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2 **Using background noise to improve sound localization following simulated hearing loss.**

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25 **Abstract**

26 Many listening abilities become more difficult in noisy environments, particularly following
27 hearing loss. Sound localization can be disrupted even if target sounds are clearly audible and
28 distinct from background noise. Since subjects locate sounds by comparing the input to the
29 two ears, sound localization is also considerably impaired by unilateral hearing loss.
30 Currently, however, it is unclear whether the effects of unilateral hearing loss are worsened
31 by background noise. To address this, we measured sound localization abilities in the
32 presence or absence of broadband background noise. Adult human subjects of either sex were
33 tested with normal hearing or with a simulated hearing loss in one ear (earplug). To isolate
34 the role of binaural processing, we tested subjects with narrowband target sounds.
35 Surprisingly, we found that continuous background noise improved narrowband sound
36 localization following simulated unilateral hearing loss. By contrast, we found the opposite
37 effect under normal hearing conditions, with background noise producing illusory shifts in
38 sound localization. Previous attempts to model these shifts are inconsistent with behavioural
39 and neurophysiological data. However, here we found that a simple hemispheric model of
40 sound localization provides an explanation for our results, and provides key hypotheses for
41 future neurophysiological studies. Overall, our results suggest that continuous background
42 noise may be used to improve sound localization under the right circumstances. This has
43 important implications for real-world hearing, both in normal-hearing subjects and the
44 hearing-impaired.

45

46 **Significance Statement**

47 In noisy environments, many listening abilities become more difficult, even if target sounds
48 are clearly audible. For example, background noise can produce illusory shifts in the
49 perceived direction of target sounds. Because sound localization relies on the two ears
50 working together, it is also distorted by a hearing loss in one ear. We might therefore expect
51 background noise to worsen the effects of unilateral hearing loss. Surprisingly, we found the
52 opposite, with background noise improving sound localization when we simulated a hearing
53 loss in one ear. A simple hemispheric model of sound localization also helped explain the
54 negative effects of background noise under normal hearing conditions. Overall, our results
55 highlight the potential for using background noise to improve sound localization.

56

57 **Introduction**

58 In everyday environments, a key challenge for the brain is to locate sounds of interest in the
59 presence of background noise. Background noise can disrupt sound localization by reducing
60 the audibility of target sounds (Good and Gilkey, 1996; Abouchacra et al., 1998; Lorenzi et
61 al., 1999a, b; Brungart et al., 2005; Kopco et al., 2010; Kerber and Seeber, 2012; Lingner et
62 al., 2012; Wood and Bizley, 2015). However, sound localization can be affected even if
63 targets are clearly audible and distinguishable from concurrent sounds. In such
64 circumstances, the perceived location of a target sound is typically pushed away from the
65 location of a concurrent sound (Suzuki et al., 1993; Canevet and Meunier, 1996; Getzmann,
66 2002; Best et al., 2005; Lee et al., 2009; Reed and van de Par, 2015). Previous attempts to
67 explain this have relied upon a neural map of space that contains an array of neurons (or
68 ‘spatial channels’) tuned to different spatial locations (Suzuki et al., 1993; Best et al., 2005).
69 However, these models predicted greater pushing effects between sounds that are closer
70 together, which is inconsistent with previous behavioral data (Best et al., 2005). They are also
71 inconsistent with neurophysiological studies in mammals, which have shown that neurons in
72 each hemisphere are broadly tuned to a single side of space (Brugge et al., 1998; Furukawa
73 and Middlebrooks, 2001; McAlpine et al., 2001; Grothe et al., 2010; Mokri et al., 2015).

74 Sound localization is additionally impaired by hearing loss, with the nature of
75 impairment depending on the type of hearing loss experienced (Lorenzi et al., 1999a; Best et
76 al., 2011; Dobreva et al., 2011; Akeroyd, 2014; Brungart et al., 2014). Under normal hearing
77 conditions, sound localization relies on the relative timing and level of input to the two ears
78 (Interaural Time Differences: ITDs; Interaural Level Differences: ILDs)(Middlebrooks and
79 Green, 1991). Binaural sound localization is therefore particularly vulnerable following
80 unilateral hearing loss, which alters and degrades these binaural spatial cues (Slattery and
81 Middlebrooks, 1994; Hawley et al., 1999; Van Wanrooij and Van Opstal, 2004; Rothpletz et
82 al., 2012; Agterberg et al., 2014; Firszt et al., 2017; Nelson et al., 2018). Key insights into
83 this problem have been obtained by using earplugs to simulate a hearing loss in one ear
84 (Slattery and Middlebrooks, 1994; Van Wanrooij and Van Opstal, 2007; Kumpik et al., 2010;
85 Irving and Moore, 2011; Strelnikov et al., 2011; Keating and King, 2013; Keating et al.,
86 2016; Asp et al., 2018). These studies have shown that sound localization is initially
87 disrupted but improves as individuals adapt. Adaptation can be achieved by learning to locate

88 sounds using the input provided to the unoccluded ear (Kumpik et al., 2010; Keating et al.,
89 2013; Keating et al., 2016). This is possible because the head and ears filter sounds (i.e.
90 change their spectrum) in a direction-dependent way (Carlile et al., 2005). However, when
91 the energy of a sound is concentrated in a narrow range of frequencies, these monaural
92 spectral cues are unavailable. In such circumstances, subjects can adapt by instead learning to
93 reinterpret the altered binaural cues (Gold and Knudsen, 2000; Keating et al., 2015; Keating
94 et al., 2016). Nevertheless, when adult humans wear an earplug for prolonged periods of
95 everyday life, they find it difficult to do so (Kumpik et al., 2010).

96 Although background noise is a common feature of everyday life, previous studies of
97 unilateral hearing loss have tested sound localization in quiet environments. For many
98 auditory abilities, individuals with hearing loss typically experience greater difficulty in the
99 presence of background noise (Moore, 1996; Bronkhorst, 2000; Lorenzi et al., 2006; Helfer
100 and Freyman, 2008; Akeroyd, 2014). Consequently, we might expect individuals with
101 simulated unilateral hearing loss to be particularly vulnerable to the effects of background
102 noise. Surprisingly, however, we found the opposite. Following simulated unilateral hearing
103 loss, background noise improved narrowband sound localization. A simple
104 neurophysiological model also provided insight into how background noise might affect
105 behavior.

106

107 **Materials and Methods**

108 **Subjects**

109 10 subjects (2 males and 8 females), aged 21-35, participated in the study. All participants
110 provided informed consent and were reimbursed for their time. Participants underwent
111 audiometry to confirm normal hearing prior to testing. Only one participant had prior
112 experience of a sound localization task. All procedures were approved by the University
113 College London Research Ethics Committee.

114 **Apparatus**

115 Sound localization was tested in a double-walled anechoic chamber. Stimuli were presented
116 from a semi-circular array of nine loudspeakers (Canton Plus XS.2; Computers Unlimited
117 London), located in the front hemifield, with a radius of 1.2m. Participants were seated on a

118 stool in the center of the speaker array, facing a central speaker at 0° azimuth. The height of
119 the stool was adjusted to ensure the participant's head was level with the speaker array; a chin
120 rest was used to minimize head movements.

121 Stimuli were generated using the Psychophysics Toolbox (Brainard, 1997) for
122 Matlab(The Mathworks, Natick, MA), sent to a MOTU 24io sound interface (MOTU,
123 Cambridge, MA), amplified (MA1250; Knoll Systems, Point Roberts, WA) and presented via
124 the appropriate loudspeaker. On each trial, a target sound was presented from a single
125 loudspeaker. Participants indicated the perceived location of this target by clicking on a
126 graphical user interface (GUI; generated in Matlab), which was presented on a screen located
127 just below the central speaker. The GUI contained an illustration of the speaker array, which
128 allowed participants to click on different response locations.

129 Procedure

130 *Familiarization*

131 Before testing began, participants were given the opportunity to familiarize themselves with
132 the sound localization task under normal hearing conditions. Throughout this familiarization
133 process, the background of the graphical user interface changed color to indicate whether a
134 behavioral response was correct (green) or incorrect (red). Following incorrect trials, the
135 same target stimulus was presented again and participants were given a second opportunity to
136 respond (referred to as 'correction trials'). Following consecutive incorrect responses, the
137 target stimulus was presented continuously for > 2s before participants were asked to respond
138 (referred to as 'easy trials').

139 *Testing*

140 Each participant was tested in the presence or absence of background noise, with either
141 normal hearing or a simulated hearing loss in one ear (see below), for a total of 4 unique test
142 conditions (i.e. normal hearing in quiet; normal hearing in background noise; earplug in
143 quiet; earplug in background noise). Within each session, participants were tested for 15 mins
144 on each of these conditions (~400 trials), with the testing order randomized across
145 participants. Participants completed two such sessions on different days, each of which lasted
146 approximately 1hr, and were given short breaks between conditions. During these test
147 sessions, participants were not given any feedback on their performance; correction trials and
148 easy trials (see above) were also turned off.

149 *Stimuli*

150 Target sounds consisted of broadband noise (0.5-20kHz) or pure tones (1, 2, 4 or 8 kHz),
151 which were identical to those used in previous work (Keating et al., 2016). Broadband and
152 narrowband sounds were presented with equal probability. Broadband targets had either a flat
153 or random spectrum, with random spectra produced by adding a random vector to the
154 logarithmic representation of the source spectrum on each trial. This random vector was
155 smoothed to remove spectral transitions > 3 cycles/octave and had an RMS of 10 dB (Keating
156 et al., 2016). All target sounds were 100ms in duration (including 10ms cosine ramps),
157 generated with a sampling frequency of 48 kHz, and presented at 56-77 dB SPL in
158 increments of 7 dB. The intensity, type and location of target stimuli were randomly
159 interleaved across trials. Background noise consisted of broadband noise (0.5-20kHz) with a
160 flat spectrum presented continuously at the midline at 56 dB SPL. By setting the background
161 noise to this level, we were able to vary target intensity (corresponding to different signal-to-
162 noise ratios: SNRs) across a relatively wide range (21 dB), whilst ensuring that all targets
163 were clearly audible (SNRs ≥ 0). Previous studies of unilateral hearing loss have shown that,
164 if target intensity is not varied, subjects can locate sounds using the sound level in the better
165 ear (Van Wanrooij and Van Opstal, 2004).

166 *Simulated unilateral hearing loss*

167 To simulate a hearing loss in one ear, participants wore a foam earplug (EAR classic) in one
168 ear (Keating et al., 2016). Each participant wore the earplug in the same ear across sessions,
169 but different participants wore the earplug in either the left (n=5) or right (n=5) ear. For each
170 subject, conventional audiometry was performed in the absence and presence of the earplug.
171 This allowed us to assess the attenuating effects of the earplug, which were very similar to
172 those observed in previous studies (Kumpik et al., 2010; Keating et al., 2016).

173 *Statistical Analyses*

174 To provide an overall measure of performance, we calculated the average magnitude of errors
175 made by each participant across trials. These values were calculated separately for different
176 hearing conditions (normal or earplug), background noise conditions (quiet or background
177 noise), sound levels and stimulus types (broadband or narrowband). The statistical
178 significance of these fixed effects was then assessed using mixed-effects ANOVAs, with

179 subject as a random effect, followed by appropriate post-hoc tests corrected for multiple
180 comparisons.

181 To facilitate comparison with previous work (Kumpik et al., 2010; Keating et al.,
182 2016), and to help understand the reasons for subjects' errors, we also performed linear
183 regression to calculate subjects' bias values as well as the slope of the relationship between
184 stimulus and response. Perfect performance on our task produces a bias of 0 and a slope of 1,
185 with deviations from these values reflecting errors in sound localization. Following previous
186 work (Kumpik et al., 2010), we restricted this analysis to stimulus locations $\leq 30^\circ$ from the
187 midline. As above, these measures were calculated separately for different hearing
188 conditions, background noise conditions, sound levels and stimulus types; significance was
189 then assessed using mixed-effects ANOVAs and post-hoc tests corrected for multiple
190 comparisons.

191 To test the predictions of the hemispheric model (see below), we calculated the mean
192 response for each stimulus location in quiet and assessed how it changes in the presence of
193 background noise. Since this requires separate measures for each stimulus location, data were
194 pooled across sound level. For normal hearing conditions, we found that our data were
195 symmetric around the midline (i.e. data for the left and right sides of space were opposite in
196 sign but were otherwise very similar). To test this symmetry directly, our statistical model
197 therefore included hemifield (left or right side of space), eccentricity (distance from the
198 midline), and stimulus type (narrowband or broadband) as factors; our dependent variable
199 was the extent to which sounds are pushed away from the midline. The significance of these
200 fixed effects was then assessed using mixed-effects ANOVAs with subject as a random
201 factor, followed by post-hoc tests corrected for multiple comparisons. Data for normal
202 hearing and plugged conditions were analysed separately. All statistical analyses were
203 conducted in Matlab.

204 Hemispheric Model

205 We implemented a simple and popular model of sound localization (McAlpine et al., 2001;
206 Keating et al., 2015) and applied it to previously published neurophysiological data
207 (Furukawa and Middlebrooks, 2001). Full details of how these neurophysiological data were
208 collected have been described previously by the authors. Briefly, neuronal responses were
209 recorded in anaesthetized cat A2 (right hemisphere). Target sounds were presented at
210 different locations (-160 to 160 in increments of 40) either in the presence or absence of

211 continuous background noise presented at 35 dB SPL. Target intensity was varied by up to 40
212 dB. Although the location of the background noise varied (-80° to 80° in increments of 40°),
213 it was always presented from a single location at any given time. Targets and background
214 noise were both broadband with flat spectra (0.5-30kHz).

215 The authors report the percentage of active neurons for various spatial configurations
216 of target and masker (Furukawa and Middlebrooks, 2001)(Fig. 3), which provides a measure
217 of the population response. We therefore fit Gaussians to these data to generate population
218 tuning curves for different background noise conditions (quiet, or background noise presented
219 at 0° , 40° and 80° away from the midline), and assume symmetric responses for the left
220 hemisphere. We then used these population tuning curves to simulate behavioral data for
221 different background noise conditions. On each simulated trial, we generated left- and right-
222 hemisphere responses for a sound presented at a specific location. This was done by
223 identifying the appropriate neural responses from the population tuning curves, and adding a
224 random term, drawn from a Gaussian distribution, to simulate neural noise. The variance of
225 this Gaussian distribution was chosen so that the overall performance of the model (mean
226 error magnitude) matched that of human participants (either for broadband or narrowband
227 stimuli, although this produced no appreciable difference in the predicted pushing effects). To
228 simulate different background noise conditions, neural responses were generated using the
229 population tuning curves appropriate to each condition.

230 On each simulated trial, we calculated the difference in response between the two
231 hemispheres. To decode this hemispheric difference, the model then identified the target
232 location that produced the most similar hemispheric difference under quiet conditions. This
233 was then used to generate the behavioral output of the model. When background noise was
234 absent, this led to accurate performance. However, when background noise was present,
235 neural responses were often decoded incorrectly, which led the model to make systematic
236 errors in sound localization.

237 To better understand the link between changes in population tuning curves and
238 changes in model output, we also ran the model above using population tuning curves that
239 were manipulated in specific ways (i.e. tuning width was sharpened or responses were
240 reduced). In such cases, we started with population tuning curves that were Gaussian fits to
241 real neurophysiological data obtained in the absence of background noise (Furukawa and

242 Middlebrooks, 2001). We then changed the standard deviations of these Gaussians (to
243 sharpen tuning) or multiplied the Gaussians by a scale factor (to reduce responses).

244 Code Accessibility

245 All relevant code is available on request from the corresponding author.

246

247 **Results**

248 **Background noise reduces sound localization errors following simulated unilateral** 249 **hearing loss**

250 We began by measuring the impact of background noise on sound localization under normal
251 hearing conditions, focusing on the role of binaural spatial cues (Interaural Time Differences:
252 ITDs; Interaural Level Differences: ILDs). To do this, we used narrowband target sounds,
253 which prevent subjects from using monaural spectral cues to sound location. Target sounds
254 were presented at various locations in the front hemifield, either in quiet or in the presence of
255 continuous broadband noise located directly in front of the listener (Fig. 1A). This was done
256 to facilitate comparison with previous work (Furukawa and Middlebrooks, 2001). Targets
257 also varied in frequency and intensity (corresponding to different signal-to-noise ratios
258 (SNRs) in the background noise condition; all SNRs ≥ 0), but the effects of background noise
259 were very similar in each case and so are plotted together (no significant interactions between
260 frequency/intensity and noise condition, mixed-effects ANOVA, $p > 0.05$).

261 With normal hearing, subjects performed this task well in a quiet environment,
262 making relatively small errors (Fig. 1B,C). Performance was worse, however, in the presence
263 of background noise, with subjects making larger errors ($p < 0.05$, post-hoc test; Fig. 1B,D).
264 We then asked whether individuals are more vulnerable to background noise if they
265 experience a hearing loss in one ear. To do this, we simulated a partial unilateral hearing loss
266 by requiring the same subjects to wear an earplug in one ear. This delays and attenuates the
267 input to the plugged ear (Kumpik et al., 2010; Keating et al., 2016), which alters the two
268 primary sound localization cues (ITDs and ILDs). When subjects wore an earplug, sound
269 localization was considerably impaired relative to normal hearing conditions, irrespective of
270 whether the background noise was off ($p < 0.05$, post-hoc test; Fig. 1B,E) or on ($p < 0.05$, post-
271 hoc test; Fig. 1B,F).

272 However, when subjects wore an earplug, the effect of background noise was opposite
273 to that observed with normal hearing (significant interaction between background noise and
274 hearing loss conditions; mixed effects ANOVA, $F_{(1,576)} = 45.1$, $P < 0.001$; Fig. 1B).
275 Surprisingly, we found that background noise improved sound localization when subjects
276 wore an earplug ($p < 0.05$, post-hoc test; Fig. 1B). This result was not limited to a specific
277 target frequency, with similar results observed if we conducted separate analyses for low-
278 frequency targets (< 1.5 kHz; where ITDs are the primary cue to sound location) or high-
279 frequency targets (> 1.5 kHz; where ILDs are the primary cue to sound location). In each
280 case, background noise improved sound localization following simulated unilateral hearing
281 loss (post-hoc tests, $p < 0.05$; significant interactions between background noise and hearing
282 loss conditions; mixed effects ANOVAs, Low Frequency Targets: $F_{(1,144)} = 5.8$, $P = 0.018$;
283 High Frequency Targets: $F_{(1,464)} = 42.5$, $P < 0.001$).

284 **Background noise improves performance by reducing bias and increasing perceptual** 285 **discriminability**

286 Previous studies have shown that an earplug impairs sound localization because sounds are
287 mislocalized toward the side of the open ear (i.e. subjects are biased) (Kumpik et al., 2010;
288 Keating et al., 2016). This occurs because the earplug changes ITDs and ILDs in ways that
289 favor the side of the open ear. Localization is also impaired because subjects are less able to
290 discriminate between sounds presented at different locations, which flattens the relationship
291 between stimulus and response (slope of the stimulus-response relationship becomes closer to
292 0) (Kumpik et al., 2010; Keating et al., 2016). To better understand our results in light of
293 previous work, we therefore used linear regression to estimate bias and slope values for
294 different conditions. To facilitate comparison with previous work (Kumpik et al., 2010), we
295 restricted this analysis to stimulus locations $< 45^\circ$ from the midline (Fig. 1C-F, red lines; see
296 Methods).

297 Under normal hearing conditions, subjects showed very little bias, with similar bias
298 values observed in the presence and absence of background noise ($p > 0.05$, post-hoc test,
299 Fig. 1C,D,G). Although an earplug produced a large bias toward the side of the open ear (bias
300 values > 0 ; $p < 0.05$, post-hoc tests; Fig. 1E,G), the magnitude of this bias was reduced in the
301 presence of background noise ($p < 0.05$, post-hoc test; significant interaction between
302 background noise and hearing loss conditions; mixed effects ANOVA, $F_{(1,576)} = 18.5$, $P <$
303 0.001 ; Fig. 1F,G). In other words, background noise reduced subjects' tendency to

304 mislocalize sounds toward the side of the open ear following simulated unilateral hearing
305 loss.

306 If subjects were to perform our task perfectly, the slope of the relationship between
307 stimulus and response would be equal to 1, with deviations above or below this value
308 reflecting errors in sound localization. When locating narrowband sounds in a quiet
309 environment, normal hearing subjects showed slope values very close to 1 (Fig. 1C,H).
310 However, in the presence of background noise, slope values increased ($p < 0.05$, post-hoc
311 test; Fig. 1D,H). This occurs because the perceived locations of target sounds are pushed
312 away from the location of the background noise (i.e. the midline). For example, when a target
313 sound is presented at 30° , it tends to be perceived further to the right ($\sim 50^\circ$; Fig. 1D), with
314 symmetric errors observed on the left hand side. This means that background noise increases
315 sound localization errors under normal hearing conditions.

316 Conversely, when subjects wore an earplug, slope values were < 1 when locating
317 sounds in a quiet environment, and were considerably lower than the slope values observed
318 with normal hearing ($p < 0.05$, post-hoc test; Fig. 1C,E,H). This is because subjects are less
319 able to distinguish between sounds presented at different locations. However, in the presence
320 of background noise, slope values increased ($p < 0.05$, post-hoc test; Fig. 1F,H) and became
321 very close to 1. This means that background noise increased slope values similarly for both
322 normal hearing and earplug conditions (no significant interaction between background noise
323 and earplug conditions, mixed effects ANOVA, $F_{(1,576)} = 2.8$, $P = 0.092$; Fig. 1H). However,
324 whilst this increase moved slope values away from 1 under normal hearing conditions (post-
325 hoc test, $p < 0.05$), it moved slope values closer to 1 when subjects were wearing an earplug
326 (post-hoc test, $p < 0.05$). Consequently, background noise improves narrowband sound
327 localization following simulated unilateral hearing loss by both reducing bias and returning
328 slope values closer to their optimal value (i.e. 1). In this way, background noise partly
329 reverses the two main effects of simulated unilateral hearing loss.

330 **Broadband sound localization is more robust to the effects of background noise**

331 Since we presented our background noise directly in front of the listener, a simple
332 explanation for a reduction in bias is that the background noise acts as a reference point that
333 informs subjects where the midline is. When wearing an earplug, subjects could therefore use
334 the perceived location of the background noise to estimate how biased they are and shift their
335 localization responses to compensate (note that this could be a useful strategy in everyday

336 life, not only in our task). However, if this were the case, bias would be shifted by the same
337 amount for all target sounds, including those with broadband spectra. To test this, we
338 therefore investigated the effect of background noise on sound localization using broadband
339 targets.

340 Contrary to this hypothesis, we found that background noise changed bias values (and
341 overall errors) in a stimulus-specific way (i.e. data obtained using broadband targets differed
342 from that obtained using narrowband targets; significant 3-way interactions between
343 background noise, hearing loss and stimulus conditions; mixed-effects ANOVAs; bias
344 values: $F_{(1,928)} = 10.9$, $P = 0.001$; overall errors: $F_{(1,928)} = 23.6$, $P < 0.001$). In particular, when
345 subjects located broadband sounds, background noise had no effect on bias values or overall
346 errors ($p > 0.05$ for both normal-hearing and hearing loss conditions, post-hoc tests; Fig. 2A-
347 F). For broadband targets, the effects of background noise were therefore both less
348 detrimental (normal hearing) and less beneficial (plugged hearing) than those observed for
349 narrowband targets. This means that broadband sound localization is relatively robust to the
350 effects of background noise. It also suggests that our subjects are not simply using the
351 background noise as a reference point and therefore requires an alternative explanation.

352 **Background noise produces pushing effects in the hemispheric model of sound** 353 **localization**

354 We next considered previous work that investigated the spatial tuning of auditory neurons
355 (cat A2) for normal hearing conditions whilst continuous broadband noise was presented
356 directly in front of the listener (Furukawa and Middlebrooks, 2001). One key result from this
357 work is that background noise suppresses neuronal responses in a location-specific way. In
358 particular, when sounds are presented in a quiet background, neurons in cat auditory cortex
359 tend to be broadly tuned to sounds presented on the contralateral side of space. This is
360 reflected in the population response for each hemisphere (Fig. 3A; see Methods). However,
361 when continuous background noise is presented at the midline, the population responses to
362 target sounds become more tightly tuned to spatial location (Fig. 3A). Sharper tuning is a
363 robust effect of continuous background noise, and is also observed for single neurons in both
364 A1 (Brugge et al., 1998; Wood et al., 2018) and A2 (Furukawa and Middlebrooks, 2001). In
365 addition, it has been suggested that these effects may partly reflect corresponding changes in
366 the responses of inferior colliculus (IC) neurons (Mokri et al., 2015).

367 To assess how sharper spatial tuning might influence behavior, we implemented a
368 popular and simple model of sound localization (McAlpine et al., 2001; Grothe et al., 2010;
369 Keating et al., 2015). According to this model (the hemispheric model), sound location is
370 represented by the difference in mean activity between the two hemispheres (hemispheric
371 difference). We therefore calculated hemispheric differences in activity for different
372 background noise conditions (quiet background or continuous background noise presented at
373 the midline; Fig. 3B), using Gaussian fits to previously published neurophysiological data
374 (Fig. 3A; see Methods) (Furukawa and Middlebrooks, 2001).

375 For target sounds presented in the front hemifield background noise exaggerated
376 differences in activity between left and right auditory cortex, particularly for locations $\sim 45^\circ$
377 from the midline (Fig. 3B). For example, when a target sound was presented 15 degrees to
378 the right in the presence of background noise, it produced the same population response (i.e.
379 difference in activity between two hemispheres) as a target sound presented further to the
380 right in the absence of background noise. Symmetric effects were observed for sounds
381 located on the left. In the model, background noise is therefore expected to push target
382 sounds away from the midline (i.e. the location of the background noise) relative to quiet
383 conditions.

384 To illustrate this, we simulated neural responses for quiet and noisy conditions using
385 the hemispheric responses in Fig. 3A. Trial-to-trial variability was simulated by adding a
386 random term to the neural responses on each trial (constrained to match the overall errors
387 observed for our behavioral data). These neural responses were then decoded by the model
388 (see Methods). When we simulated quiet conditions, the model performed well (Fig. 3C).
389 However, when we simulated noisy conditions, the ‘perceived’ (i.e. decoded) locations of
390 target sounds were pushed away from the midline (Fig. 3D). This increased the slope of the
391 relationship between stimulus and response (Fig. 3D, red line), but had no effect on overall
392 bias. This is broadly consistent with what we observed in our behavioral data for narrowband
393 sounds under normal hearing conditions.

394 **Pushing effects depend on spatial separation between target and background noise**

395 In the model, we next tested the effect of background noise for each target location. To do
396 this, we calculated the mean response for each target location and assessed how much it
397 changed in the presence of background noise (Fig. 3E). In the model, pushing effects were
398 symmetric around the midline (i.e. in each hemifield, target sounds were pushed away from

399 the midline). The greatest pushing effect also occurred for intermediate separations between
400 target and background noise (± 30 deg), and declined for greater separations. To test these
401 predictions, we therefore reanalysed our normal-hearing behavioral data to estimate the
402 degree of pushing observed for targets presented at different locations.

403 In our behavioral data, we found that the pushing effect is also symmetric around the
404 midline (no significant main effect or interaction effects of hemifield; mixed-effects
405 ANOVA, $p > 0.05$; Fig. 3F). We additionally found that the pushing effect is greatest for
406 intermediate separations between target and background noise (30 deg for narrowband
407 sounds, 60 deg for broadband sounds), and declines for greater separations. However,
408 narrowband targets showed greater pushing effects than broadband targets, particularly close
409 to the midline (significant differences between narrowband and broadband data at 15° and
410 30° ; post-hoc tests, $p < 0.05$). The pushing effect for narrowband targets was also more
411 sensitive to the separation between target location and background noise (relative to
412 broadband targets; significant interaction between stimulus type and target eccentricity;
413 mixed-effects ANOVA, $F_{(3,152)} = 2.7$, $P = 0.048$).

414 **Sharper spatial tuning produces pushing effects that vary with target location**

415 In the neurophysiological data, background noise reduces the magnitude of neural responses
416 and sharpens their spatial tuning (Fig. 3A) (Furukawa and Middlebrooks, 2001). To isolate
417 the role of each of these factors, we therefore used the hemispheric model to simulate what
418 happens when we vary each of these factors separately. When we reduced the magnitude of
419 the neural responses, but kept the tuning widths constant (Fig. 4A), the hemispheric
420 differences in activity were reduced. In the hemispheric model, the ‘perceived’ locations of
421 target sounds were therefore pulled toward the midline (Fig. 4B), which is opposite to what
422 we observed in our behavioral data (Fig. 3F).

423 However, when we sharpened the spatial tuning of the neural responses, but kept their
424 maxima constant (Fig. 4C), the hemispheric model produced pushing effects (Fig. 4D) that
425 are broadly similar to those observed behaviorally (Fig. 3F). As the tuning width becomes
426 sharper, the model predicts an increase in the magnitude of the pushing effect, particularly for
427 targets located close to the midline. Consequently, the model predicts a relationship between
428 the magnitude of the pushing effect and the target location that exhibits the greatest amount
429 of pushing. Interestingly, this relationship parallels the differences we observed in our
430 behavioral data between narrowband and broadband targets (Fig. 3F). This means that the

431 stimulus differences we observed in our behavioral data are consistent with differences in a
432 single parameter (i.e. degree to which spatial tuning is sharpened by background noise).

433 **Effects of lateralized background noise in the hemispheric model**

434 Previous neurophysiological studies have not investigated the effects of background noise
435 following unilateral hearing loss. However, researchers have shown changes in the spatial
436 tuning of neurons if they are exposed to background noise presented away from the midline
437 (Fig. 5A) (Furukawa and Middlebrooks, 2001). In such circumstances, the background noise
438 produces binaural spatial cues (ITDs and ILDs) that favor one side of space. Under these
439 conditions, the balance of neural activity between the two hemispheres in response to target
440 sounds is altered. For example, when background noise is presented 40° to the right of the
441 midline, a target located in front of the listener produces a hemispheric difference equivalent
442 to that produced by a target on the left in a quiet environment (Fig. 5B). In the model, the
443 ‘perceived’ location of target sounds is therefore pushed away from the side of the
444 background noise. Similar changes in the hemispheric difference are observed if background
445 noise is presented further from the midline (80°; Fig. 5B,C).

446 Interestingly, when background noise is presented on one side of space, the
447 population response in each hemisphere is affected in a different way. For example, in the
448 hemisphere ipsilateral to the background noise, spatial tuning is primarily sharpened by
449 background noise whilst the peak response remains relatively unchanged (Fig. 5A,C).
450 Conversely, in the hemisphere contralateral to the background noise, the peak response is
451 considerably reduced by background noise whilst the tuning curve width remains less
452 affected (Fig. 5A,C). To illustrate the role played by each hemisphere in the hemispheric
453 model, we therefore considered what would happen to the hemispheric difference if
454 background noise affected only a single hemisphere (i.e. we calculated the hemispheric
455 difference using spatial tuning curves obtained in the presence of noise for one hemisphere,
456 and in quiet for the other hemisphere). If we simulate the effects of background noise solely
457 for the hemisphere contralateral to the background noise, the hemispheric difference shifts
458 toward more negative values (blue, Fig. 5D). This is consistent with target sounds being
459 pushed away from the side of the background noise. By contrast, if we simulate the effects of
460 background noise solely for the hemisphere ipsilateral to the background noise, the
461 hemispheric difference shifts toward more positive values (yellow, Fig. 5D). This is
462 consistent with target sounds being pulled toward the side of the background noise. When the

463 hemispheric difference is computed, the effects of lateralized background noise in each
464 hemisphere therefore oppose one another and partly cancel.

465 **Background noise produces greater pushing effects on the side of the earplug**

466 If subjects wear an earplug, background noise presented at the midline produces binaural
467 spatial cues that favour the side of the open ear (Eric Lupo et al., 2011; Keating et al., 2016).
468 Consequently, subjects perceive the background noise on the side of the open ear (all subjects
469 reported this, but it is also evident in their responses to identical stimuli of short duration; Fig.
470 2 E). In light of the modelling results above, we might expect background noise to push target
471 sounds away from the side of the open ear, which is the side on which the background noise
472 is perceived. For narrowband sounds, this is precisely what we found (Fig. 1G). However, we
473 wanted to know whether this pushing effect varies with target location. We therefore
474 reanalysed our behavioral data for subjects wearing an earplug.

475 In particular, we calculated the mean behavioral response for each target location and
476 assessed how much it changed in the presence of background noise (Fig. 5E). Although
477 background noise pushed narrowband targets away from the side of the open ear (change in
478 response < 0), this pushing effect was greater on the side opposite the open ear (significant
479 effect of hemifield, post-hoc test, $p < 0.05$). However, very different effects of background
480 noise were observed for broadband targets (significant interaction between stimulus type and
481 hemifield, mixed-effects ANOVA, $F_{(1,144)} = 41.8$, $p < 0.001$), particularly on the side opposite
482 the open ear (significant effect of stimulus type on that side; post-hoc test, $p < 0.05$; Fig. 5E).
483 This is primarily because background noise had very little effect on broadband localization.

484

485 **Discussion**

486 Many auditory abilities are impaired in the presence of background noise, particularly in
487 individuals who suffer from hearing loss (Moore, 1996; Lorenzi et al., 1999a; Bronkhorst,
488 2000; Lorenzi et al., 2006; Helfer and Freyman, 2008; Akeroyd, 2014). Surprisingly,
489 however, we found that background noise improved narrowband sound localization when
490 subjects experienced a simulated hearing loss in one ear. By contrast, localization of
491 broadband sounds was more robust, and was less affected by either simulated hearing loss or
492 background noise. A simple neurophysiological model also provided insight into how the
493 behavioral effects of background noise might arise.

494 **Background Noise Distorts Sound Localization Under Normal Hearing Conditions**

495 Under normal hearing conditions, sound localization was relatively unaffected by background
496 noise, with errors only increasing for narrowband targets. However, we ensured that target
497 sounds were clearly audible by using signal-to-noise ratios (SNRs) ≥ 0 . Previous work
498 suggests that background sounds impair sound localization by reducing target audibility
499 (Good and Gilkey, 1996; Abouchacra et al., 1998; Lorenzi et al., 1999a, b; Brungart et al.,
500 2005; Kopco et al., 2010; Kerber and Seeber, 2012; Lingner et al., 2012; Wood and Bizley,
501 2015). Greater effects of background noise may therefore occur at more adverse SNRs.
502 Nevertheless, we found that the perceived location of targets was pushed away from the
503 location of the background noise. Although previous studies have observed ‘pulling’ effects
504 between sounds that are grouped together (Lee et al., 2009), our target sounds were clearly
505 distinct from the background noise, which tends to produce ‘pushing’ effects (Suzuki et al.,
506 1993; Canevet and Meunier, 1996; Getzmann, 2002; Best et al., 2005; Reed and van de Par,
507 2015). We also found greater pushing effects for narrowband targets, which indicates that the
508 pushing effect is a feature of binaural spatial processing. Previous studies have shown that the
509 pushing effect increases with spatial separation between target and background noise (Best et
510 al., 2005). However, because we tested a wider range of spatial separations, we found that the
511 pushing effect declines for even greater spatial separations. By using broadband and
512 narrowband targets, we also found that the effect of spatial separation is stimulus-specific.

513 To explain the behavioral effects of background noise, previous models have relied
514 upon a neural map of space with an array of neurons (or ‘spatial channels’) tuned to different
515 locations (Suzuki et al., 1993; Best et al., 2005). In these models, sound location is
516 represented by the neurons (channels) that fire most, and competing sounds repel one another
517 because of competitive interactions between neurons tuned to adjacent locations in space.
518 These models therefore predict greater pushing effects for targets that are closer to the
519 background noise, which is not observed behaviorally (Best et al., 2005). A second difficulty
520 for these models is that neurophysiological studies in mammals are inconsistent with an array
521 of neurons tuned to different spatial locations. Instead, neurons within a single hemisphere
522 tend to be broadly tuned to sounds presented in the contralateral hemifield (Brugge et al.,
523 1998; Furukawa and Middlebrooks, 2001; McAlpine et al., 2001; Grothe et al., 2010; Mokri
524 et al., 2015). This has led to the suggestion that sound location is represented by the
525 difference in activity between the two hemispheres (hemispheric model) (McAlpine et al.,
526 2001; Grothe et al., 2010). When applied to data recorded from cat A2 (Furukawa and

527 Middlebrooks, 2001), the hemispheric model captured key features of our behavioral data.
528 This includes a predicted relationship between the magnitude of the pushing effect and the
529 target location that exhibits the greatest amount of pushing. In the model, these effects occur
530 because background noise sharpens spatial tuning, which has been observed in a number of
531 different studies (Brugge et al., 1998; Furukawa and Middlebrooks, 2001; Mokri et al., 2015;
532 Wood et al., 2018).

533 Nevertheless, the greater robustness of broadband sound localization (relative to
534 narrowband) suggests that the brain may do more than simply average the activity of neurons
535 tuned to different frequencies (Day and Delgutte, 2013; Goodman et al., 2013). If this is the
536 case, then the effects of background noise may be smaller in neurons that integrate
537 information across frequency. One implication of this is that spatial representations may
538 become more robust at higher levels of the auditory system, where frequency tuning tends to
539 be broader. Greater robustness may also be achieved by taking into account differences in the
540 spatial selectivity of individual neurons (Stecker et al., 2005; Keating et al., 2015), or by
541 relying on a sub-population of noise-robust neurons (Mokri et al., 2015). However, our
542 results suggest that the effects of background noise are not entirely eliminated, even when
543 target sounds are clearly audible.

544 **Beneficial Effects of Background Noise Following Simulated Unilateral Hearing Loss**

545 Consistent with previous studies, we found that sound localization was impaired when
546 subjects experienced a hearing loss in one ear (Slattery and Middlebrooks, 1994; Wightman
547 and Kistler, 1997; Hawley et al., 1999; Van Wanrooij and Van Opstal, 2004, 2007; Kumpik
548 et al., 2010; Irving and Moore, 2011; Strelnikov et al., 2011; Rothpletz et al., 2012; Agterberg
549 et al., 2014; Keating et al., 2016; Parisa et al., 2017; Asp et al., 2018; Nelson et al., 2018).
550 This disruption of sound localization was greater for narrowband sounds (relative to
551 broadband), which suggests that the effects of unilateral hearing loss may be mitigated by
552 combining information across frequency. Previous work has shown that subjects rely more on
553 the spectral cues provided to the intact ear following unilateral hearing loss (Van Wanrooij
554 and Van Opstal, 2004, 2007; Kumpik et al., 2010; Keating et al., 2013; Keating et al., 2016).
555 However, these spectral cues are unavailable if narrowband sounds are used, which would
556 explain worse localization performance for these stimuli. Nevertheless, when subjects wore
557 an earplug, they were still able to locate narrowband sounds, albeit less well. Since this
558 requires subjects to compare the input to the two ears, it indicates that subjects used the

559 residual input to the occluded ear. We would therefore expect greater disruption of sound
560 localization following more severe forms of unilateral hearing loss (Wightman and Kistler,
561 1997; Van Wanrooij and Van Opstal, 2004; Agterberg et al., 2014; Firszt et al., 2015; Asp et
562 al., 2018).

563 Although many auditory abilities are impaired by background noise following hearing
564 loss (Moore, 1996; Lorenzi et al., 1999a; Bronkhorst, 2000; Lorenzi et al., 2006; Helfer and
565 Freyman, 2008; Akeroyd, 2014), we found that background noise improved narrowband
566 sound localization following simulated unilateral hearing loss. Since similar results were
567 observed for both low- and high-frequency targets, which respectively rely on ITDs and ILDs
568 (Middlebrooks and Green, 1991), this beneficial effect appears to be a general feature of
569 binaural processing. However, background noise had much less effect on broadband targets.
570 This is consistent with our normal-hearing data, which means that broadband sound
571 localization is more immune to both the negative (normal hearing) and positive (plugged
572 hearing) effects of background noise. Although we investigated what happens when targets
573 and background noise overlap in time, auditory spatial processing can adapt to sounds that
574 precede a target sound but do not overlap (Dahmen et al., 2010; Maier et al., 2012; Stange et
575 al., 2013; Phillips, 2014; Kopco et al., 2017; Tolnai et al., 2017; Ferger et al., 2018).
576 However, previous work has shown that adaptation cannot fully explain the effects of
577 concurrent background noise on sound localization (Best et al., 2005), which points toward
578 additional mechanisms. Similarly, whilst background noise can improve the audibility of sub-
579 threshold sounds via stochastic resonance (Zeng et al., 2000; Itzcovich et al., 2017), we saw
580 similar results across a wide range of SNRs, which argues against this.

581 To understand the beneficial effects of background noise at a neurophysiological
582 level, new studies will be necessary. However, previous work has shown that simulated
583 unilateral hearing loss changes the balance of target responses between the two hemispheres
584 (Keating et al., 2015). When background noise (or preceding sounds) are presented on one
585 side of space, they also alter the balance of target responses between the two hemispheres
586 (Furukawa and Middlebrooks, 2001; Dahmen et al., 2010). Additionally, when subjects wore
587 an earplug, the background noise produced binaural cues that favored the side of the open ear
588 (and was perceived on that side). Consequently, a key hypothesis for future work is that
589 background noise helps rebalance activity between the two hemispheres following unilateral
590 hearing loss (Fig. 5F). When subjects wear an earplug for prolonged periods of everyday life,
591 they show no adaptation to the abnormal binaural cues when tested in quiet environments

592 (Kumpik et al., 2010). This is surprising because subjects can learn to do this if given
593 appropriate training (Keating et al., 2016). However, our results show that subjects rapidly
594 reinterpret abnormal binaural cues in the presence of background noise. If subjects rely on
595 this to maintain accurate sound localization following earplugging, they might not show
596 binaural adaptation in quiet environments. Consequently, whilst the enormous diversity of
597 environmental sounds may affect perception and adaptation in different ways, our results
598 suggest that background noise may be part of the solution as well as the problem.

599

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742

743 **Figure legends**

744 **Figure 1.** Behavioral effects of background noise on narrowband sound localization. **A**
745 Schematic of speaker array used to test sound localization. On each trial, a target sound was
746 presented from one of the loudspeakers shown. Subjects sat at the centre of the array and
747 used a graphical user interface to indicate their response. To create a noisy background,
748 broadband noise was presented continuously at the midline (0°, black). **B** Magnitude of sound
749 localization errors (black: mean \pm SEM; gray: individual subject data) are plotted for
750 different experimental conditions. Subjects located sounds with normal hearing or with an
751 earplug in one ear, and with background noise turned either off (Q: quiet) or on (N: noisy). **C**
752 Localization data for normal hearing condition with background noise off. Joint distribution
753 of stimulus and response is shown averaged across all subjects. Circle size is proportional to
754 the number of trials corresponding to each unique combination of stimulus and response.
755 Results of linear regression (restricted to stimulus locations $\pm 30^\circ$ away from the midline) are

756 shown for actual data (red) and perfect performance (gray). Mean error magnitude is
757 displayed above main plot. **D-F** Identical to (C) but showing localization data for normal
758 hearing condition with background noise on (D), earplug condition with background noise off
759 (E), or earplug condition with background noise on (F). **G** Identical to (B) but showing
760 subjects' bias values. Positive values indicate a tendency to mislocalize sounds toward the
761 side of the ear that did not receive an earplug. **H** Identical to (B) but showing slopes of linear
762 regression lines fit to localization data. Perfect performance on task is associated with a slope
763 of 1 (dashed line); values above or below this reflect errors.

764 **Figure 2.** Behavioral effects of background noise on broadband sound localization. **A**
765 Localization data for normal hearing condition with background noise off. Joint distribution
766 of stimulus and response is shown averaged across all subjects. Circle size is proportional to
767 the number of trials corresponding to each unique combination of stimulus and response.
768 Results of linear regression (restricted to stimulus locations $\pm 30^\circ$ away from the midline) are
769 shown for actual data (red) and perfect performance (gray). Mean error magnitude is
770 displayed above main plot. **B-D** Identical to (A) but showing localization data for normal
771 hearing condition with background noise on (B), earplug condition with background noise off
772 (C), or earplug condition with background noise on (D). **E** Bias values (black: mean \pm SEM;
773 gray: individual subject data) are plotted for different experimental conditions. Positive
774 values indicate a tendency to mislocalize sounds toward the side of the ear that did not
775 receive an earplug. Subjects located sounds with normal hearing or with an earplug in one
776 ear, and with background noise turned either off (Q: quiet) or on (N: noisy). **F** Identical to (E)
777 but showing average magnitude of errors made by subjects for different conditions.

778 **Figure 3.** Effect of background noise under normal hearing conditions in the hemispheric
779 model of sound localization. **A** Neural responses to target sounds for left and right auditory
780 cortex either in the presence or absence of continuous background noise located at the
781 midline (0° ; arrow). Stimulus locations on the right are represented by positive values.
782 Markers indicate data obtained in cat A2 by Furukawa and Middlebrooks (2001; see also
783 Methods). Lines show Gaussian fits to their data; responses for the left hemisphere are
784 mirrored versions of right-hemisphere responses. **B** Difference in neural response between
785 the left and right hemispheres plotted as a function of target location, calculated using the
786 Gaussian fits in (A). Positive hemispheric differences indicate a greater response in the left
787 hemisphere. Data are shown for conditions in which the background noise was either absent
788 (gray) or present (black). In general, background noise located directly in front exaggerates

819 hemispheric differences in activity, albeit in a location-specific way. **C,DS** Sound localization
820 data simulated using the hemispheric differences in (B), either with the background noise off
821 (C) or on (D). For each of these conditions, the joint distribution of stimulus and response is
822 shown. Circle size is proportional to the number of trials corresponding to each unique
823 combination of stimulus and response. Results of linear regression (restricted to stimulus
824 locations $\pm 30^\circ$ away from the midline) are shown for actual data (red) and perfect
825 performance (gray). Overall errors are constrained to match human behavioral data for
826 narrowband targets. **E** Change in response produced by background noise plotted for each
827 target location. Positive changes in response indicate that background noise shifts responses
828 toward the right; negative changes in response indicate shifts toward the left. Positive target
829 locations are on the right. Data show that target sounds are pushed away from the location of
830 the background noise (midline; arrow). Data are shown for simulations that match overall
831 errors to human behavioral data obtained using narrowband targets (black; computed from
832 data in panels C and D) or broadband targets (red). **F** Identical to (E) except data have been
833 calculated using subjects' behavioral responses. Data are shown for narrowband targets
834 (black; see also Fig. 1C,D) and broadband targets (red; see also Fig. 2A,B). Asterisks indicate
835 significant differences between narrowband and broadband data (mixed-effects ANOVA,
836 post-hoc tests, $p < 0.05$). Pale lines show data for individual subjects; dashed lines show data
837 averaged across subjects. Continuous dark lines show data (mean \pm SEM) averaged across
838 subjects and hemifields. Close correspondence between continuous and dashed lines indicate
839 that data are symmetric around the midline.

840 **Figure 4.** Dissociable effects of sharper tuning and reduced responsiveness in the
841 hemispheric model. **A** Population responses for left hemisphere plotted as a function of
842 stimulus location. Positive stimulus values correspond to locations on the right. Lightest gray
843 shows Gaussian fit to real neural responses obtained in quiet (identical to Fig. 3A). These
844 responses can be reduced artificially using a scaling factor that keeps the tuning width
845 constant. Progressively greater reductions in neural response correspond to progressively
846 darker shades. For clarity, data are shown for right hemisphere only; left-hemisphere data are
847 symmetric around the midline. **B** Reducing neural responses produces changes in the
848 behavioral output of the hemispheric model. Changes in model output (relative to baseline)
849 are plotted as a function of stimulus location. Positive target locations are on the right.
850 Positive changes indicate that the model 'perceives' (i.e. decodes) target sounds further to the
851 right (relative to baseline). Overall, reducing neural responses pulls the 'perceived' location

822 of target sounds toward the midline, particularly for peripheral sounds. **C** Identical to (A)
823 except the tuning of neural responses has been progressively sharpened whilst keeping the
824 maximum neural response constant. Darker shades correspond to sharper tuning curves. **D**
825 Identical to (B) but showing the impact of sharper tuning on model output. Overall, sharper
826 neural tuning (darker shades) pushes the ‘perceived’ location of sounds away from the
827 midline, particularly for target sounds that are located intermediate distances from the
828 midline (for comparison, see also Fig. 3 E,F). As tuning width is progressively sharpened, the
829 target location associated with the greatest change in response shifts toward the midline
830 (arrows).

831 **Figure 5.** Effects of lateralized background noise. **A** Neural responses to target sounds in the
832 presence or absence of continuous background noise to the right of the midline (40° ; arrow).
833 Data are shown for the left hemisphere (contralateral to background noise) and right
834 hemisphere (ipsilateral to background noise). Stimulus locations on the right are represented
835 by positive values. Markers indicate data obtained from cat A2 by Furukawa and
836 Middlebrooks (2001). Lines show Gaussian fits to their data; responses for the left
837 hemisphere are mirrored versions of right-hemisphere responses. **B** Difference in neural
838 response between the left and right hemispheres plotted as a function of target location,
839 calculated using the Gaussian fits in (A). Positive hemispheric differences indicate a greater
840 response in the left hemisphere. Data are shown for conditions in which the background noise
841 was absent (gray), presented 40° to the right (continuous black), or 80° to the right (dashed).
842 **C** Identical to (A) but showing data for background noise located 80° to the right of the
843 midline. **D** Identical to (B), but shows what happens if we simulate the impact of background
844 noise for the right hemisphere only (yellow; hemisphere ipsilateral to the background noise)
845 or left hemisphere only (blue; contralateral to the background noise). Data are shown for
846 background noise located 40° (continuous coloured lines) or 80° (dashed lines) to the right of
847 the midline, as well as for the quiet condition (gray). Effects of background noise in the two
848 hemispheres oppose one another (shift in opposite directions relative to gray line) and partly
849 cancel each other out when the hemispheric difference is computed. **E** Behavioral effects of
850 background noise following simulated unilateral hearing loss for different target locations.
851 Change in response produced by background noise is plotted for each stimulus location.
852 Negative stimulus locations are on the side of the plugged ear. Negative changes in response
853 indicate that background noise shifts responses toward the side of the plugged ear; positive
854 changes in response indicate shifts toward the side of the unoccluded ear. Data are shown for

855 narrowband (black) and broadband (red) targets. Pale lines show data for individual subjects.
856 Continuous dark lines show data (mean \pm SEM) averaged across subjects. **F** Hypothesis to
857 explain beneficial effects of background noise following simulated unilateral hearing loss. (1)
858 when a simulated unilateral hearing loss (simUHL) is induced in the left ear, responses to
859 target sounds are reduced in the right hemisphere (middle; Keating et al., 2015), which alters
860 the balance of activity between the two hemispheres (bottom). Background noise presented at
861 the midline (filled black circle, top) is also perceived on the right (dashed circle) because it
862 produces binaural cues that favor that side. (2) When background noise is presented on the
863 right (filled black circle, top), responses to target sounds are reduced in the left hemisphere
864 (middle; Furukawa and Middlebrooks, 2001), which alters the balance of activity between the
865 two hemispheres (bottom; opposite direction to simUHL). Background noise may therefore
866 help rebalance activity between the two hemispheres following simUHL.

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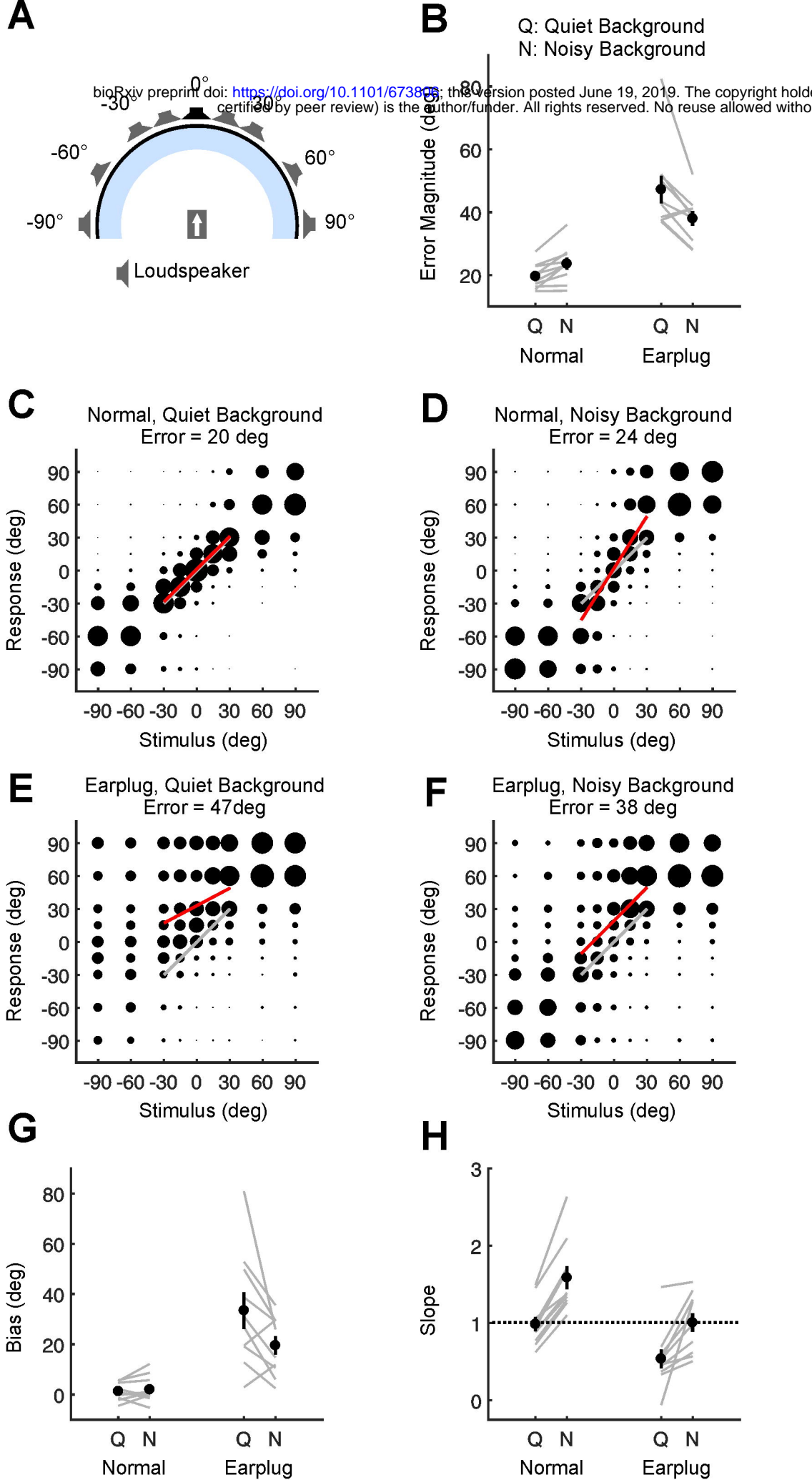


Figure 1

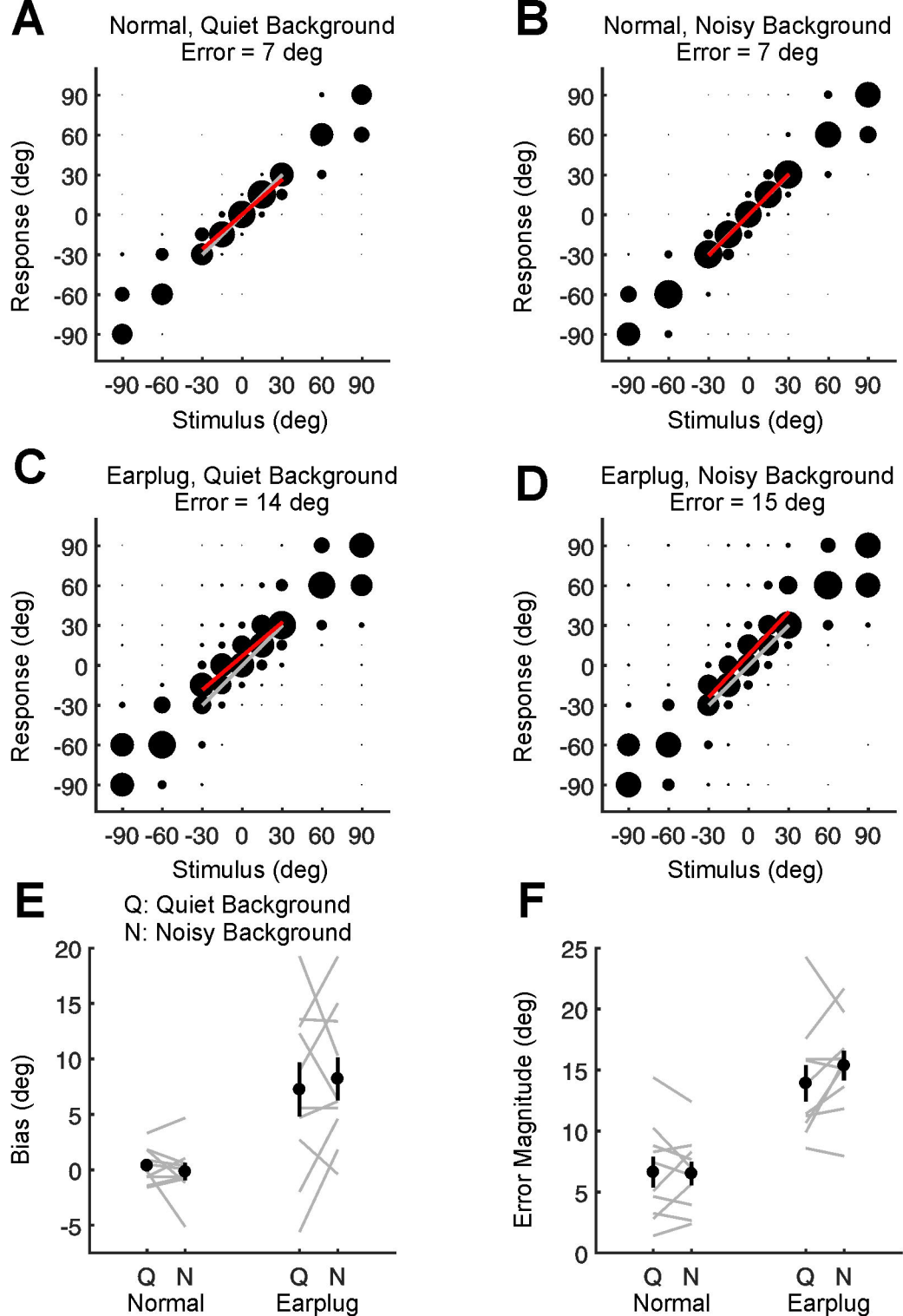


Figure 2

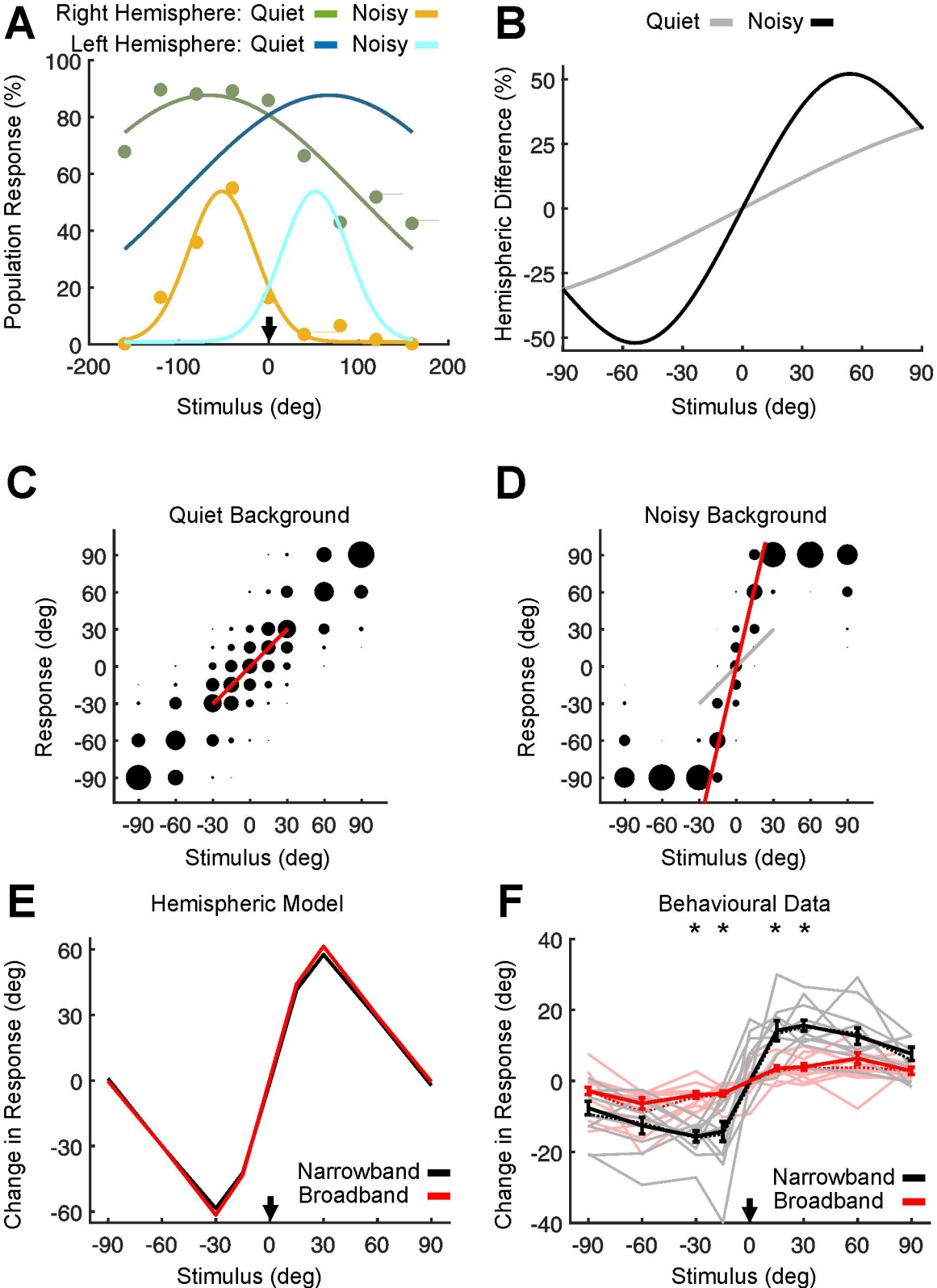


Figure 3

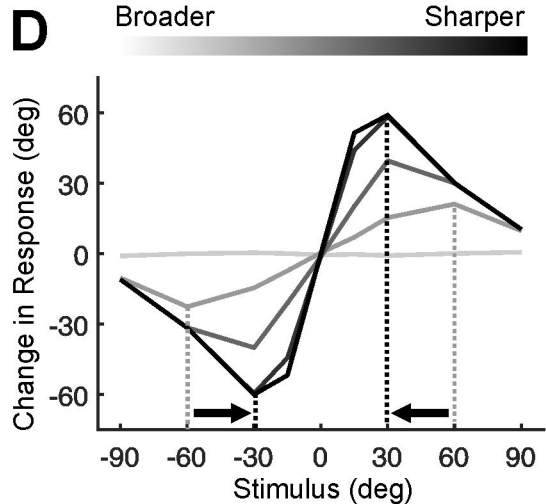
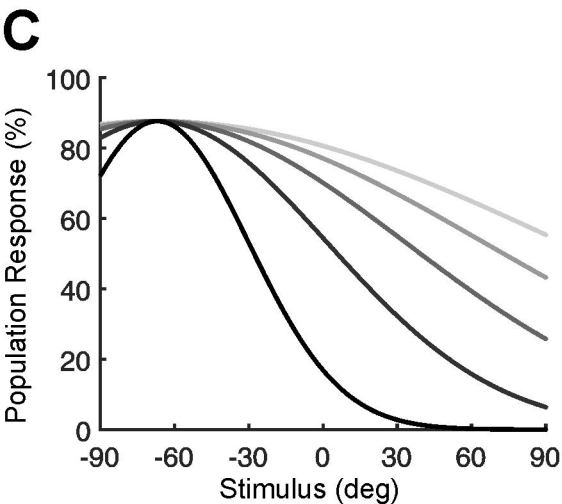
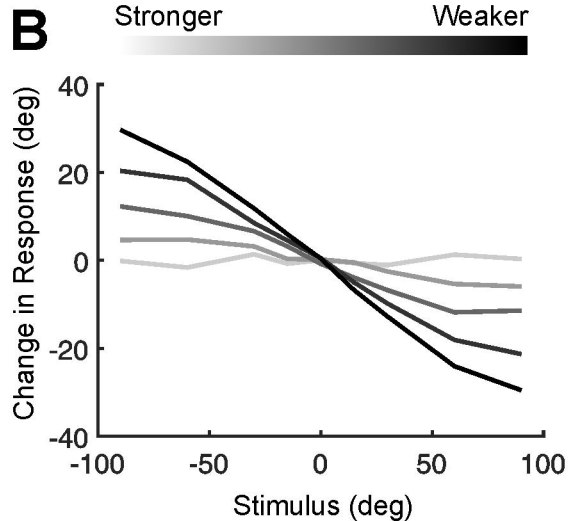
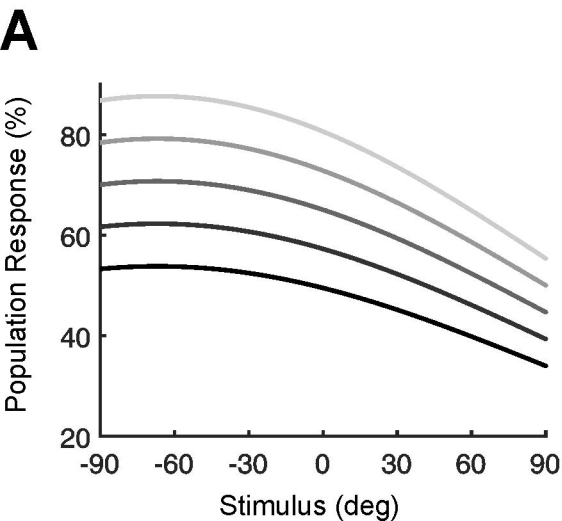


Figure 4

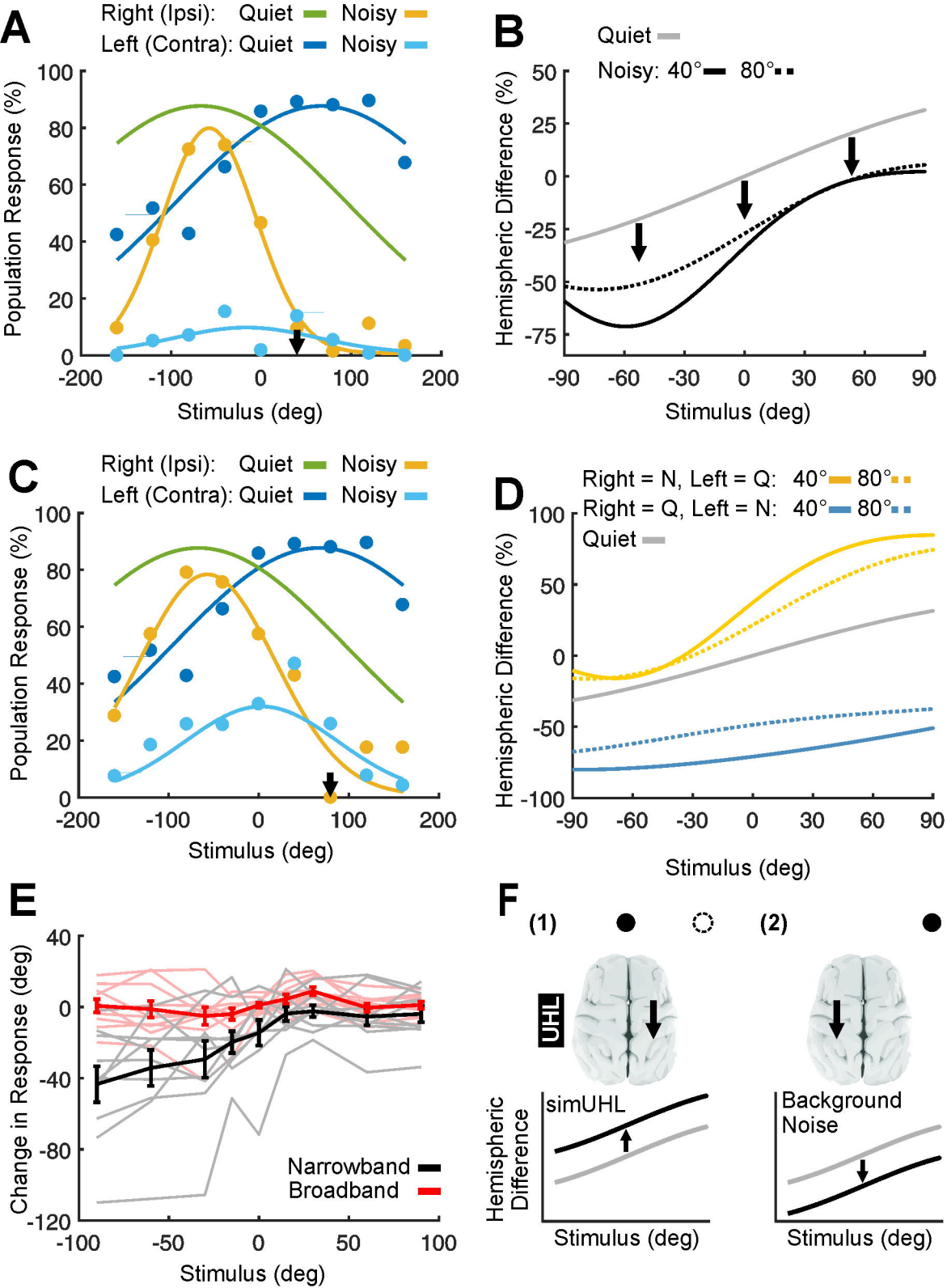


Figure 5