Individual differences show that only some bats can cope with noise-induced masking and distraction

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Anthropogenic noise is a widespread pollutant that has received considerable recent attention. While alarming effects on wildlife have been documented, we have limited understanding of the perceptual mechanisms of noise disturbance, which are required to understand potential mitigation measures. Likewise, individual differences in response to noise (especially via perceptual mechanisms) are likely widespread, but lacking in empirical data. Here we use the echolocating bat *Phyllostomus discolor*, a trained discrimination task, and experimental noise playback to explicitly test perceptual mechanisms of noise disturbance. We demonstrate high individual variability in response to noise treatments and evidence for multiple perceptual mechanisms. Additionally, we highlight that only some individuals were able to cope with noise, while others were not. We tested for changes in echolocation call duration, amplitude, and peak frequency as possible ways of coping with noise. Although all bats strongly increased call amplitude and showed additional minor changes in call duration and frequency, these changes could not explain the differences in coping and non-coping individuals. Our understanding of noise disturbance needs to become more mechanistic and individualistic as research knowledge is transformed into policy changes and conservation action.

1 **Individual differences show that only some bats can cope with noise-induced masking and**

2 **distraction**

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17 We dedicate this research to Lutz Wiegrebe, who passed away in November 2019. Lutz was a

18 great friend and a brilliant scientist with a sharp mind. We will miss his thoughts and jokes

19 forever.

22 **Abstract**

23 Anthropogenic noise is a widespread pollutant that has received considerable recent attention.

24 While alarming effects on wildlife have been documented, we have limited understanding of the

25 perceptual mechanisms of noise disturbance, which are required to understand potential

26 mitigation measures. Likewise, individual differences in response to noise (especially via

27 perceptual mechanisms) are likely widespread, but lacking in empirical data. Here we use the

28 echolocating bat *Phyllostomus discolor*, a trained discrimination task, and experimental noise

29 playback to explicitly test perceptual mechanisms of noise disturbance. We demonstrate high

30 individual variability in response to noise treatments and evidence for multiple perceptual

31 mechanisms. Additionally, we highlight that only some individuals were able to cope with noise,

32 while others were not. We tested for changes in echolocation call duration, amplitude, and peak

33 frequency as possible ways of coping with noise. Although all bats strongly increased call

34 amplitude and showed additional minor changes in call duration and frequency, these changes

35 could not explain the differences in coping and non-coping individuals. Our understanding of

36 noise disturbance needs to become more mechanistic and individualistic as research knowledge

37 is transformed into policy changes and conservation action.

39 **Introduction**

40 Anthropogenic noise is a global pollutant that is pervasive even in protected areas (Buxton et al.,

41 2017), is increasing over time (Luther and Baptista, 2009), and has recently gained considerable

42 attention by behavioral biologists (Barber et al., 2010). Noise can disrupt animal behavior, such

43 as communication (Brumm and Slabbekoorn, 2005; Rabin et al., 2003) and foraging (Gomes et

44 al., 2016; Purser and Radford, 2011; Siemers and Schaub, 2011), reduce reproductive success

45 (Halfwerk et al., 2011), increase mortality (Simpson et al., 2016), change biological communities

46 (Francis et al., 2011), and alter ecological services (Francis et al., 2012). Yet it is not often

47 understood what mechanisms drive these changes, and if and how different individuals are

48 affected by these mechanisms differently. Individual differences in response to noise has been

49 documented in humans (Furnham and Strbac, 2002; Standing et al., 1990), birds (Naguib et al.,

50 2013), fish (Bruintjes and Radford, 2013), mongooses (Eastcott et al., 2020), and bats (Luo et al.,

51 2015a; Luo et al., 2015b; Simmons et al., 2018), among many others (reviewed in Harding et al.,

52 2019), yet individual differences are often overlooked as individuals are more often grouped

53 together for analysis than analyzed individually (Harding et al., 2019).

54 Similarly, only a few studies to date have investigated the mechanisms of noise disturbance.

55 Some have used bands of noise that are both overlapping or non-overlapping with signals or cues

56 of interest to demonstrate evidence of masking (e.g. Gomes et al., 2016; Zhou et al., 2019).

57 Others have shown that noise can disrupt behaviors across sensory modalities (where masking

58 cannot work) via distraction (e.g. Chan et al., 2010; Morris-Drake et al., 2016). Understanding

59 how we may be able to mitigate the consequences of noise relies heavily on knowledge of direct

60 mechanisms of noise disturbance on individuals. Dominoni et al. (2020), for example, highlight

61 three main perceptual mechanisms of noise disturbance – masking, distraction, and misleading.

62 While these mechanisms apply to all senses, we here consider them specifically in the auditory

63 domain.

64

65 Masking is a mechanism whereby noise overlaps in frequency with important signals or cues,

66 thus making the detection and auditory analysis of the signal difficult, if not impossible, and

67 occurs at the auditory periphery (Clark et al., 2009; Fay and Wilber, 1989; Gomes et al., 2016;

68 Tanner Jr, 1958). Distraction, on the other hand, occurs when noise competes for the finite

69 attention (i.e. central processing) of an organism, and is not limited to frequencies that overlap

70 with a signal or cue of interest (Chan et al., 2010). Misleading occurs when noise is interpreted

71 as something that it is not, similar to a false alarm (Wiley, 2013) or a sensory trap (Christy, 1995;

72 West-Eberhard, 1984). Some have shown, for example, that beaked whales respond to Navy

73 sonar similarly as they do killer whales, perhaps indicating that they misinterpret this noise as a

74 predator or something unknown that might be dangerous (Tyack et al., 2011). Other mechanisms

75 of disturbance have been proposed, such as stress, fear, and avoidance (Campo et al., 2005; Luo

76 et al., 2015a; Voellmy et al., 2014), yet these physiological and behavioral responses must occur

77 downstream of the initial perceptual mechanism (i.e. masking, distraction, or misleading).

78

79 Here, we use a behavioral experiment to tease apart the effects of both masking and distraction

80 as perceptual mechanisms on individual echolocating bats. Echolocating bats are a worthwhile

81 system to study these questions because they actively sense their world via sound. Thus, by

82   monitoring how they adjust the characteristics of their echolocation calls in response to noise, we

83   can easily study how they are responding to changes in the sensory environment.

84   Anthropogenic noise arises from diverse sources (e.g. automobile and airplane traffic, energy

85   extraction, and urban cities) and generally contains more energy in lower rather than in higher

86   frequencies (Bondello and Brattstrom, 1978; Bunkley and Barber, 2015; Bunkley et al., 2015;

87   Cinto Mejia et al., 2019; Nemeth and Brumm, 2010; Schaub et al., 2008; Siemers and Schaub,

88   2011; Sierro et al., 2017). Despite this, anthropogenic noise can contain considerable energy in

89   the ultrasonic range, particularly at close distance to the noise source (Siemers and Schaub,

90   2011). As the echolocation call frequencies of different bat species also span a wide frequency

91   range (Fenton and Bell, 1981), anthropogenic noise can overlap bat echolocation in frequency in

92   a species-, distance- and noise-source specific manner, potentially affecting bats via multiple

93   mechanisms (Dominoni et al., 2020).

94

95   We trained pale spear-nosed bats (*Phyllostomus discolor*) to discriminate surface structures with

96   increasing level of difficulty and under three noise treatments (see Methods). We made distinct

97   predictions for each of the tested perceptual mechanisms. By broadcasting noise that does and

98   does not spectrally overlap with echolocation calls, we directly tested the role of masking. We

99   predicted that masking should only reduce the discrimination performance for spectrally

100   overlapping noise, but not for non-overlapping noise. Since distraction assumes that deficits

101   result from limited attentional resources, we predicted that distraction should be independent of

102   the noises' spectral overlap with echolocation calls (distinguishing it from masking), but should

103   depend on the noises' temporal structure. We thus also presented a spectrally overlapping

104   'sparse' noise with random temporal gaps, making the noise less predictable, and thus, more

105   distracting (Glass and Singer, 1972; Kjellberg et al., 1996; Matthews et al., 1980). At the same

106   time, sparse noise might allow bats to listen in-between the noise gaps ("dip listening"), reducing

107   its masking effect (Vélez and Bee, 2011). Thus, if distraction is the primary mechanism of

108   disturbance, then sparse noise should decrease discrimination performance and increase trial

109   duration, while we would expect an increase in discrimination performance and a decrease in

110   trial duration under sparse noise if masking is the primary mechanism of disturbance.

111

112

Materials and methods

Experimental Animals and Husbandry

The pale spear-nosed bat (*Phyllostomus discolor*; Wagner, 1843) is an omnivorous neotropical bat (Kwiecinski, 2006) that emits multi-harmonic, downward frequency-modulated echolocation calls of short duration (0.3 – 2.5 ms) and most energy in the range of ~40-100 kHz (Goerlitz et al., 2008; Kwiecinski, 2006). A captive colony of *P. discolor* was kept in a temperature (~25 °C) and humidity (~70%) controlled room at the Max Planck Institute for Ornithology, Seewiesen, Germany, where the bats had access to water *ad libitum*, and were fed a fruit-based diet. During experimental days, bats were first only fed during experiments (mealworm reward; *see below*), to maintain motivation. At the end of the day, several hours later, bats were fed fruit. Experiments were carried out in a nearby, but separate room (~21 °C / 65% rel. hum). Bat housing and all research was approved by the German authorities under the permit numbers 311.5-5682.1/1-2014-023 (Landratsamt Starnberg) and 55.2-1-54-2532-18-15 (Regierung von Oberbayern), respectively.

Experimental Setup

Experiments were conducted in a dark chamber within a dark room (see below for light levels). Walls of both the chamber and the room were covered in anechoic foam to reduce echoes. The chamber held a custom-built mushroom maze (87 cm x 65 cm x 18 cm, W x H x D), which was a fully enclosed mesh-cage (Baier et al., 2019). The mesh (12 mm x 12 mm mesh grid with wires of <1 mm diameter) is acoustically transparent for the echolocation calls of P. discolor (wavelength: ~3-9 mm). This maze allowed the bats perceptual access by echolocation to two simultaneously presented stimulus discs (reference plus test disc) on either side of the maze (**Figure 1A**). One infrared light barrier next to each of the disc positions objectively recorded the choice of the bat via a custom-written Matlab code (The Mathworks, Nattick, MA, USA), avoiding observer bias and potential observer errors. Two loudspeakers (Vifa, Peerless by Tymphany, San Rafel, CA, USA; connected to power amplifier TA-FE330R, Sony, Tokyo, Japan, and soundcard Fireface 802, RME, Haimhausen, Germany) were mounted on either side of the setup for noise playback (**Figure 1A**). The experimenter (stationed outside of the chamber) observed the experiment via a red-filtered computer screen displaying a live-feed from

144   an infrared camera (Foculus FO432SB; NET-GmbH, Finning, Germany; 880 nm infrared LED-

145   illumination, TV6818; ABUS, Wetter, Germany).

146

147   ***Stimuli***

148   We used an established behavioral assay that has been previously used to test perceptual

149   performance in bats (Baier et al., 2019). We used eight discs with 45 cm diameter as physical

150   stimuli. The stimulus discs were made by a milling cutter (Modellbau Grossmann, Calw,

151   Germany) and then spray-painted with multiple coats to be smooth-textured. One disc

152   ("reference disc") had a completely flat surface. The seven other discs had concentric ripples,

153   resembling concentric sinusoidal standing waves. All rippled discs had the same spatial

154   frequency of 17.8 ripples per meter, corresponding to eight full sinusoidal ripples per disc, but

155   different ripple heights increasing from 2 to 32 mm peak-to-peak height (2, 4, 5.6, 8, 11.2, 16, 32

156   mm; **Figure 1B**).

157

158   ***Noise Treatments***

159   In addition to silence, used as a control, we tested the bats under three band-limited white noise

160   treatments (**Figure 2**): 1) Smooth non-overlapping noise: band-limited white Gaussian noise not

161   overlapping in frequency with the echolocation calls of *P. discolor*, ranging from 5-35 kHz (10th-

162   order Butterworth filter). 2) Smooth-overlapping noise: band-limited white Gaussian noise

163   overlapping in frequency with the echolocation calls of *P. discolor*, ranging from 40-90 kHz

164   (10th-order Butterworth filter). 3) Sparse-overlapping noise: derived from the smooth-

165   overlapping noise (40-90 kHz) with additional short silent gaps between all adjacent samples

166   (Hübner and Wiegrebe, 2003). These silent gaps generate fluctuations in the temporal envelope

167   of the noise, causing the noise to sound rougher in comparison to the smooth noise. The duration

168   of the silent gaps was drawn from a uniformly random duration (mean: 0.3 ms, range: 0-0.6 ms).

169   The roughness is quantified by the base-10 logarithm of the waveform's fourth moment

170   (Hartmann and Pumplin, 1988), and is calculated as the summed amplitude values raised to the

171   power of 4, divided the squared sum of all squared amplitude values raised to the power of 2.

172   LogM4 was 1.44 logM4 for the sparse-overlapping noise, compared to 0.48 logM4 for the two

173   smooth noises (cf. Grunwald et al., 2004). For all three noise types, we generated uncorrelated

174   stereo noise files of 60 min duration (192 kHz sampling rate, 16 bit resolution) and corrected

175   each channel for the corresponding speaker's frequency response. At each daily experimental

176   session, noise playback was started at least 30 s prior to the beginning of the first trial at a

177   random position within the 60-min long noise files, and continued throughout the session.

178   Playback level was 70 dB SPL RMS re. 20 µPa at the bat's starting position. It is important to

179   note that the perceived loudness was likely different, since the noise treatments had different

180   bandwidths and the auditory sensitivity of *P. discolor* varies over their range of hearing (Esser

181   and Daucher, 1996; Hoffmann et al., 2008). However, this should not affect any interpretation of

182   the designed tests of masking and distraction.

183

184   ***Training and testing***

185   Nine bats were initially trained in a two-alternative forced-choice paradigm to discriminate the

186   flat reference disc from the stimulus disc with the highest ripples (32 mm). During training, bats

187   received mealworms (larvae of *Tenebrio molitor*) as reward when approaching the flat reference

188   disc only. Two bats did not learn this task at all, and three bats appeared to learn somewhat but

189   never showed consistent performance after three months of training (including one bat that had

190   already been trained successfully in a previous experiment; Baier et al., 2019). There appears to

191   be no consistent patterns between failure to train and previous experience or age of the bats.

192   Only four bats (3 males, 1 female) reached the training criterion (>70% correct approaches to the

193   flat reference disc over three consecutive days; the three males were previously trained in Baier

194   et al., 2019) and were subsequently tested during the data acquisition stage. Throughout testing

195   and training, the flat reference disc was pseudo-randomly (Gellermann, 1933) alternated between

196   each side of the experimental setup to avoid any biases in location preferences by the bats.

197

198   Prior to each trial, bats were encouraged to enter a small Tupperware 'starting' box in the middle

199   of the experimental setup by offering blended banana as a food reward via a syringe tube that

200   was mounted inside this starting box (**Figure 1A**). While in the starting box, bats had no

201   perceptual access to the discs since the solid bottom door was closed upon entering. The discs

202   were then placed in their positions. Once the starting box opened, the trial started. Bats were

203   allowed to crawl through the setup towards the discs. When they broke the IR light barrier, the

204   trial ended, and the bat was rewarded with a mealworm when it chose the flat reference disc.

205

206   Bats were initially tested in a silent (*i.e.* ambient sound level) experimental room to generate

207   baseline psychometric curves with discs of 5 different ripple heights (2 mm, 4 mm, 8 mm, 16

208   mm, and 32 mm). For the subsequent tests, we added two additional discs with intermediate

209   ripple heights (5.6 mm and 11.2 mm) to get better resolution around the turning point of the

210   psychometric function measured in silence. The bats were then tested with all seven discs in each

211   of the three noise conditions. Per individual, the noise conditions were presented in pseudo-

212   random sequence, and a new noise condition was presented only after the individual had

213   completed all trials of the previous noise condition. Finally, each bat was retested a second time

214   in silence with all seven discs, to assure that differences in performance were not due to learning

215   or other order effects. Testing each bat in the same noise conditions over multiple trials and days

216   (as opposed to changing noise treatment for each trial) may lead to more habituation to that noise

217   treatment. However, as the opportunity for habituation was consistent across treatments, any

218   differences amongst noise treatments are due to the noise treatments themselves. Additionally, as

219   randomizing noise treatments across trials would only exacerbate any differences amongst noise

220   treatments, the differences we report here are conservative. Each bat was tested 30 times for

221   every ripple height and noise treatment combination, totaling 990 trials per individual bat.

222

223   To motivate the bats, each day was started with easier discrimination tasks (higher ripple

224   heights) and gradually moved towards more difficult tasks (lower ripple heights). Bats were

225   allowed to continue testing until satiated or no longer food-motivated, which was determined by

226   the bat attempting to leave the mushroom maze via an exit door in the top of the setup.

227

228   ***Aborted trials***

229   If the bat did not exit the starting box within 5 minutes after starting a trial, the trial was aborted

230   and repeated. As the bats did not make a decision in those aborted trials, they were not included

231   in further analyses. The one exception, however, is that we analyzed the number of these aborted

232   trials as a measure of aversion to the noise. Abortion was behaviorally distinguished from

233   satiation, as bats would crawl toward the door to exit the maze when they were seemingly no

234   longer food-motivated. It is likely that bats aborted trials not only because of the noise, but also

235   for potential other reasons. However, as those other reasons are constant within the controlled

236 setting of an experiment, any *difference* in the number of aborted trials (as in any other

237 behavioral measure) can be attributed to the experimental treatment (i.e., the type of noise).

238

239 ***Echolocation call recording and analysis***

240 We continuously recorded the bats' echolocation calls into a 4-sec-long ring-buffer. When a bat

241 made a decision by interrupting a light barrier, only the sound of the four seconds prior to the

242 decision were automatically saved into a WAV-file. Recordings were performed with two

243 microphones (Knowles SPU0410) positioned just behind each light barrier, a sound card

244 (Fireface 802, RME, Haimhausen, Germany; 192 kHz sampling rate, 16-bit resolution) and

245 playrec (V2.1.0, playrec.co.uk) for Matlab (V2007b, The Mathworks, Nattick, MA, USA).

246

247 Echolocation calls were analyzed automatically by custom-written scripts in Matlab (V2016a,

248 The Mathworks, Nattick, MA, USA), advanced from previous work (Goerlitz et al., 2008; Luo et

249 al., 2015a). First, we filtered all recordings with each microphone's compensatory impulse

250 response (511-order finite impulse response filter) to compensate for the microphone's frequency

251 response, and a band-pass filter (38-95 kHz, 8th-order elliptic filter). Second, we used a

252 threshold detector to broadly determine the timing of all acoustic events: we additionally band-

253 pass-filtered recordings around the bats' main call energy (45-90 kHz, 4th-order elliptic filter),

254 calculated their low-pass filtered (500 Hz, 4th-order elliptic filter) Hilbert-envelope, and detected

255 all acoustic events that surpassed a threshold (mean + 2x STD of the envelope), excluding events

256 that were too close to the preceding event (< 20 ms) and too short (< 0.75 ms). We then added an

257 additional 0.5 ms on both sides of the detected acoustic events, which, together with the previous

258 low-pass-filtering of the envelope, ensured that the determined time window included the full

259 call flanked by non-call samples. Third, we detected the actual call within this time window of

260 the recording, and analyzed its acoustic parameters.

261

262 Call duration was determined from the low-pass filtered (5000 Hz, 2nd-order butterworth filter)

263 Hilbert envelope of the originally filtered recording (38-95 kHz) at -12 dB below the envelope's

264 peak value. Peak frequency (frequency with highest amplitude), frequency centroid (dividing the

265 call energy into two halves along the frequency axis; Au, 2012) and the lowest and highest

266 frequency (defined as the lowest and highest frequencies whose amplitudes were at -12 dB below

267   the highest amplitude) were calculated from the time-averaged call spectrogram (1024 FFT of

268   100 samples, 95% overlap). Relative call level was calculated as the root mean square (RMS) of

269   all samples within the -12 dB duration criterion and expressed in dB FS, i.e., negative dB values

270   relative to the full scale of the recording system.

271

272   If a call was detected on both microphones, we only analyzed the call with the higher signal-to-

273   noise-ratio (SNR: call-RMS relative to RMS of all parts of the recording that were not classified

274   as acoustic events). Of all recorded calls (N = 287,061), we excluded for further analysis calls

275   shorter than 0.3 ms and longer than 2 ms, with too high (>-0.5 dB FS, to avoid clipping) or too

276   low recorded peak amplitudes (<-15 dB FS), with a SNR of less than 20 dB, and whose ratio

277   between the -12 dB duration and the -6 dB duration was larger than 1.5 (to exclude calls with

278   long echoes). All remaining calls (N = 63,990) were manually viewed as spectrogram (256 FFT,

279   50 time slices over full call length, 95% overlap), blind to bat individual and noise treatment, to

280   exclude ambiguous recordings and obvious artefacts, e.g., overlapping call-echo-pairs and non-

281   multiharmonic sounds (e.g., clicks, external noise). This resulted in a final data set of 59,173

282   calls (0-83 calls per trial). Of the 3960 total trials, 3469 trials (87.6%) included at least one

283   recorded call, 3166 trials (80.0%) at least 3 calls, 2912 trials (73.5%) at least 5 calls, and 2265

284   trials (57.2%) included at least 10 recorded calls. For further analysis, we used the mean call

285   parameters of each trial in statistical models. Note that the background noise affects our call level

286   measurements only negligibly (<0.05 dB) because we only analyzed calls with a SNR >20 dB.

287

288   *Visual system and light levels*

289   Light levels in the experimental room were extremely low (1.39 x 10^{-5} lux; SPM068 with

290   ILT1700 light detector, resolution 10^{-7} lux, International Light Technologies, Peabody, MA,

291   USA), precluding the use of vision to discriminate between discs. Many other laboratory

292   experiments, which have similarly excluded the use of vision due to an assumed unavailability of

293   light, have either reported higher light levels than us or did not measure or report light levels.

294   Additionally, it has been experimentally shown that another related phyllostomid bat (*Macrotus*

295   *californicus*) only has visual acuity to light levels as low as 2 x 10^{-3} lux (Bell and Fenton, 1986),

296   which is nearly two orders of magnitude higher than our light levels. Furthermore, *M.*

297   *californicus* has one of the highest sensitivities to low light levels known (Bell and Fenton, 1986;

298 Eklöf et al., 2014). Thus, it is extremely unlikely that the *Phyllostomus discolor* used here were

299 able to visually discriminate between the discs.

300

301 ***Statistical analysis***

302 We fitted (generalized) linear models to the behavioral data of each individual, using R (R Core

303 Team, 2017). Response variables were analyzed with different distribution families and link

304 functions based on theoretical sampling distributions of the data, and model fits were validated

305 with plots of model residuals, and were checked for collinearity.

306

307 We used a binomial distribution family and logit link function to analyze differences in

308 discrimination performance and number of aborted trials, since these were binary data. We used

309 an inverse Gaussian distribution family with an identity link function to analyze trial time data

310 (Baayen and Milin, 2010). Log-normal linear models (Gaussian family with an identity function)

311 were used to analyze log-transformed received call level, duration, peak frequency, and

312 frequency centroid. Peak frequency and frequency centroid measure similar aspects of

313 vocalization frequency and are both used in the literature (Goerlitz et al., 2008; Holderied et al.,

314 2005; Lattenkamp et al., 2018; Lazure and Fenton, 2011). We therefore included both metrics in

315 our analyses for comparability, but report only peak frequency in the main text because it is the

316 most commonly used metric, and present frequency centroid data in the supplementary

317 information (**Table S6**).

318

319 We initially checked that discrimination performance did not change between the first and last

320 (pre- and post-treatment) silent conditions with a logistic regression including noise treatment (as

321 factors) and ripple height. Since the performance across the two silent noise conditions did not

322 change for any of the bats (see Results), we pooled these data for analysis, and thus present both

323 'silent' conditions together.

324

325 For all models we used noise treatment, ripple height, and their interaction as explanatory

326 variables, while the number of days that bats were in our experiment was included as a covariate,

327 all fitted as fixed effects. The number of days an animal is in an experiment may influence

328 performance because animals may learn over time, become faster at a given task, or, conversely,

329 give up on difficult tasks. We thus included this term as a covariate in our model to control for it

330 (and show its effect in the model output tables), but focused our main analysis and interpretation

331 on more pertinent variables.

332

333 We fitted individual models for each bat, instead of single models for every response variable,

334 with bats as random effects terms (*e.g.* Gomes et al., 2017), for two reasons. Firstly, it has been

335 suggested that random effects terms should have a minimum of five groups; otherwise estimates

336 of variance become imprecise (Harrison et al., 2018). As we only had four bats that completed

337 the experiment, we were unable to fulfill this requirement. Secondly, and more importantly,

338 fitting models to each individual bat allowed us to understand the nuanced differences between

339 them, which an all-bats-combined model would not achieve. Since we fitted four models per

340 response variable (one for each bat), we used conservative Bonferroni corrections to correct p

341 values for these multiple comparisons by multiplying p values by four. All differences reported

342 in results due to noise treatments are model estimates, and not differences in raw data.

343

344 *Performance thresholds*

345 We used a binomial generalized linear model with a probit link (constrained between 0.5 and 1

346 with the link function `mafc.probit` in the R package `psyphy`; Knoblauch, 2007) to generate

347 estimates of ripple height thresholds at which bats exceed correct responses at least 70% of the

348 time. For each bat, 1000 simulated discrimination performance (0 or 1) datasets were generated

349 based on the above model estimates for each bat, at each ripple height, within each noise

350 treatment. Then the lower 0.025 and upper 0.975 percentiles of those data gave us a 95%

351 confidence interval band around our performance threshold.

352

353 **Results**

354

355 ***Discrimination performance***

356 All four bats learned to discriminate the smooth disc from the rippled disc with the highest

357 ripples (32 mm) in silence (88-100% correct), and showed reduced discrimination performance

358 with decreasing ripple height (**Figure 3**, orange line; logistic model $p < 0.001$; **Table 1**). In

359 silence, performance dropped below our 70% threshold criterion for ripple heights around

360   7.9 mm (mean; range = 5.4 – 11.4 mm; **Figure 3; Table 2**), matching the mean threshold found

361   by (Baier et al., 2019) of 8.0 mm (range: 3.7 – 12.3 mm). As the performance in silence did not

362   change for any bat between the first and last silence condition (Bat A: $p = 0.21$, B: $p = 0.89$, C: p

363     $= 0.81$, D: $p = 0.39$), demonstrating a lack of order (e.g. learning) effects, we pooled all silence

364   trials. Noise treatments did not change the discrimination performance of bats A and B (hereafter

365   'coping' bats; **Table 1**), and the 95% confidence intervals of their thresholds in noise overlapped

366   with those in silence. In contrast, discrimination performance decreased for bats C and D

367   (hereafter 'non-coping' bats) both under smooth-overlapping noise ($z = -3.2$, $p = 0.008$; $z = -3.2$,

368     $p = 0.004$) and sparse-overlapping noise ($z = -3.7$, $p < 0.001$; $z = -3.1$, $p = 0.008$; indicated as

369   blue and purple lines in **Figure 3** respectively). The same is true for the smooth non-overlapping

370   noise for bat C ($z = -2.5$, $p = 0.047$, green line), yet not for bat D ($z = 1.8$, $p = 0.24$).

371

372   *Trial duration*

373   The time to complete trials differed between some noise treatments for some bats (**Figure 4**).

374   Both bats A and D made faster decisions during smooth-overlapping noise compared to silence

375   (model estimated trial durations of bat A and D under noise and silence, respectively: 28.8 s

376   vs. 30.0 s (A) and 10.3 s vs. 14.8 s (D); $z = -3.4$, $p = 0.004$ (A); $z = -4$, $p < 0.001$ (D); **Table S1**).

377   However, bat C took longer to complete trials during sparse-overlapping noise (48.6 s vs. 18.5 s;

378     $z = 4.8$, $p < 0.001$), while noise treatments did not affect the trial time of bat B (**Table S1**).

379

380   *Aborted Trials*

381   The bats aborted 297 trials of 4,257 total trials (7 %; bats A: 54; B: 92; C: 101; D: 50).

382   Compared to silence, both bats B and C significantly aborted more trials under both smooth non-

383   overlapping ($z = 4.0$, $p < 0.001$; $z = 3.0$, $p = 0.01$) and smooth-overlapping noise ($z = 3.9$, $p <$

384   0.001; $z = 4.2$, $p < 0.001$). In addition, bat B and also bat D aborted more trials under sparse-

385   overlapping noise compared to silence ($z = 5.2$, $p < 0.001$; $z = 3.8$, $p < 0.001$; **Figure 5**; **Table**

386   **S2**).

387

388   *Echolocation call parameters*

389   We recorded at least one call for most (87.6%) of the 3960 total trials, and at least ten calls for

390   more than half of the trials (57.2%), and used the mean call parameters of each trial in the

391   analysis. Mean call duration ranged from 0.38 ms (bat A) to 0.47 ms (bat C), matching previous

392   results in confined space (Goerlitz et al., 2008; Luo et al., 2015b). All bats increased call

393   duration under smooth-overlapping noise. Coping bats (A and B) increased call duration by an

394   estimated 0.07 ms, while non-coping bats (C and D) only increased call duration by 0.05 ms and

395   0.04 ms (bat A: t = 20.4, $p < 0.001$; B: t = 9.1, $p < 0.001$; C: t = 7.9, $p < 0.001$; D: t = 6.0, $p <$

396   0.001; **Table S3**). Similarly, coping bats increased call duration in sparse-overlapping noise

397   (increase of 0.06 ms and 0.07 ms, A and B respectively), while non-coping bats did not (A: t =

398   15.1, $p < 0.001$; B: t = 9.3, $p < 0.001$; C: t = 1.2, $p = 0.22$; D: t = 1.8, $p = 0.07$; **Figure 6**). Oddly,

399   bats B and C decreased call duration by 0.03 ms and 0.02 ms in non-overlapping noise relative to

400   silence (B: t = -4.1, $p < 0.001$; C: t = -3.8, $p < 0.001$).

401

402   Relative to silence, all bats increased their call sound pressure level in both overlapping noise

403   treatments by about 10-13 dB (smooth overlapping noise: bats A: 11.8 dB; B: 9.7 dB; C: 9.6 dB;

404   D: 13.3 dB (t = 46.1; t = 31.8; t = 33.0; t = 25.8); sparse overlapping noise: A: 12.6 dB; B: 8.7

405   dB; C: 10.5 dB; D: 13.3 dB; (t = 47.4; t = 29.8; t = 37.6; t = 19.8), all $p < 0.001$; **Figure 7**; **Table**

406   **S4**). Additionally, bat A also increased call level during the smooth non-overlapping noise,

407   though by a much lower magnitude of only 1.5 dB (t = 4.7, $p < 0.001$).

408

409   The mean peak frequency was 69.8 kHz (bats A: 71.8 kHz; B: 69.9 kHz; C: 69.6 kHz; D: 67

410   kHz). Of all 12 comparisons, only three showed significant, yet small changes of call frequency

411   with no clear pattern: Bat A increased peak frequency in smooth non-overlapping noise by

412   1.2 kHz, and decreased peak frequency in smooth overlapping noise by 1.4 kHz (t = 3.8, $p <$

413   0.001; t = -4.5, $p < 0.001$). Bat C increased peak frequency by 2.1 kHz only in sparse

414   overlapping noise (t = 5.5, $p < 0.001$; **Figure 8**). Bats B and D never changed their peak

415   frequency (**Table S5**).

416

417

418   **Discussion**

419   We tested the ability of four bats to discriminate increasingly rippled surface structures from a

420   flat surface under silence and three different noise types. By comparing the bats' discrimination

421   performance, behavior, and echolocation parameters, we address the perceptual mechanism of

422 noise disturbance, and how bats may be able to cope with noise disturbance. The individual bats

423 in our experiments responded to noise in varying ways. Two bats (A and B; "coping") were able

424 to cope with all three noise types, as their discrimination performance was not affected by noise.

425 In contrast, the other two bats (C and D; "non-coping") were not able to cope with the noise, yet

426 in different ways. Bat C had decreased discrimination performance in all three noise types, took

427 longer in sparse-overlapping noise, and aborted more trials in smooth-overlapping and smooth

428 non-overlapping noise. Bat D had strongly reduced discrimination performance in both smooth

429 and sparse overlapping noise types (but not in non-overlapping noise), made faster decisions in

430 smooth-overlapping treatments, and aborted more trials only in sparse-overlapping noise. Of the

431 changes in echolocation call parameters, the increase in call level was the most prominent one,

432 and shown by both coping and non-coping bats in response to both overlapping noise types.

433 Changes in call frequency were much smaller and without a clear pattern, while call duration

434 increased slightly more for the coping than the non-coping bats. Based on our predictions both

435 perceptual mechanisms tested, masking and distraction, appeared to contribute to the bats'

436 performance. In the following, we will discuss all measured parameters in relation to our

437 predictions about the perceptual mechanisms of noise disturbance.

438

439 *Discrimination performance (masking vs distraction)*

440 We analyzed the ripple discrimination performance to address the perceptual mechanisms of

441 masking and distraction. Masking should only reduce the performance in overlapping noise, and

442 more so for smooth than sparse overlapping noise. In contrast, distraction should reduce the

443 performance in all noise types, and most so for sparse overlapping noise. Overall, our results do

444 not match those predictions: the coping bats (A and B) showed no decreased performance in any

445 of the noise treatments, excluding masking and distraction. Bat C seemed to suffer from

446 distraction, as its discrimination performance was affected by all noise types. In contrast to our

447 prediction, however, sparse overlapping noise did not reduce performance more than the other

448 noises. Lastly, bat D seemed to suffer from masking, as, in line with our prediction, its

449 discrimination performance was only reduced in both overlapping noise types – yet again

450 without difference between the smooth and sparse noise (in contrast to our prediction). The

451 sparse noise had temporal gaps with a mean duration of 0.3 ms (range: 0-0.6 ms), which is

452 slightly shorter than the average *P. discolor* call here (0.43 ms in silence). Although the detection

453 performance of the gleaning bat *Megaderma lyra* for rustling sounds improved at around this gap

454 duration (Hübner and Wiegrebe, 2003), it is possible that the temporal gaps in the sparse noise

455 were not sufficiently long to provide sufficient release from masking for echo detection in our

456 species *P. discolor, despite similar*ly short *call duration*s of <1 ms in confined spaces (Goerlitz

457 et al., 2008; Schuchmann et al., 2006). Therefore, our prediction that sparse-overlapping noise

458 would allow bats to listen in between the gaps of the noise may be false, and further tests with

459 larger gap widths are required. It is also possible that any release from masking that bats had

460 gained might have been opposed by an additional distracting effect of the sparse-overlapping

461 noise opposes, but this seems less likely than the lack of release from masking.

462

463 *Trial duration (masking vs distraction)*

464 To further differentiate between masking and distraction as perceptual mechanisms, we also

465 analyzed trial duration as a proxy for task difficulty. Only bat C showed a change in line with our

466 predictions, namely a 26% increase in trial duration in sparse overlapping noise, indicative of

467 stronger distraction by this temporally fluctuating noise. This matches our previous interpretation

468 of this bat's discrimination performance, suggesting that this bat was mostly affected by

469 distraction, which should be strongest for the sparse noise. In contrast, the trial durations in

470 smooth-overlapping noise of both the coping bat A and the non-coping bat D was even shorter

471 than in silence, by 13 and 18%, respectively. In the coping bat A, this faster decision making did

472 not reduce the discrimination performance, thus rather indicating reduced task difficulty due to

473 the smooth overlapping noise, which however seems unlikely. In the non-coping bat D, the

474 shorter trial duration might indicate the bat has stopped attempting to complete the task

475 accurately, due to the increased task difficulty by the smooth overlapping noise. This matches

476 our previous interpretation that this bat was affected by masking. However, it is unclear why this

477 bat had equally reduced discrimination performance in sparse overlapping noise, but trial

478 duration was not affected. In summary, trial duration partially supports distraction and masking

479 as perceptual mechanisms of noise disturbance for bats C and D, respectively, but this evidence

480 is not conclusive.

481

482 *Echolocation call characteristics (masking)*

483   Several bat species change echolocation call parameters in response to noise (Bunkley et al.,

484   2015; Hage et al., 2013; Luo et al., 2017; Tressler and Smotherman, 2009), which is a potential

485   mechanism to mitigate masking effects of noise (Brumm, 2013). Thus, we next discuss whether

486   the differences in coping ability (discrimination performance) can be explained by changes in

487   echolocation call parameters. The most prominent change was an increase in call level by around

488   10-13 dB, shown by all four bats (coping and non-coping) in both overlapping noise types

489   (smooth and sparse). This Lombard effect, the increase of vocalization amplitude in response to

490   noise, is found in many animals from birds to humans (Brumm and Zollinger, 2011). Our

491   species, *Phyllostomus discolor*, also exhibits an increasing Lombard effect with increasing noise

492   level, amounting to on average +4 dB for overlapping (40-90 kHz) noise with a level of 52 dB

493   SPL (Luo et al., 2015b). Here, we show that the Lombard effect increases even further up to 10-

494   13 dB when noise levels are higher (70 dB SPL). This increase in call level is likely a direct

495   response to masking (*c.f.* Fig 3 Brumm and Todt, 2002), as only one of the bats (bat A) increased

496   call amplitude in non-masking noise, and this effect was an order of magnitude smaller (+1.5 dB,

497   c.f. Luo et al., 2015b). Interestingly, however, although the reaction in call level was equal across

498   all four bats, only two bats (A and B) were able to cope with masking overlapping noise in the

499   discrimination task, while the other two bats (C and D) showed strongly reduced discrimination

500   performance. If we assume that the increased call amplitude provides equal release from masking

501   for all four bats, another perceptual mechanism instead of masking must be responsible for the

502   reduced discrimination performance of the non-coping bats.

503

504   In addition to increasing call level, increased call duration improves signal detection in noise

505   because the mammalian ear integrates sound intensity over time (Heil and Neubauer, 2003).

506   Indeed, bats increased call duration under noise both in laboratory (Luo et al., 2015b) and field

507   environments (Bunkley et al., 2015). Here, our bats also increased call duration, and did so only

508   in overlapping noise types, suggesting that this was a direct response to masking. We found

509   some differences between coping and non-coping bats. While the coping bats increased call

510   duration by 14-16% in both overlapping noise types (smooth and sparse), the non-coping bats

511   increased their call duration only in the smooth overlapping noise, and only by 9%. At first view,

512   these patterns are consistent that coping bats mitigate noise masking by increasing call duration,

513   while non-coping bats fail to do so. However, the rather small increase in call duration found

514 here improves signal detectability by only about 1 dB (assuming a gain of 6 dB per doubling of
515 call duration; Luo et al., 2015b). This is much less than the direct increase in call level (10-13
516 dB) shown by both coping and non-coping bats, making it unlikely the slight differences in call
517 duration change can explain the differences in discrimination ability.

518

519 Shifting call frequency away from the frequency of a masker is another perceptual mechanism to
520 improve signal detection by reducing spectral overlap, shown by bats when foraging in crowded
521 situations (Bates et al., 2008; Gillam et al., 2007; Ratcliffe et al., 2004) or near loud ultrasonic
522 insect choruses (Gillam and McCracken, 2007). In lower-frequency (5-35 kHz) non-overlapping
523 noise, bat A indeed showed frequency changes consistent with avoiding spectral overlap by
524 increasing its call peak frequency by 1.2 kHz. In contrast, the decrease of its peak frequency
525 around 70 kHz by 1.4 kHz in the higher frequency (40-90 kHz) smooth-overlapping noise is
526 unlikely to improve signal detectability; and correspondingly this bat did not change its peak
527 frequency in the other overlapping noise type (sparse). Bat C increased peak frequency in sparse-
528 overlapping noise only; and the bats B and D showed no response. It is unlikely that such small
529 (≤ 2 kHz) changes in frequency have large effects on call detectability in noise, and thus do not
530 seem insightful for making predictions on the ability of bats to cope with noise.

531

532 *Aborted trials*
533 Lastly, the bats avoided the noise types differently. While the coping bat A did not abort more
534 trials under any noise type compared to silence, the other coping bat B aborted more trials in all
535 three noise types (6.0, 4.9, and 11.8 times more in smooth non-overlapping, smooth-overlapping,
536 and sparse-overlapping noise, respectively). This pattern is suggestive of the noise being
537 interpreted as novel or dangerous, perhaps causing fear (i.e. misleading), since the noise type did
538 not affect the discrimination performance and trial duration in this bat (which we would expect if
539 the bat was masked or distracted). The two non-coping bats showed opposite patterns in the
540 number of aborted trials. Bat C aborted more trials in both smooth noise types (2.4 and 5.9 times
541 more in smooth non-overlapping and smooth overlapping noise, respectively), but not in sparse
542 overlapping noise. The response of bat C might indicate that smooth noise types might be more
543 misleading or fear-inducing, as it cannot be linked to masking or distraction. In contrast, bat D
544 aborted more trials in the sparse overlapping noise only (3.9 times more), but not in the two

545 smooth noise types. It is possible here that the sparse overlapping noise was more distracting

546 than the smooth overlapping noise, causing more trials to be aborted (somehow without affecting

547 discrimination performance).

548

549 *Conclusion*

550 Understanding how echolocating bats deal with noise pollution will be important for their

551 conservation. Additionally, such a mechanistic understanding may also inform the design of

552 noise-based deterrence systems to protect bats from being killed by wind turbines (Arnett et al.,

553 2013). Recent studies have shown that echolocating bats avoid noise in the field and lab, when it

554 is possible (Bunkley et al., 2015; Luo et al., 2015a; Schaub et al., 2008), but as noise sources

555 expand and foraging habitat shrinks, avoidance will become more difficult. Here, when

556 avoidance is impossible, we show that the effects of noise and the underlying perceptual

557 mechanism of disturbance differ at the individual level. It is likely that masking affected all bats,

558 as all of them strongly increased their call levels. However, only two of four bats were able to

559 maintain discrimination performance in noise. Therefore, other perceptual mechanisms, in

560 addition to masking, likely affect signal perception by bats in noise, and probably to different

561 extents for each individual.

562

563 By grouping all individuals of one species, we may miss important differences in how

564 individuals deal with noise (reviewed in Harding et al., 2019). By ignoring variation across

565 individuals, we may be missing the potential for rapid evolution to occur in response to

566 anthropogenic changes (Sih et al., 2011). Noise (or other sensory pollutants) can filter

567 individuals over time by selecting for individuals that can cope with noise. Understanding the

568 variation in the ability to cope with noise is paramount to predicting which species may adapt

569 well to encroaching urbanization, and which will not. It is possible that this variation is

570 maintained in natural systems by individual microhabitat selection, because although natural

571 noise is ubiquitous in nature, it is spatially and temporally heterogeneous across the landscape.

572

573

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584

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Figure 1

Experimental setup and stimuli of the discrimination experiment.

A) Sketch of the experimental setup. The bat could freely move within the mushroom-shaped mesh-cage, allowing simultaneous perceptual access to both discs from multiple angles. Each trial started when the bat left from within the starting box and ended when the bat crossed an infrared light barrier next to each disc, objectively determining decision and duration of each trial. The bat received a food reward for approaching the flat reference disk. Noise treatments were presented via two speakers from similar directions as the returning disc echoes. Echolocation calls were recorded via microphones next to the light barriers. B) Cross-sections of the stimulus discs. The peak-to-peak height of the ripples is scaled to size and given on the right (but the shown distance between ripple peaks is shorter, i.e., higher spatial frequency, than in the experiment for better visualization). As ripple height gets smaller, the task to discriminate the rippled disk from the flat reference disc becomes more difficult, as indicated by the arrow.

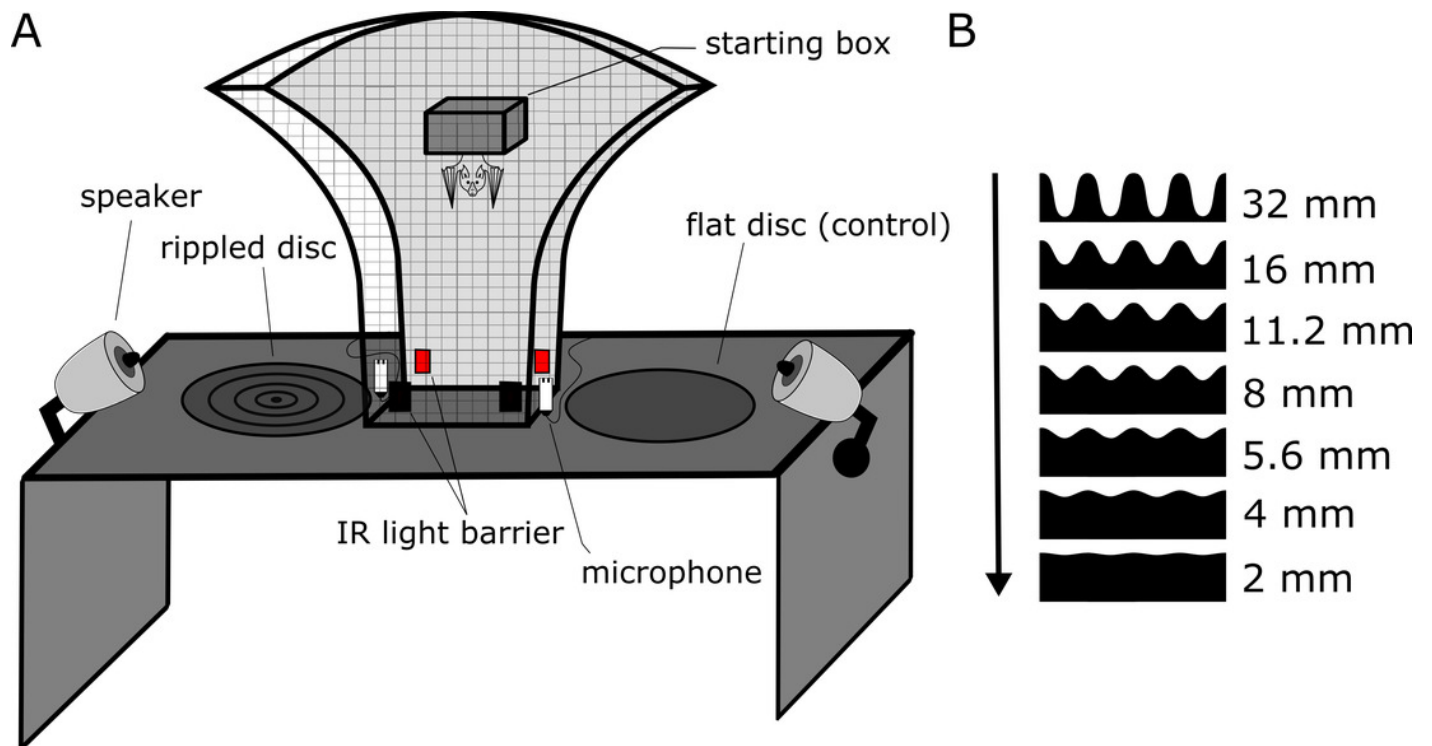



Figure 2

Experimental playback treatments.

Representative echolocation calls of *Phyllostomus discolor* in A) silence (control), B) smooth non-overlapping noise (5-35 kHz), C) smooth overlapping noise (40-90 kHz), and D) sparse overlapping noise (40-90 kHz with additional silent gaps of variable duration introduced between all adjacent noise samples; the duration of the silent gaps was drawn from a uniform distribution that ranged from 0 to 0.6 ms and had a mean value of 0.3ms). Echolocation call is based on Goerlitz et al. 2008.

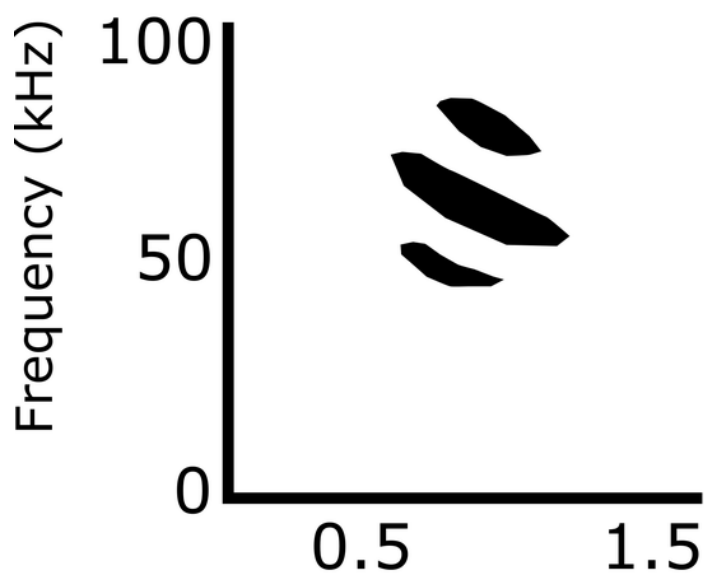
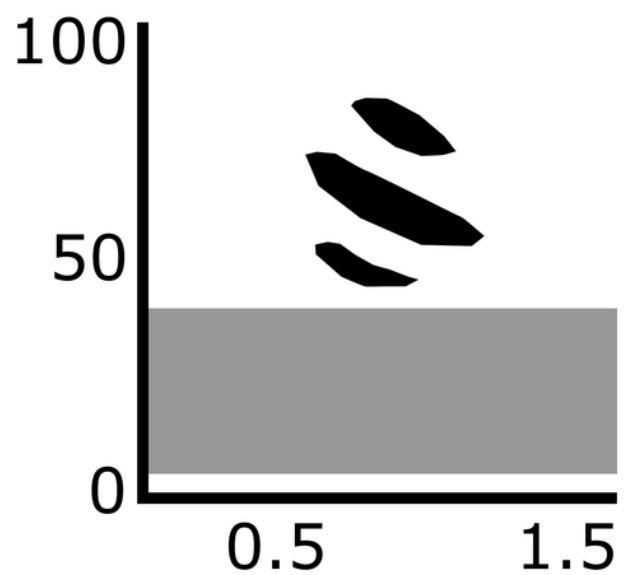
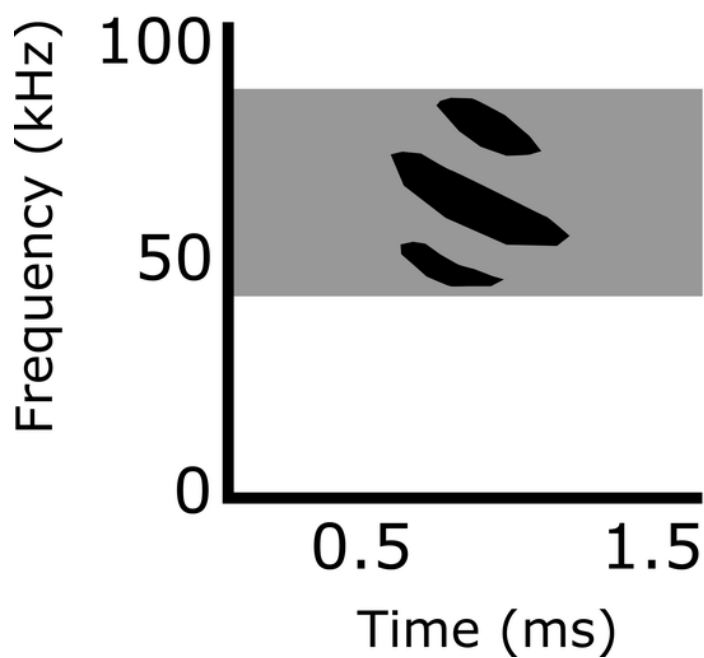
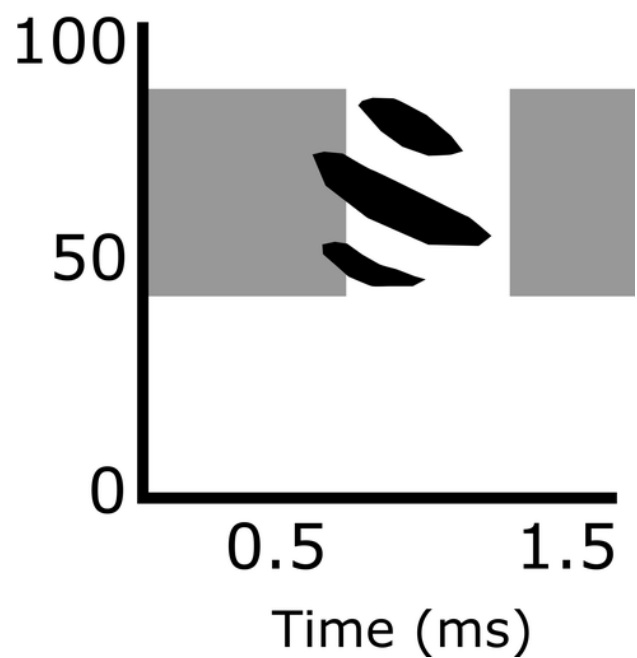



Figure 3

Discrimination performance of four bats as a function of peak-to-peak disc ripple height during silent control and three noise treatments.

Shown are raw data (dots) and the fitted performance curve (colored lines; constrained probit function) for each noise treatment. The discrimination threshold is indicated by the vertical line, with its 95% confidence interval. Discrimination performance of 'coping' bats (A and B) did not differ between silence and noise treatments. In contrast, discrimination performance of 'non-coping' bats (C and D) was reduced under both overlapping noise treatments (blue and purple lines), while discrimination performance of bat C was also reduced in non-overlapping smooth noise (green line). Noise treatments have been abbreviated here (as compared to the text) to reduce visual clutter (smooth non-overlapping noise = "Non-overlap"; smooth-overlapping noise = "Smooth-overlap"; sparse-overlapping noise = "Sparse-overlap"). Asterisks denote that the interaction between noise treatment and ripple height differs significantly ($p < 0.05$) from the silent controls (orange lines) in generalized linear models.

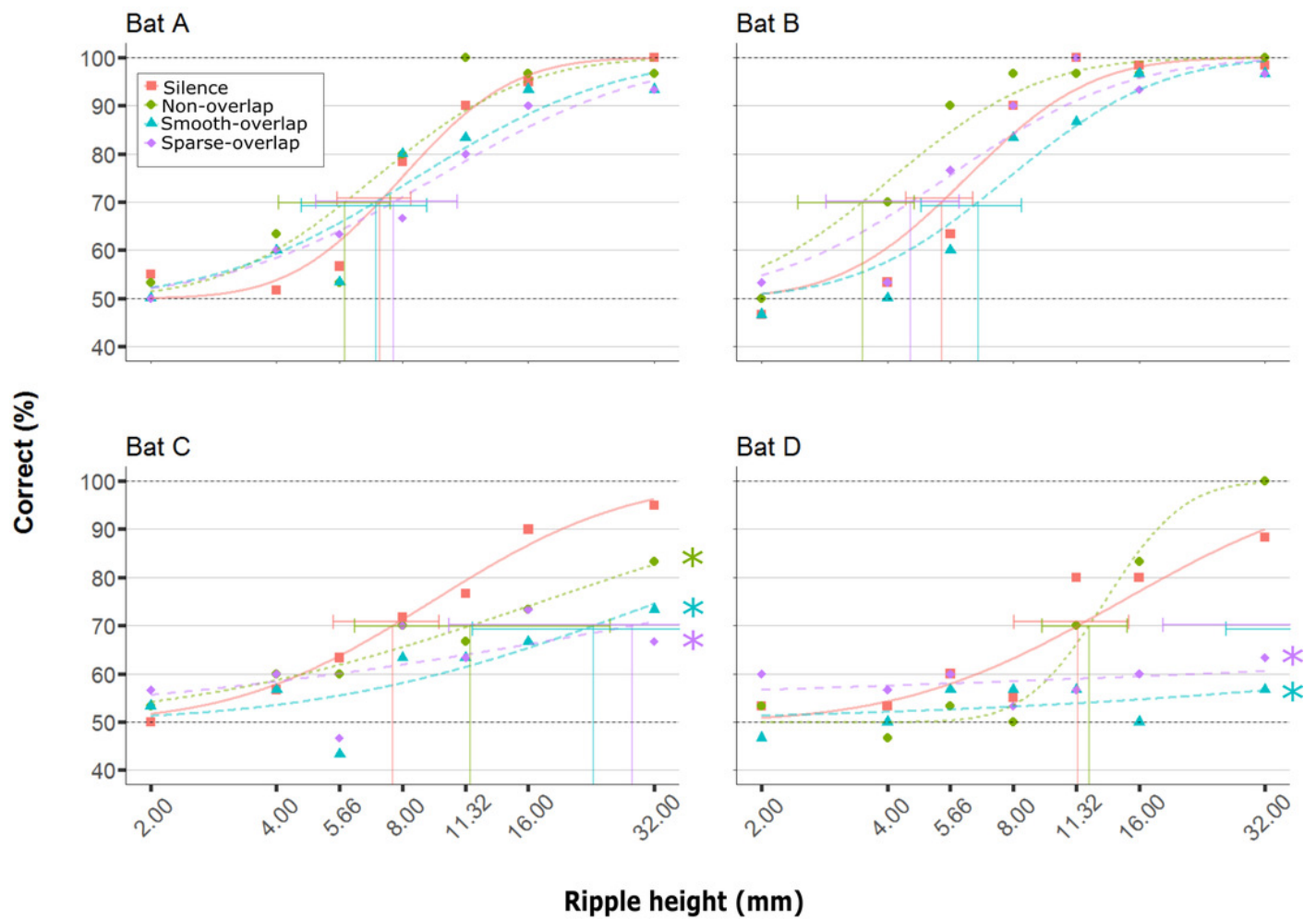



Figure 4

Trial duration of the discrimination task by noise treatment.

Smooth-overlapping noise reduced trial duration of bats A and D, and sparse-overlapping noise increased trial duration of bat C. Box plots show median (solid line) and first and third quartiles (edges of box); whiskers extend to the rest of the data minus outliers (more than 1.5 times the interquartile range), which are shown as points. Noise treatments have been abbreviated here (as compared to the text) to reduce visual clutter (smooth non-overlapping noise = "Non-overlap"; smooth-overlapping noise = "Smooth-overlap"; sparse-overlapping noise = "Sparse-overlap"). Asterisks denote significant differences (p < 0.05) in trial duration relative to the silence control.

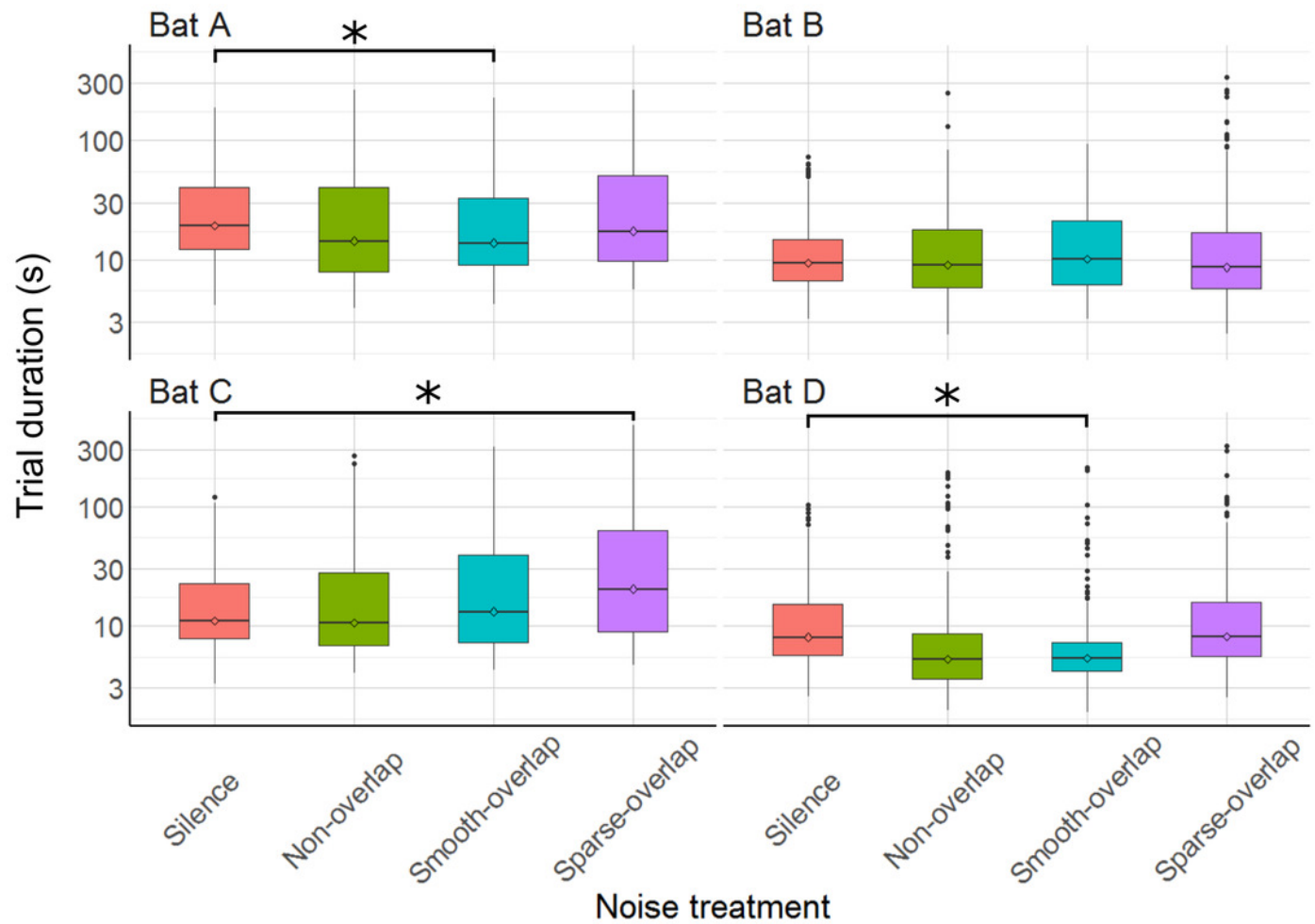



Figure 5

Percentage of aborted trials during the discrimination task by noise treatment.

Both bats B and C aborted significantly more trials for both non-overlapping and overlapping noise. Yet, bats B and D aborted significantly more trials for sparse-overlapping noise. Box plots show median (solid line) and first and third quartiles (edges of box); whiskers extend to the rest of the data minus outliers (more than 1.5 times the interquartile range), which are shown as points. Noise treatments have been abbreviated here (as compared to the text) to reduce visual clutter (smooth non-overlapping noise = "Non-overlap"; smooth-overlapping noise = "Smooth-overlap"; sparse-overlapping noise = "Sparse-overlap"). Asterisks denote significant differences (p < 0.05) in the percentage of aborted trials relative to the silence control.

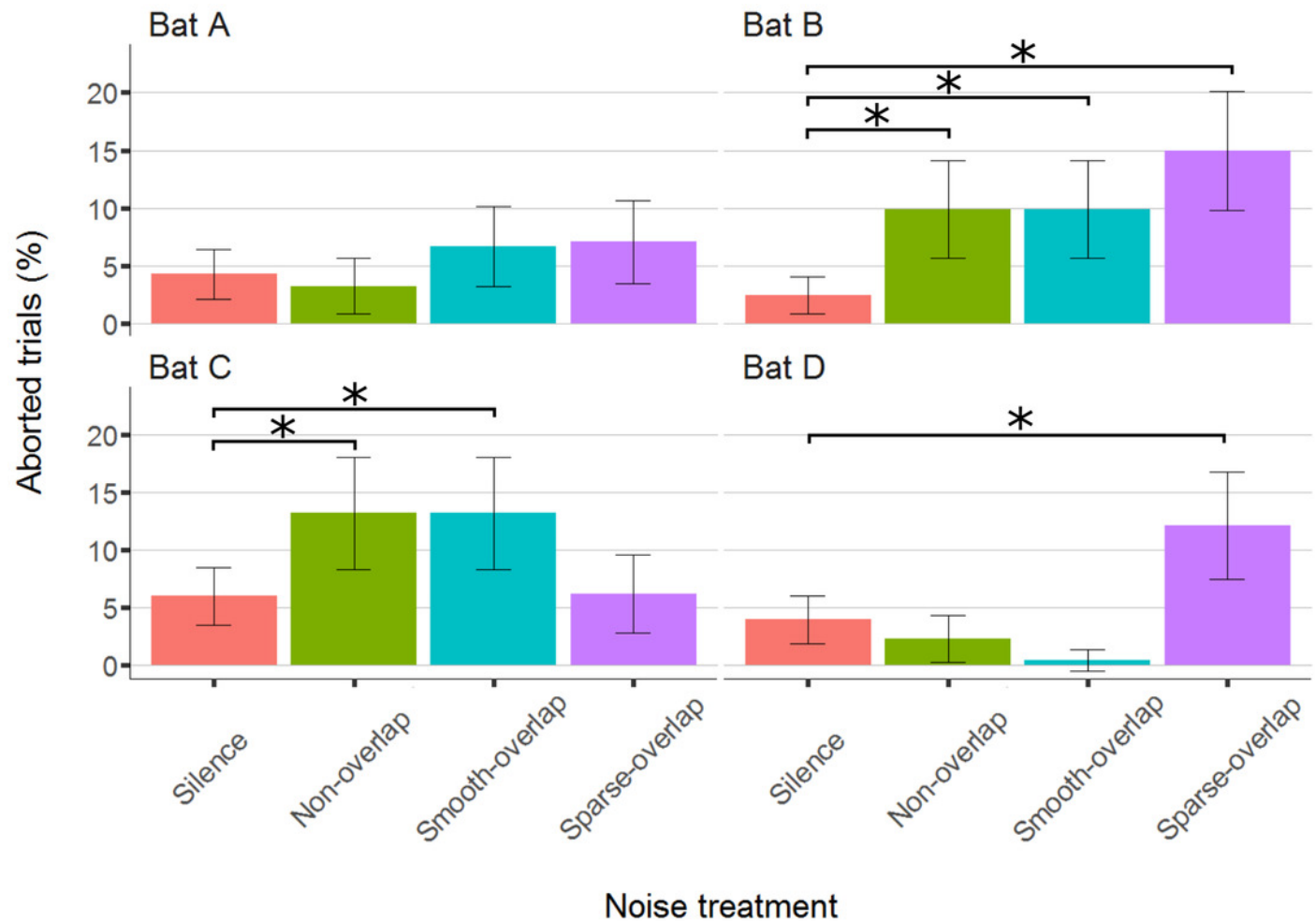



Figure 6

Duration of echolocation calls during the discrimination tasks by noise treatment.

All bats increased call duration under smooth-overlapping noise, and bats A and B also increased call duration under sparse-overlapping noise. Box plots show median (solid line) and first and third quartiles (edges of box); whiskers extend to the rest of the data minus outliers (more than 1.5 times the interquartile range), which are shown as points. Noise treatments have been abbreviated here (as compared to the text) to reduce visual clutter (smooth non-overlapping noise = "Non-overlap"; smooth-overlapping noise = "Smooth-overlap"; sparse-overlapping noise = "Sparse-overlap"). Asterisks indicate significant differences (p < 0.05) of call duration relative to the silence control.

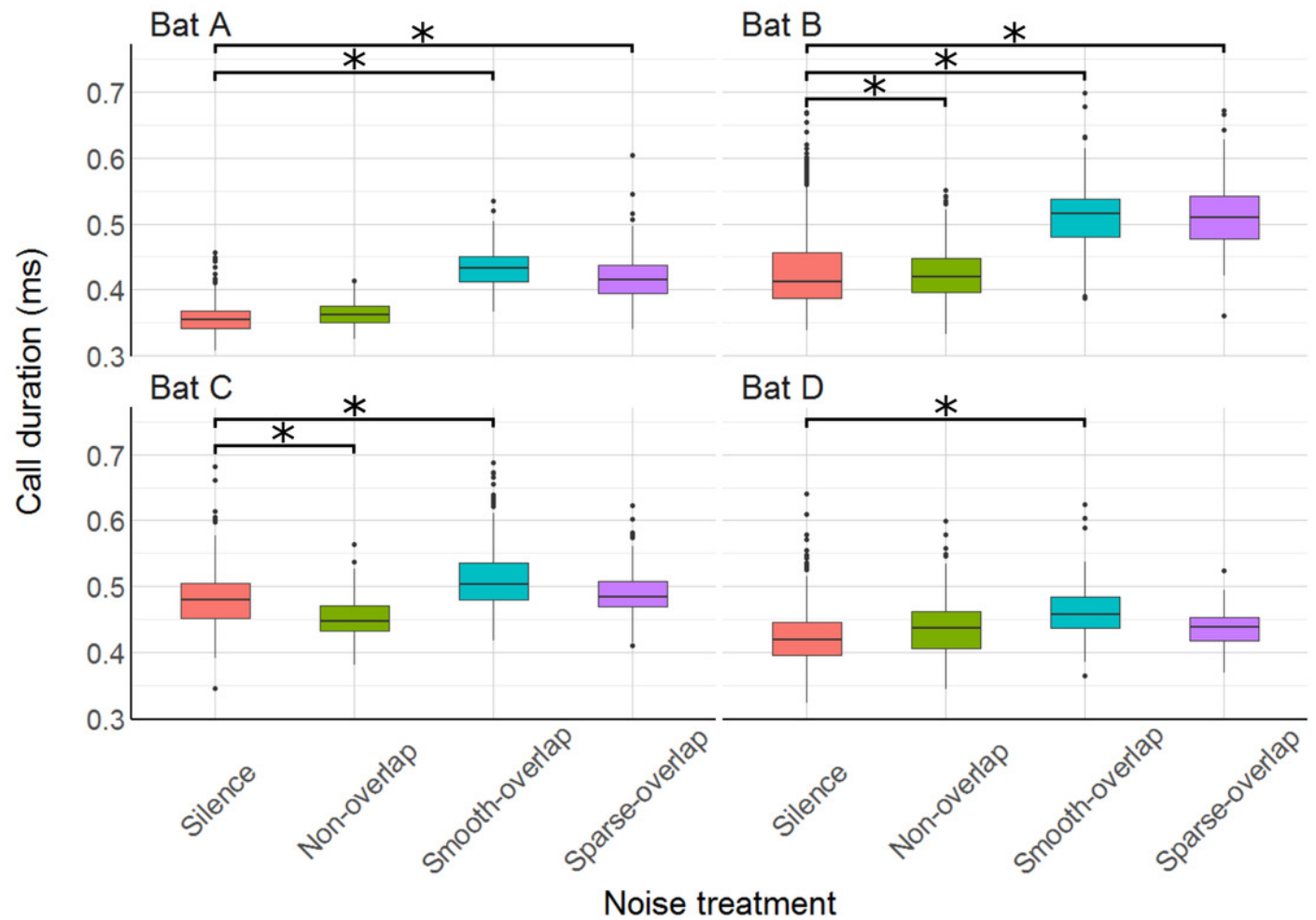



Figure 7

Relative sound pressure level of echolocation calls during the discrimination tasks by noise treatments.

All four bats significantly increased call level under both smooth- and sparse-overlapping noise. Only bat A also increased call level under smooth non-overlapping noise, and this change was much smaller. Box plots show median (solid line) and first and third quartiles (edges of box); whiskers extend to the rest of the data minus outliers (more than 1.5 times the interquartile range), which are shown as points. Noise treatments have been abbreviated here (as compared to the text) to reduce visual clutter (smooth non-overlapping noise = "Non-overlap"; smooth-overlapping noise = "Smooth-overlap"; sparse-overlapping noise = "Sparse-overlap"). Asterisks denote significant differences (p < 0.05) relative to the silence control.

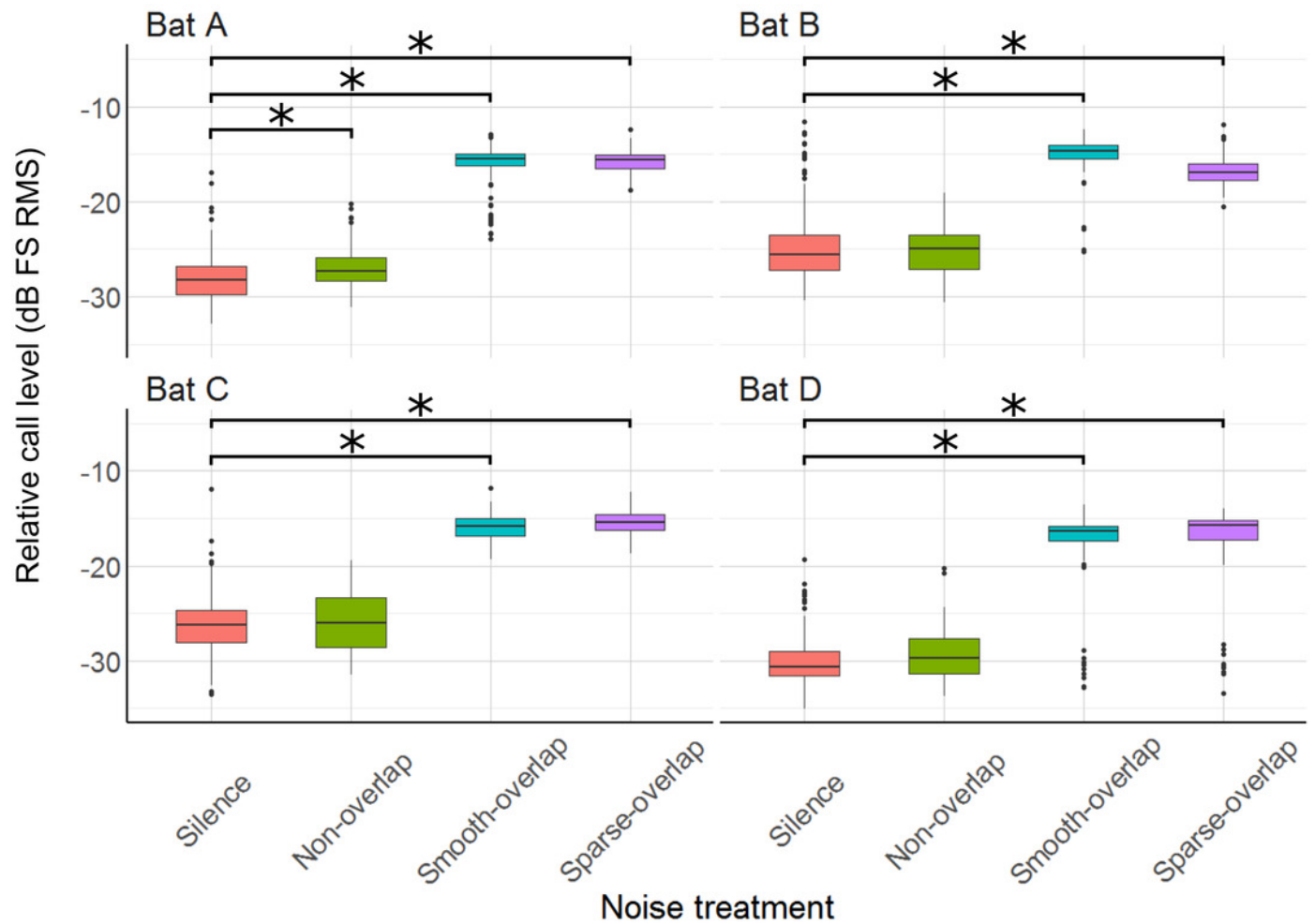
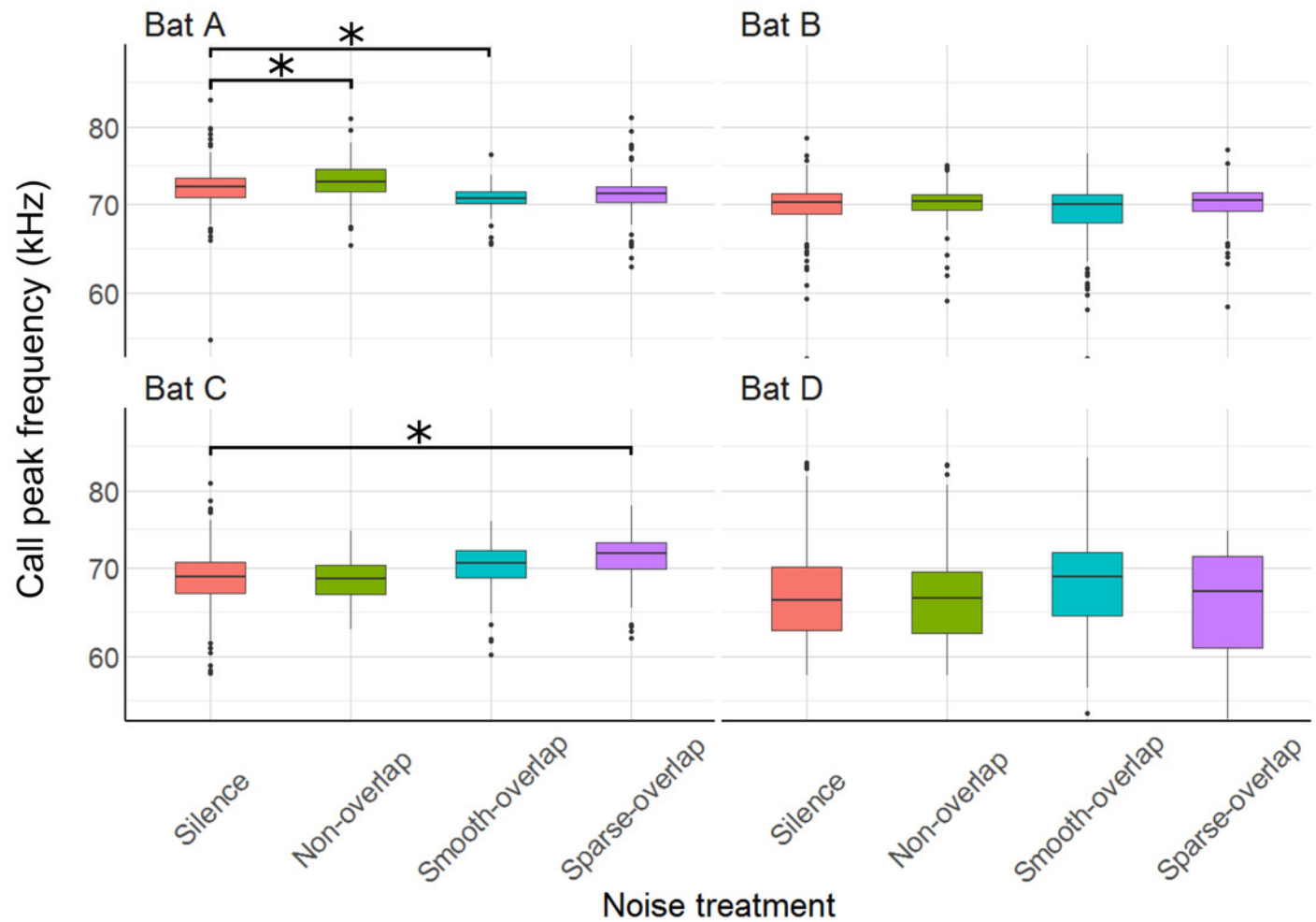



Figure 8

Peak frequency of echolocation calls during the discrimination tasks by noise treatment.

Peak frequency of bat A increased under smooth non-overlapping noise and decreased under smooth overlapping noise. Peak frequency of bat C increased under sparse-overlapping noise. Box plots show median (solid line) and first and third quartiles (edges of box); whiskers extend to the rest of the data minus outliers (more than 1.5 times the interquartile range), which are shown as points. Noise treatments have been abbreviated here (as compared to the text) to reduce visual clutter (smooth non-overlapping noise = "Non-overlap" here; smooth-overlapping noise = "Smooth-overlap" here; sparse-overlapping noise = "Sparse-overlap" here). Asterisks denote significant differences ($p < 0.05$) relative to the control treatment.

Results from generalized linear models for discrimination performance in various noise treatments.

Model results show the estimated differences in discrimination performance (relative to control trials) for the three noise treatments, ripple height, the number of days the bat was in the experiment, and the interaction between each noise treatment and ripple height (i.e. the shape of each performance curve as a function of ripple height), separately for each bat. Data were analyzed with binomial distribution and logit link function. Noise treatments have been abbreviated here (as compared to the text) to reduce visual clutter (smooth non-overlapping noise = "Non-overlap"; smooth-overlapping noise = "Smooth-overlap"; sparse-overlapping noise = "Sparse-overlap").

Bat	Variable	Estimate	SE	Z value	p value
A	(Intercept)	-0.766	0.275	-2.791	0.02
A	Non-overlap	0.228	0.521	0.438	0.987
A	Smooth-overlap	0.317	0.423	0.749	0.911
A	Sparse-overlap	0.544	0.447	1.216	0.637
A	Ripple height	0.294	0.047	6.222	<0.001
A	Day of experiment	0.110	0.095	1.165	0.673
A	Non-overlap:Ripple height	0.079	0.099	0.798	0.891
A	Smooth-overlap:Ripple height	-0.096	0.064	-1.504	0.435
A	Sparse-overlap:Ripple height	-0.088	0.069	-1.265	0.603
B	(Intercept)	-0.544	0.243	-2.240	0.096
B	Non-overlap	0.200	0.412	0.486	0.981
B	Smooth-overlap	0.441	0.377	1.171	0.668
B	Sparse-overlap	0.490	0.364	1.346	0.543
B	Ripple height	0.216	0.036	6.082	<0.001
B	Day of experiment	0.003	0.107	0.025	1
B	Non-overlap:Ripple height	-0.012	0.059	-0.209	0.999
B	Smooth-overlap:Ripple height	-0.091	0.048	-1.905	0.209
B	Sparse-overlap:Ripple height	-0.109	0.045	-2.405	0.062
C	(Intercept)	-0.130	0.200	-0.649	0.945
C	Non-overlap	0.277	0.312	0.888	0.847
C	Smooth-overlap	0.228	0.305	0.745	0.912
C	Sparse-overlap	0.433	0.298	1.451	0.471
C	Ripple height	0.118	0.022	5.465	<0.001
C	Day of experiment	-0.071	0.087	-0.817	0.882
C	Non-overlap:Ripple height	-0.071	0.028	-2.518	0.047
C	Smooth-overlap:Ripple height	-0.085	0.027	-3.157	0.008
C	Sparse-overlap:Ripple height	-0.100	0.027	-3.726	<0.001
D	(Intercept)	-0.069	0.177	-0.387	0.992
D	Non-overlap	-0.486	0.327	-1.487	0.445
D	Smooth-overlap	0.118	0.278	0.422	0.989
D	Sparse-overlap	0.280	0.283	0.990	0.789
D	Ripple height	0.074	0.015	4.937	<0.001
D	Day of experiment	0.085	0.076	1.129	0.699
D	Non-overlap:Ripple height	0.060	0.033	1.832	0.242
D	Smooth-overlap:Ripple height	-0.066	0.021	-3.179	0.004
D	Sparse-overlap:Ripple height	-0.066	0.021	-3.141	0.008

Threshold of the discrimination performance for ripple detection.

The threshold is the ripple height where bats exceeded a 0.7 probability of a correct choice. For each bat, 1000 simulated discrimination thresholds were generated with a binomial generalized linear model. The lower 0.025 and upper 0.975 percentiles of those data give lower and upper values of the 95% confidence intervals. Noise treatments have been abbreviated here (as compared to the text) to reduce visual clutter (smooth non-overlapping noise = "Non-overlap"; smooth-overlapping noise = "Smooth-overlap"; sparse-overlapping noise = "Sparse-overlap").

Noise	*p*	Threshold	Bat	Lower 95% CI	Upper 95% CI
Silent (Control)	0.7	7.05	A	5.57	8.37
Silent (Control)	0.7	5.39	B	4.42	6.41
Silent (Control)	0.7	7.58	C	5.47	9.81
Silent (Control)	0.7	11.42	D	8.02	15.14
Non-overlap	0.7	5.83	A	4.05	7.49
Non-overlap	0.7	3.49	B	2.44	4.63
Non-overlap	0.7	11.62	C	6.16	25.07
Non-overlap	0.7	12.14	D	9.37	14.98
Smooth-overlap	0.7	6.91	A	4.59	9.15
Smooth-overlap	0.7	6.60	B	4.81	8.38
Smooth-overlap	0.7	22.92	C	11.77	702.42
Smooth-overlap	0.7	621.33	D	25.87	>100000
Sparse-overlap	0.7	7.63	A	4.97	10.81
Sparse-overlap	0.7	4.54	B	2.85	5.95
Sparse-overlap	0.7	28.40	C	10.32	>100000
Sparse-overlap	0.7	4395.17	D	18.24	>100000