sound level increases by 5 dB when the compression factor is

489   increased from 0.2 to 0.5, but the sound level increases by only 2 dB when the compression

490   factor increased from 0.7 to 1. However, the subjects' ratings changed the same amount from

491   0.2 to 0.5 as from 0.7 to 1, the same amount as the relative change in BRIR compression

492   factor. This suggests that subjects relied more on stimulus factors directly related to the BRIR

493   compression factor, such as reverberation time, to estimate the perceived room size. Loudness

494   and other factors not controlled for in this study may play a more important role in

495   echolocation under different circumstances (Kolarik et al., 2014).

496   *Motor activity patterns during active sensing*

497   In the neuroimaging analyses, we were interested in the brain regions with a higher

498   hemodynamic signal during all echolocation conditions (across all BRIR amplitude and

499   compression factors) compared to the null condition. This means that the sensory information

500   was very different between the conditions tested, but the motor components were the same.

501   First, we compared the active vs. active null conditions from the active vs. passive experiment

502   to the active vs. active null conditions in this experiment using a two-sample t-test. The

503   differential brain activation patterns did not significantly differ between these two

504   experiments. The activity patterns that we find for active echolocation in this experiment are

505   likely generalizable to the passive vs. active echolocation experiment..

506   We then examined the brain activity patterns that were higher during active echolocation than

507   when subjects vocalized but did not receive auditory feedback (active null). The common

508   pattern of activity across subjects included primary and higher-level auditory processing

509   centers (Fig 5B, see Table 2 for anatomical locations), which is to be expected as more

510   auditory information was present during echolocation than during the null condition.

511   Surprisingly, however, both motor and premotor centers, together with the basal ganglia and

512   parts of the cerebellum, were significantly more active during echolocation with auditory

513   feedback than without. These data clearly show that variation of sensory feedback can

514   modulate vocal-motor brain activity although vocal-motor output is unchanged.

515   It is reasonable to suggest that sensory differences in this echolocation paradigm involve

516   sensory-motor coupling (Wolpert et al., 1995), thereby reflecting the active nature of

517   echolocation. Indeed, the activity in the primary and premotor areas cannot be explained by

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518   varying motor output because the number of clicks per trial and their loudness did not differ

519   between the active echolocation and the active null conditions.

520   ***Brain activity related to perceived room size***

521   Another important question is whether the stimulus parameters and reported room sizes are

522   reflected in the brain activity on a trial-by-trial basis. In fMRI, a parametric analysis identifies

523   voxels whose BOLD response covaries with an experimental parameter. An example peak

524   voxel in a parametric analysis from one subject is shown in Fig. 6. The BOLD response of

525   this voxel, located in the supramarginal gyrus of the parietal cortex (MNI coordinates [x,y,z]=

526   57,-27,45), is plotted as a function of the three stimulus parameters. The BOLD response

527   increases significantly with increases of either the rated room size or the BRIR compression

528   factor, and does not change significantly with BRIR amplitude (cf. Fig. 6).

529   Using a single-subject statistical model that included room-size rating as well as BRIR

530   amplitude variations, we identified brain regions where the BOLD response was significantly

531   and positively correlated with the rated room size (Fig. 7 and Table 3). In line with the

532   findings from the subtractive analysis (Fig. 5B), activation in both auditory cortices and

533   cortical motor areas were found (Fig. 7). This strengthens the conclusion that activations in

534   sensory and motor cortices are tightly coupled during active echolocation.

535   In addition to cortical auditory and motor regions, activity in the medial geniculate nucleus

536   (MGN) and the inferior colliculus (IC) was correlated with room size rating. These areas are

537   well-described subcortical auditory-sensory nuclei. Activity in these areas may be driven

538   either directly by the sensory input, or by cortical feedback loops (Bajo et al., 2010). The fact

539   that the activations significantly covaried with the rated room size but not with BRIR

540   amplitude points towards an involvement of feedback loops. Indeed, we compared the results

541   of the model with room size rating and BRIR amplitude variations, to a model with BRIR

542   compression factor and amplitude variations and found that the activity in the MGN and IC

543   was not significantly correlated with BRIR compression factor. This supports the proposal

544   that the subcortical activity found is related to cognition, rather than sensory input.

545   Finally, parametric activations were seen in the parietal and occipital cortex. These activations

546   may be due to visual imagery (Cavanna and Trimble, 2006) and/or a modality-independent

547   representation of space (Weeks et al., 2000; Kupers et al., 2010). Because we find parietal and

548   occipital cortex activity in most of our analyses, it is not possible to differentiate whether the

549   activity is more linked to the perceived space than to the presence of auditory sensory

550   information in general.

551   BOLD signal activity did not significantly covary with BRIR amplitude in any voxel in the

552   brain, even at the less conservative threshold of $p < 0.001$ uncorrected for multiple

553   comparisons, and 0 voxel threshold. This lenient threshold provides a better control of false

554   negatives, but still no significant covariation of brain activity with BRIR amplitude was

555   found. This supports the behavioral evidence that our subjects were judging room size based

556   on BRIR compression factor more than on BRIR amplitude. However, with this design we

557   cannot separate out what component of the BRIR compression subjects used to solve the task.

558   ***Brain activity in a blind echolocation expert***

559   To examine the brain regions involved in active sensing when echolocation has been

560   performed from an early age, brain activity was measured from a single congenitally blind

561   echolocation expert engaged in the room size estimation task with active echolocation. Since

562   his childhood, this subject has gathered information about his surroundings by producing

563   tongue clicks and listening to how the clicks bounce back from objects around him.

564   Despite lack of previous training on the psychophysical paradigm, the blind echolocation

565   expert solved the psychophysical task in the scanner very well. His ratings of perceived room

566   size were very similar to those of the (extensively trained) sighted subjects (Fig. 8A compared

567   to Fig. 5A). Results from a subtractive analysis for this single blind subject are shown in

568   Fig. 8B and Table 4 in the same format as for the sighted subjects in Fig. 5B. This blind

23

569   subject did not show activation in primary auditory areas but strong and extended activations

570   in primary-visual areas (right occipital cortex). This confirms earlier reports showing activity

571   in primary visual areas during auditory and tactile tasks in the early blind (Kupers et al.,

572   2010). In particular, we found activity in the middle occipital gyrus which is known to be

573   specialized for spatial processing tasks in the early blind (Renier et al., 2010). The only active

574   auditory area was the left planum temporale, a part of auditory cortex involved in the

575   processing of spatial auditory information (Griffiths and Warren, 2002). Strong activations

576   are seen in (mostly right) parietal cortex. These activations partially overlap with the parietal

577   parametric activations found in the sighted subjects (cf. Fig. 7).

578   The activation pattern seen with the current experimental paradigm is qualitatively similar to

579   the activity seen in an early blind subject in a passive echolocation task compared to silence

580   (Thaler et al., 2011), in particular the lack of auditory activity when comparing the presence

581   or absence of echoes. More detailed comparisons of the two studies are difficult, however,

582   because the relative difference in auditory information between the task and control

583   conditions in the two studies were very different. Interestingly, we see very little activity in

584   the cerebellum and primary motor cortex (Table 4) in our active echolocation task. The motor

585   activity was instead seen in the parametric modulation with room size. Although otherwise

586   instructed, the current echolocation expert adjusted both emission loudness and repetition

587   frequency based on the perceived room size. While this strategy is perceptually useful, as

588   evidenced from echolocating species of bats and toothed whales, it confounds the intended

589   sensory-evoked parametric analysis. Any parametric modulation of brain activity with room

590   size in the echolocation expert can be a result of both sensory and motor effects. Thus, the

591   behavioral strategy of the echolocation expert precludes quantification of the selective

592   modulation of brain activity by sensory input.

593   To quantify the differences in brain activity between the subject groups, we used a two-

594   sample group-level general linear model to test the differences between the blind subject and

595 the sighted subjects. The pattern of brain activity seen in the single analysis for the blind

596 subject was significantly higher than in sighted individuals. However, no regions of the brain

597 showed significantly higher activity for the sighted subjects, suggesting that in the blind

598 echolocation expert, subthreshold motor activity was still present during active echolocation

599 compared to the active null.

Discussion

600

601 Echolocation is a unique implementation of active sensing that probes the spatial layout of the

602 environment without vision. Using a virtual echo-acoustic space (VEAS) technique, we were

603 able to explore the production of vocalizations and the auditory analysis of their echoes, in a

604 fully controlled, rigid paradigm. The current psychophysical results demonstrate that sighted

605 humans can be effectively trained to discriminate changes in the size of an acoustically

606 excited virtual space with an acuity comparable to visual spatial-frequency discrimination

607 (Greenlee et al., 1990). To solve this task, subjects excited the virtual room by producing a

608 series of short, loud, and broadband vocalizations (typically tongue clicks). As would be

609 expected in active sensing, the psychophysical performance was related to the vocalizations

610 produced. Subjects that produced fewer but louder clicks performed better (Fig. 3).

611 Echo-acoustic room-size discrimination in humans has previously only been characterized

612 qualitatively. McCarthy and Worchel (1954) described a blind echolocating child who

613 "entered a strange house, clicked once or twice and announced that it was a large room."

614 McGrath et al. (1999) showed that, using echoes from their own voices, humans can

615 discriminate a small room with a size of 3 m x 3 m x 2.5 m from a concert hall with the

616 dimensions of 60 m x 80 m x 20 m. Quantitative information does exist about the passive

617 evaluation of the reverberation times of rooms. When presented with synthetic BRIRs

618 consisting of temporally decaying bands of noise, subjects' JNDs are between 5 % and 10 %

619 of the reference reverberation time (Seraphim, 1958). Our subjects were similarly good at

620 estimating changes in room size, but based on the auditory analysis of active, self-generated

621   vocalizations. Passively presenting the BRIRs themselves, instead of convolving them with a

622   source sound, provides an auditory stimulation that approaches a Dirac Impulse (like a slash

623   from a whip). Self-generated vocalizations are not as broadband as synthesized BRIRs and

624   there is increased masking of the source onto the reverberation. However, in our experiment,

625   active vocalization led to better room size classification performance than passive listening

626   (Fig. 4); supporting the idea that additional and perhaps redundant information, in this case

627   from the motor system, increases performance (Schenkman and Nilsson, 2010).

628   The evaluation of room size based on the evaluation of reverberation from self-generated

629   sounds may involve the estimation of egocentric distance from sound-reflecting surfaces.

630   Perception of reverberation and its application for echo-acoustic orientation are

631   comprehensively reviewed in Kaplanis et al (2014) and Kolarik et al. (2016), respectively. For

632   instance, the direct-to-reverberant ratio of an external sound reliably encodes the distance of

633   its source, and changes thereof encode changes in source distance (Bronkhorst and Houtsma

634   (1999)). Zahorik (2002) found, however, that psychophysical sensitivity to changes of the

635   direct-to reverberant ratio is on the order of five to six dB, corresponding to an about 2-fold

636   change in the egocentric distance towards a sound source. This ratio is too large to explain the

637   high sensitivity to changes in room size that we have shown here. Instead, current

638   psychophysical performance is more likely to be governed by evaluation of changes in

639   reverberation time (Seraphim, 1958), supported also by the relatively low degree of sensitivity

640   to BRIR amplitude changes in the room size estimation experiment (Fig. 5A). Reverberation

641   time, together with inter-aural coherence, is the main perceptual cue used to assess room

642   acoustics (Hameed, 2004; Zahorik, 2009). Only Cabrera et al. (2006) has indicated that

643   perceptual clarity of reproduced speech sounds may carry even greater information about

644   room size than reverberation time.

645   Although in our paradigm active echolocation improves performance over passive

646   echolocation, assisted or passive echolocation may be more useful in other circumstances.

647 The sensory-motor coupling in active echolocation requires extensive training and even then

648 performance differs greatly across participants, similar to the ability to pronounce non-native

649 speech sounds (Kartushina et al., 2015). Participants that are naïve to active echolocation,

650 detect ensonified objects better when passive echolocation is used (Thaler and Castillo-

651 Serrano, 2016). After training with multisensory sensory substitution devices using passive

652 auditory information, navigation performance can improve to a level similar to sighted

653 navigation, although many limitations still exist (Chebat et al., 2015).

654

655 Using the VEAS we were able to investigate brain activity while subjects are engaged in

656 echolocation, and thereby separate out the individual sensory and motor components of

657 human echolocation. Primary and secondary motor cortices have previously been found in

658 both blind and sighted subjects during passive echolocation (Thaler et al. (2011)), although

659 there the activity may be a result of motor imagery, or motor activity during action

660 observation (Cattaneo and Rizzolatti, 2009; Massen and Prinz, 2009). In the current study,

661 both auditory and motor cortices were more active when auditory feedback was present

662 (Fig. 5B) than when subjects vocalized without auditory feedback. Primary somatosensory

663 and motor cortex activity together with the cerebellum were significantly more active during

664 echolocation than when one of the modalities, audition or motor control was present without

665 the other. These motor areas also showed activity that was correlated with the auditory

666 percept. Together these results provide strong evidence that motor feedback is a crucial

667 component of echolocation.

668 The vast majority of animal sensory systems (also in humans) passively sample the

669 environment, i.e. extrinsic energy sources like light or sound stimulate sensory receptors.

670 Still, animals generally use the motor system to sample the environment, e.g. to focus the eyes

671 or turn the ears, but truly active senses, where the animal itself produces the energy used to

672 probe the surroundings, are rare in the animal kingdom (Nelson and Maciver, 2006).

673 Examples comprise the active electric sense by weakly electric fishes (Lissmann and Machin,

674 1958) and echolocation, where sensing of the environment occurs through auditory analysis

675 of self-generated sounds (Griffin, 1944). The advanced echolocation systems of bats and

676 toothed whales involve dynamic adaptation of the outgoing sound and behavior, e.g. head aim

677 and flight path, based on perception of the surroundings through auditory processing of the

678 information carried by returning echoes.

679 The motor system can modulate sensory information processing; independent of whether the

680 energy sensed is also produced. Temporal motor sequences, or rhythmic movements, sharpen

681 the temporal auditory stimulus selection through top-down attentional control (Morillon et al.

682 2014). Motor output is regulated in part by slow motor cortical oscillatory rhythms that have

683 also been shown to affect the excitability of task-relevant sensory neurons (Schroeder et al.

684 2010). Our results support this idea in a classical active sensing task. If the temporal

685 comparison between call and reverberation is used in evaluating room size, as it appears to be,

686 then this may be a possible neural mechanism that would explain both our behavioral and

687 neuroimaging results.

688 In addition to the motor system, active echolocation recruited cortical and subcortical auditory

689 processing regions, as well as visual and parietal areas not typically known for auditory

690 processing. As in the visual cortex, the auditory cortex is thought to comprise two processing

691 streams, the dorsal or "where" stream, and the ventral or "what" stream (Rauschecker and

692 Tian, 2000). Sound localization and spatial hearing recruit early auditory areas posterior and

693 lateral to the primary auditory cortex, extending into the parietal cortex both in humans and

694 non-human primates (Rauschecker and Tian, 2000; Alain et al., 2001; van der Zwaag et al.,

695 2011) Recently the function of the dorsal auditory stream was reconceptualized to involve

696 sensory-motor control and integration in speech (Rauschecker, 2011; Chevillet et al., 2013).

697 While our experimental paradigm involved spatial auditory processing (classically the

698 'where' stream), the vocal-motor requirements of human echolocation also challenge sensory-

28

699 motor integration making it conceivable with a non-spatial task to further delineate auditory

700 processing streams.

701 Auditory midbrain (IC) and thalamus (MGN) activity was modulated by the behavioral output

702 variable on a trial-by-trial basis. Both the IC and MGN are part of the ascending auditory

703 system, but cortico-collicular feedback was shown to play a crucial role in auditory spatial

704 learning and plasticity (Bajo et al., 2010). Based on our results, cortico-collicular feedback

705 may also contribute to sonar processing.

706 Both the sighted subjects and the blind echolocation expert had visual and parietal activity

707 during echolocation. For the sighted subjects, activity in the precuneus, in the medial parietal

708 cortex, may be a result of visual imagery (Cavanna and Trimble, 2006). Sighted persons

709 typically visualize non-visual tasks and visual imagery is positively correlated with

710 echolocation performance (Thaler et al., 2014a). Alternatively, the parietal activity may

711 reflect a modality independent representation of space. Auditory localization activated the

712 medial parietal areas including the precuneus in both sighted and blind subjects (Weeks et al.,

713 2000), and is active during imagined passive locomotion without visual memory (Wutte et al.,

714 2012). Parietal areas were active in when both blind and sighted subjects used passive

715 echolocation for path finding (Fiehler et al., 2015). Route navigation using a tactile sensory

716 substitution device activates the precuneus in congenitally blind subjects and in visual route

717 navigation in sighted subjects (Kupers et al., 2010). This evidence speaks for multimodal

718 spatial processing for action in the parietal cortex in humans.

719

Figure captions

720

721 **Figure 1**. Binaural room impulse response (BRIR) of a real enclosed space. (**Top**) A

722 photograph of the acoustically excited room (old St. Stephanus, Gräfelfing, Germany) with

723 the head-and-torso simulator. (**Row 2**) Spectrograms of the left and right BRIRs are shown.

724 Sound pressure level is color coded between -60 and 0 dB. (**Row 3**) Changes of the size of a

725 virtual room with an equivalent reverberation time after it is compressed with factors of 0.7,

726 0.5, and 0.2, respectively. (**Bottom**) Spectrograms of the left-ear room impulse response

727 corresponding to the three compression factors are shown. The color scale is identical to the

728 second row.

729

730 **Figure 2**. Just noticeable differences (JND) in room size. (**Top**) The average JNDs illustrated

731 in terms of the changes in the size of a cubic room with equivalent reverbration time (Sabine,

732 1923). (**Bottom**) Individual JNDs are plotted for each subject and each room size and the

733 mean on the far right. The individual data reveal that subjects performed quite differently with

734 some subjects having JNDs as low as 3-4% and others having JNDs between 20 and 35 %.

735 The across-subjec mean is shown as the right.

736

737 **Figure 3**. Examples of the subjects' vocalizations produced to solve the echo-acoustic task.

738 (**Top**) Exemplary spectrograms (**Row 1**) and oscillograms (**Row 2**) are shown for three

739 typical participants. (**Bottom**) A detailed correlation analysis between the individual

740 psychophysical performances and specific call parameters is shown. The correlation

741 coefficients (Spearman's Rho) are given in the top right of each panel. The analysis shows

742 that overall, JNDs improve with increasing call level and decrease with increasing number of

743 calls per trial.

744

745   **Figure 4**. Active vs. passive echolocation. (**A)** Behavior: subjects' rating of the perceived

746   room size, in both active (blue) and passive (red) echolocation for the four BRIR compression

747   factors (room sizes). Error bars represent standard error across subjects. (**B**) Neuroimaging:

748   differential activations between active and passive echolocation show stronger motor activity

749   during active echolocation, although the motor behavior was subtracted from the activity:

750   (active echolocation minus active null condition) minus (passive echolocation minus silence).

751   Significant voxels (p<0.05 FDR corrected) are shown as a heat map overlaid on the mean

752   structural image from all subjects from the control experiment. Coordinates are given in MNI-

753   space (see Table 1 for details).

754

755   **Figure 5**. Active echolocation only. (**A**) The room-size rating is shown for the four different

756   BRIR compression factors and as a function of BRIR amplitude. Error bars represent standard

757   error across subjects. The data show that while the BRIR compression factor is strongly

758   reflected in the subjects' classifications, the BRIR amplitude has a much smaller effect on the

759   perceived room size. (**B**) Regions of activity during active echolocation (active sound

760   production with auditory feedback) compared to sound production without feedback. The

761   auditory cortex was active bilaterally as well as primary motor areas, cerebellum and the

762   visual pole (see Table 2 for details). Activity maps were thresholded at p<0.05 (FDR

763   corrected) and overlaid on the mean structural image of all subjects in the study. X and Z

764   values refer to MNI coordinates of the current slice.

765

766   **Figure 6**. An example of the parametric modulations in the hemodyamic response with

767   respect to the experimental parameters. The BOLD signal values in a single voxel (MNI-

768   coordinates [x,y,z]= 57,-27,45) in the right supramarginal gyrus of the inferior parietal lobe

769   were averaged over room size rating (**A**), reverberation scaling (**B**) and amplitude (**C**) in an

770   example subject. It is clear here that activity in this voxel was related to both the reverberation

31

771   scaling and room size rating but not the amplitude. All three experimental parameters were

772   used to model activity across the brain (see Fig. 7). Means and standard error of the mean are

773   shown here.

774

775   **Figure 7**. Areas of activity that were significantly linearly modulated by room size rating.

776   Interestingly, both the MGN and the inferior colliculus were modulated by room size rating

777   but not by amplitude. In addition to primary auditory centers, visual cortical areas and vocal-

778   motor areas were also modulated by room size. The parametric vocal-motor activation is

779   especially intriguing because the vocal-motor output does not vary with perceived room size,

780   but still the motor-cortical activation does. Activity maps were thresholded at p<0.05 (FDR

781   corrected) and overlaid on the mean structural image of all subjects in the study. X,Y,Z values

782   represent MNI coordinates of the current slice.

783

784   **Figure 8**. Blind echolocation expert. (**A**) Psychophysical performance as in Figure 5A. Bars

785   show the mean room-size classification as a function of BRIR compression factor (grey scale

786   of the bars) and BRIR amplitude (bar groups). Error bars represent standard errors across trial

787   repetitions. Without any prior training, the classification is very stable and similar to that of

788   the extensively trained, sighted subjects. (**B**) Regions of activity in an echolocation expert

789   during active echolocation compared to sound production without auditory feedback. The

790   strongest regions of activations in the fMRI data were found in visual and parietal areas (cf.

791   Table 4). Activity maps were thresholded at p<0.05 (FDR corrected) and overlaid on the

792   subject's normalized structural image.

793

32

794 **Tables**

795 **Table 1**. Spatial coordinates of the local hemodynamic activity maxima for active

796 echolocation – the active null, without auditory feedback, vs passive echolocation compared

797 to the baseline null condition. In other words, both auditory stimuli and motor output were

798 subtracted out of the brain activity, but activity in the motor cortices and cerebellum remains.

799 MNI-coordinates (p < 0.05 FDR-corrected, minimum spatial extent threshold of 5 voxels) are

800 shown as well as the z-score and spatial extent in voxels (see also Fig. 4B). * Significant after

801 clusterwise FWE-correction (p < 0.05)

Region	[x,y,z] in mm	Z-score	Extent
Cerebellum vermis V*	[16, -64, -20]	7.14	4634
	[-20, -64, -20]	6.69	
Postcentral gyrus, somatosensory cortex*	[-56, -12, 26]	6.83	4769
Precentral gyrus*	[60, 2, 28]	6.44	4159
Precuneus	[-4, -40, -50]	4.74	172
Thalamus	[16, -18, -2]	3.40	52
	[-2, -4, -4]	3.26	27
Middle frontal gyrus	[34, 0, 62]	3.38	27
Anterior insular cortex	[36, 18, 0]	3.40	65
Frontal pole	[42, 42, 10]	3.19	95
Caudate nucleus	[-18, 28, 6]	3.15	138
	[10, 16, -2]	2.80	6

802

803 **Table 2**. Spatial coordinates of the local hemodynamic activity maxima during echolocation

804 versus null (click production without auditory feedback). All coordinates are from the group

805 analysis (p < 0.05 FDR-corrected, spatial extent threshold of 5 voxels) given in MNI-space, as

806 well as the z-score and the cluster extent size (see also Fig. 5). Coordinates without extent

807 values are subclusters belonging to the next closest cluster. • Significant after clusterwise

808 FWE-correction (p<0.05), ζ Belongs to cluster [54, -6, -3]

Region	[x,y,z] in mm	Z-score	Extent
Subcortical			
Thalamus, premotor	[-15, -18, 9]	3.06	5
Cortical auditory			
Temporal pole*	[54, -6, -3]	4.67	1126
Heschl's gyrus (H1, H2)	[48, -24, 9]	4.09	
Superior temporal lobe	[-39, -27,0]	3.45	181
Heschl's gyrus (H1,H2)	[-51, -12, 3]	3.24	
Planum temporale	[-60, -21, 6]	3.29	
Cortical sensorimotor, frontal			
Precentral gyrus*	[-48, -3, 18]	4.48	970
Precentral gyrus, BA6	[-63, 0, 18]	4.29	
Middle cingulate cortex	[-9, -3, 30]	4.34	
Juxtapositional cortex, BA6	[-3, -6, 51]	3.08	11
Precentral gyrus ζ	[54, 3, 21]	4.26	
Cortical visual			
Occipital Pole	[3, -93, 24]	3.11	8
Cerebellum			
Right I-V	[3, -51, -6]	3.98	18
Right VI, Crus I	[24, -66, -21]	3.60	18
Vermis VI	[3, -66, -21]	3.57	38

809

810 **Table 3**. Spatial coordinates of the local hemodynamic activity maxima for the linear

811 correlation with subjective room size rating. All coordinates are from the group analysis

812 (p < 0.05 FDR-corrected, spatial extent threshold of 5 voxels) given in MNI-space, as well as

813 the z-score and the cluster extent size (see also Fig. 8). Coordinates without extent values are

814 subclusters belonging to the next closest cluster. * Significant after clusterwise FWE-

815 correction (p<0.05)

Region	[x,y,z] in mm	Z-score	Extent
Subcortical			
Medial geniculate body*	[-15, -27, -6]	5.37	1634
Inferior colliculus	[0, -42, -9]	3.95	
Thalamus:			
- premotor, prefrontal	[-12, -15, -3]	3.46	
- acoustic radiation	[15, -24, -3]	4.77	
- acoustic radiation	[-12, -33, 6]	3.57	
- corticospinal tract	[-15, -24, 12]	3.51	
Pallidum	[-18, -3, 0]	3.79	
Putamen	[-33, -18, -6]	3.22	
Cortical auditory			
Heschl's gyrus (H1,H2)	[48, -21, 6]	4.83	
Planum temporale	[57, -15, 6]	4.62	
Superior temporal lobe*	[-57, -24, 3]	4.53	267
Planum polare	[-51, -3, 0]	3.77	
Cortical sensorimotor, frontal			
Primary somatosensory cortex, BA3a	[42, -6, 30]	3.58	
Superior frontal gyrus, BA6	[-27, -6, 60]	3.82	
Superior frontal gyrus, BA6	[-9, 6, 69]	3.49	
Middle frontal gyrus	[-51, 9, 48]	3.48	
Premotor cortex, BA6*	[9, 0, 54]	3.97	188
Precentral gyrus, BA6*	[51, -3, 48]	4.97	136
Precentral gyrus BA4a*	[-42, -12, 51]	4.32	268
Anterior insular cortex	[-36, 12, -12]	3.84	
Cortical visual, parietal			
Calcarine sulcus	[21, -57, 21]	3.37	9
Precuneus	[-15, -63, 51]	3.74	48
	[15, -60, 42]	4.06	46
Posterior cingulate gyrus	[-3, -33, 45]	3.46	27
	[-9, -27, 39]	3.21	

816 **Table 4**. Spatial coordinates of the local hemodynamic activity maxima during echolocation

817 verses null (click production without auditory feedback) in an echolocation expert. MNI-

818 coordinaces (p < 0.05 FDR-corrected, spatial extent threshold of 5 voxels), together with the

819 z-score, and the cluster extent are shown (see also Fig. 9B). * Significant after clusterwise

820 FWE-correction (p < 0.05)

Region	[x,y,z] in mm	Z-score	Extent
Inferior parietal cortex, supramarginal gyrus*	[48, -44, 42]	5.07	1027
Temporal-parietal-occipital junction*	[-52, -46, 8]	4.69	2162
Fusiform gyrus	[32, -60, -12]	4.30	424
Calcarine cortex, cuneus, posterior cingulum, V1*	[16, -54, 18]	4.21	1722
Cerebellum crus 1	[-38, -58, -34]	4.06	244
Precuneus and posterior cingulum	[8, -40, 42]	3.49	128
Inferior temporal gyrus, bordering occipital cortex	[50, -54, -8]	3.27	49
Paracentral lobule	[-14, -26, 72]	3.42	53
Occipital pole	22, -90, 32	3.22	23
Cerebellum, Crus II	[-16, -72, -36]	3.03	14
Precentral gyrus	[-56, -10, 40]	3.03	18
Cuneus, V2	[8, -88, 24]	2.99	7

821

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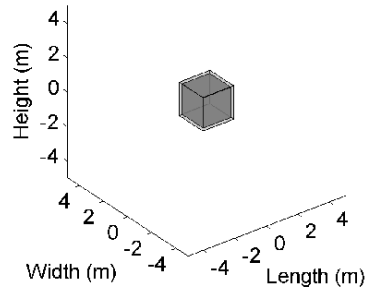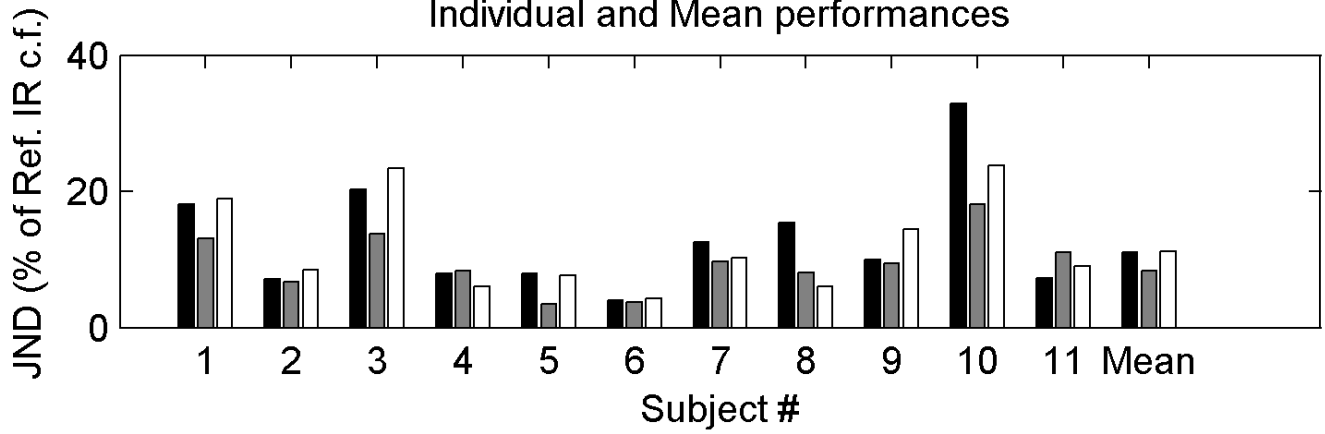953   room acoustics. J Acoust Soc Am 126:776-791.
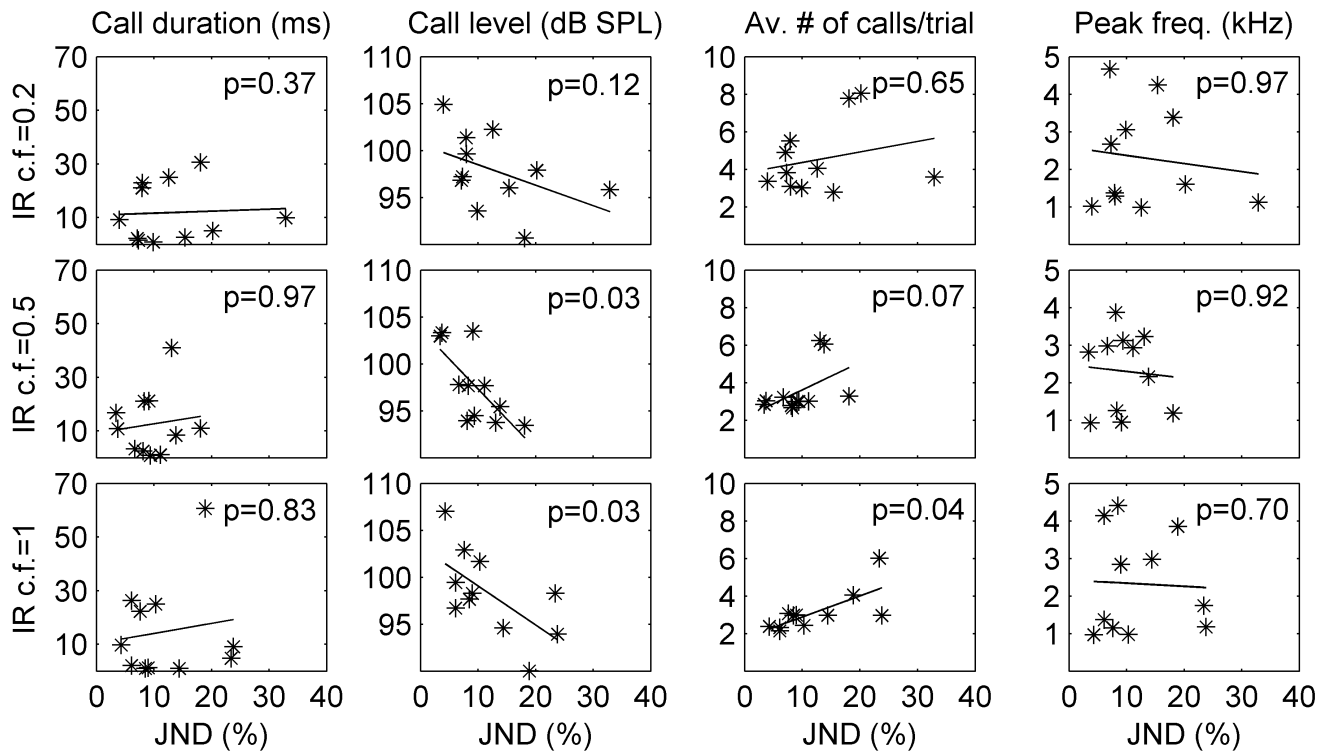
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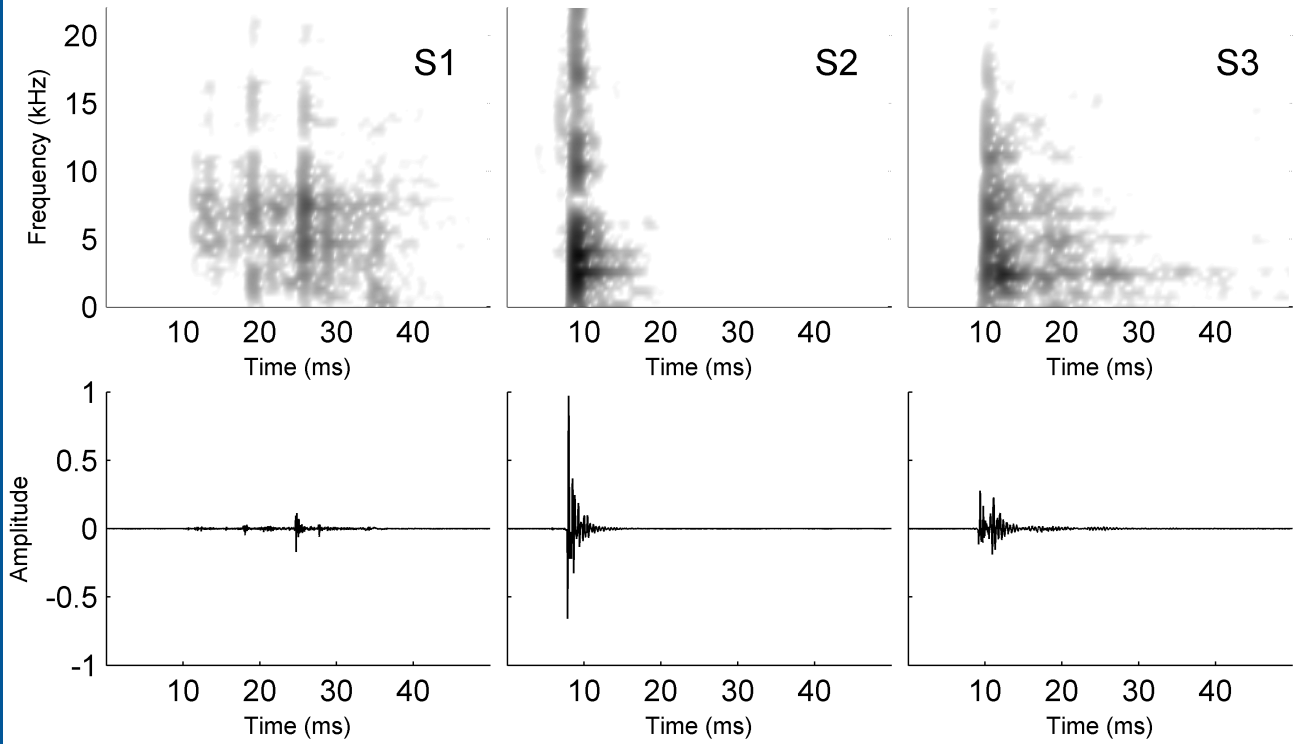
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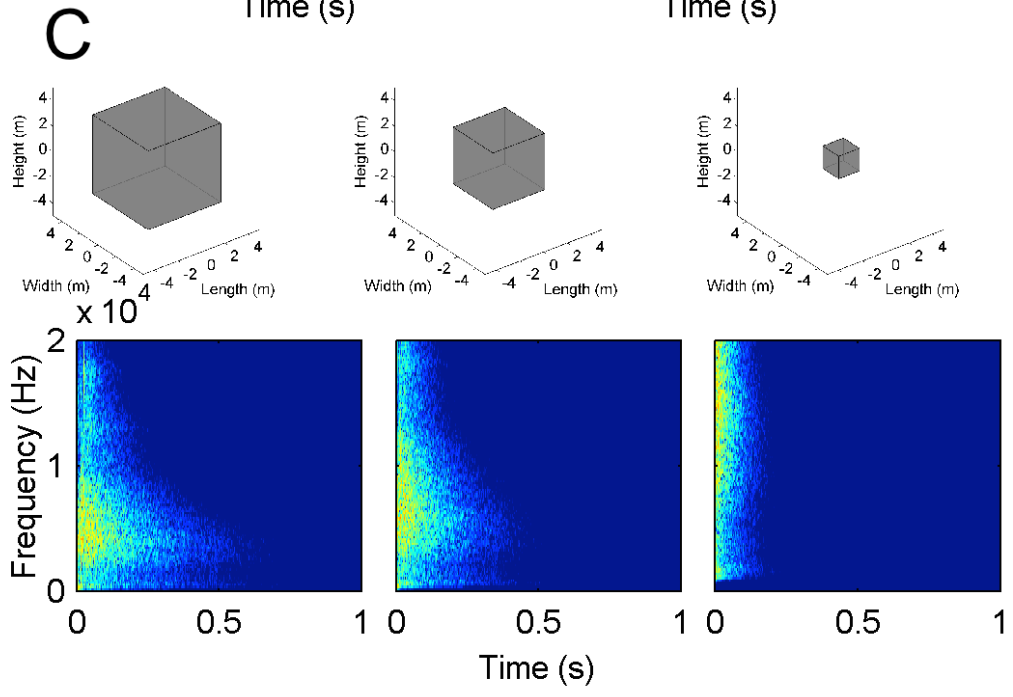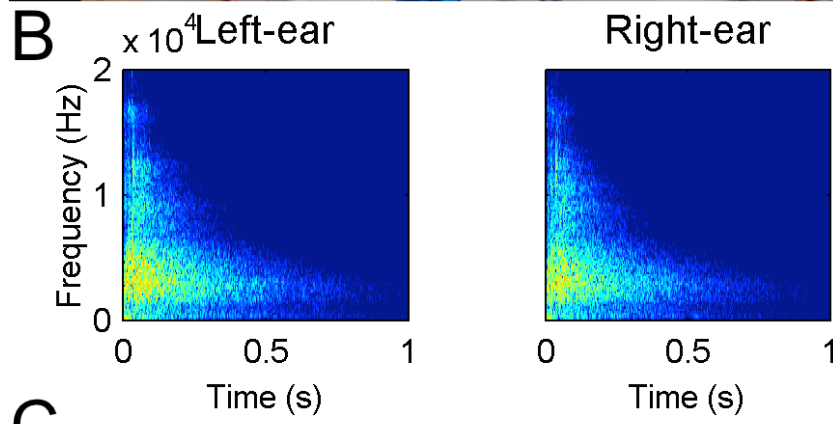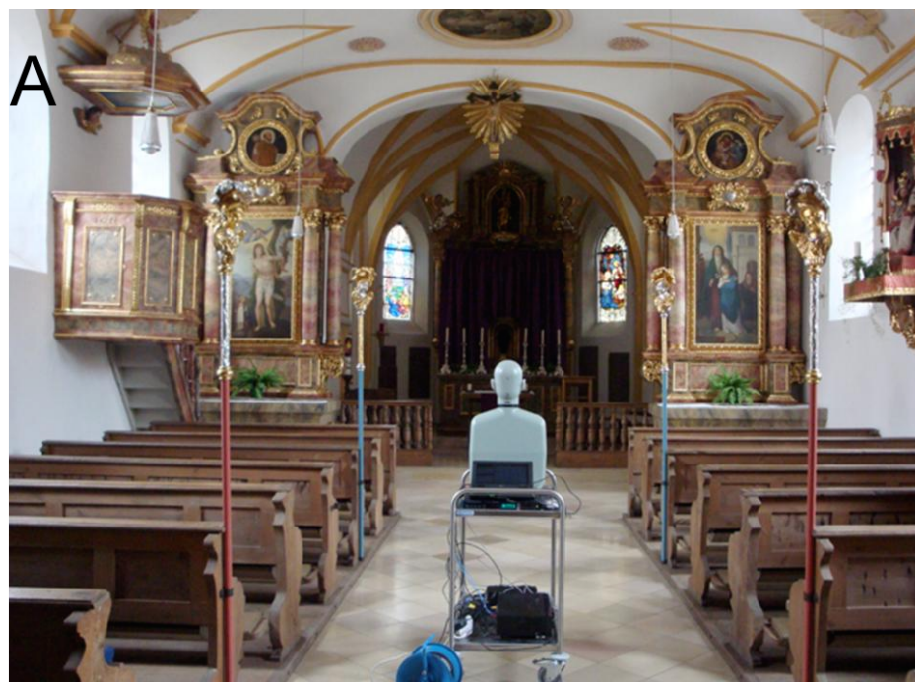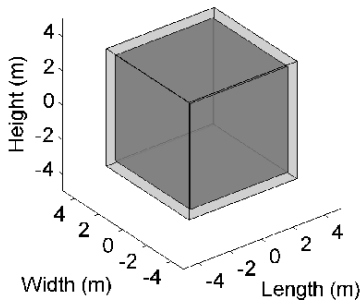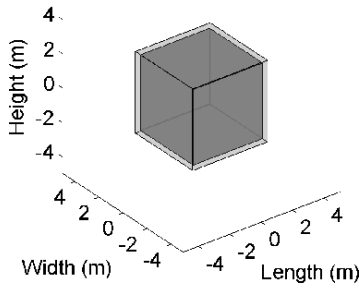
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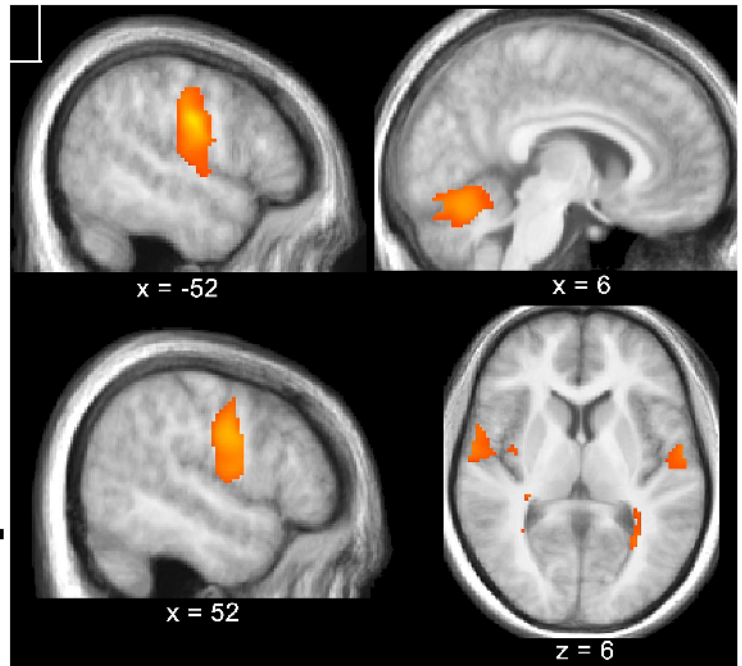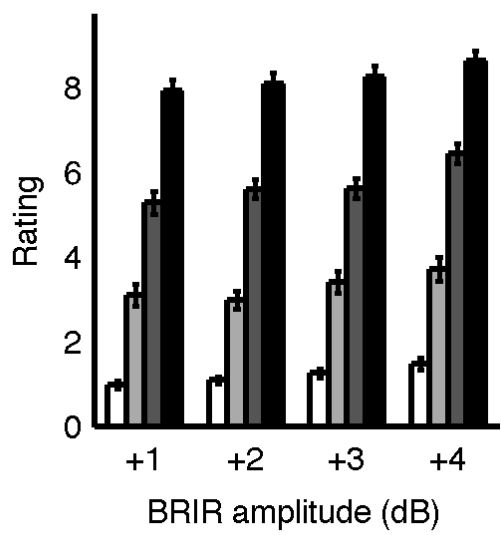
A Active vs. Passive Echolocation

Room size ratings

B

A Active echolocation only

Rating

BRIR amplitude (dB)

BRIR c.f.
0.2
0.5
0.7
1.0

B

x = -52   x = 6   z = 6

x = 52

Parametric fMRI signal change in a single voxel

MGN

IC

L   R

Echolocation expert

A

B

BRIR c.f.
0.2
0.5
0.7
1.0

x = -52   x = 6   z = 6

x = 52