

1 **Title**

2 Full: Female Bengalese finches recognize their father's song as sexually attractive

3 Short: Sexual preference for father's song in female Bengalese finches

4

5 **Authors**

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13 **Abstract**

14 Birdsong is an important communication signal used in mate choice. In some songbirds,
15 only males produce songs while females do not. Female birds are sensitive to inter- and intra-species
16 song variation. Some aspects of female song preference depend on developmental experiences. For
17 example, in Bengalese finches and zebra finches, adult females prefer the song to which they were
18 exposed early in life, such as the father's song. However, it is unclear whether such song preference
19 in females is sexually motivated. The purpose of our study is to test if female Bengalese finches
20 recognize their father's song as sexually attractive. We measured copulation solicitation displays
21 during playbacks of the father's song vs. unfamiliar conspecific songs and found that across
22 individuals, the father's song elicited more displays than other songs. In addition, we analyzed if a
23 bird's response to a given song could be predicted by the level of similarity of that song to the father's
24 song. The results suggest that preference for the father's song in this species is actually relevant to
25 mate choice. Although more precise control is necessary in future studies to elucidate the process of
26 preference development, our results imply the significance of early-life experience in shaping female
27 song preference.

28 **Introduction**

29 Song is an important communication signal used for mate choice in songbirds [1]. In some
30 species of songbirds, only males produce songs. While females do not sing, they can perceive inter-
31 and intra-species song variations and change their behavior depending on features of the song that
32 reflect the sex, species, and condition of the signaler [2]. For example, female birds selectively respond
33 to conspecific songs over heterospecific ones [3–5]. In some species, this preference seems to be a
34 common tendency across individuals that develops independent of experience after hatching [6,7].
35 However, developmental experience plays a significant role in shaping other aspects of female song
36 preference. A cross-fostering study in the zebra finch (*Taeniopygia guttata*) demonstrated that
37 recognition of a subspecies based on song depends on auditory experience with the foster father’s song
38 [8]. Early-life song exposure in this species is also critical to be able to discriminate song quality [7]
39 or song performance related to social context [9].

40 In addition, developmental experience might be an important source of individual
41 differences in song preference. Previous studies in zebra finches and Bengalese finches (*Lonchura*
42 *striata* var. *domestica*) found that females prefer songs to which they were exposed early in life, such
43 as the father’s song [10–15]. These studies clearly show that female birds acquire and retain an ability
44 to discriminate their (foster) father’s song from other songs, but it is not clear whether such song
45 preference is sexually motivated. Although the possibility of sexual imprinting on the father’s song

46 has already been discussed in some literature [10,14], the idea has not yet been directly tested. Because
47 in these previous studies preference was measured by behaviors such as approach to sound sources
48 [10,11,15] or operant behaviors associated with song playback [13,14], the results could be interpreted
49 as either general selectivity to a familiar stimulus or as a sexual response in the context of mate choice.
50 Likewise, from the perspective of adaptation, it is not clear if preference for a trait similar to that of
51 the parents actually increases an animal's fitness [16–18]. Some studies in songbirds and other bird
52 taxa indicate that memorizing the traits of parents is a possible strategy for kin recognition to avoid
53 inbreeding [19,20]. Therefore, elucidating why birds prefer their father's song over unfamiliar
54 conspecific songs is important for a deeper understanding of female mate choice.

55 In the current study, we aimed to test whether adult female Bengalese finches recognize
56 their father's song as a sexually attractive signal. To meet this purpose, we measured copulation
57 solicitation displays (CSDs) in response to song playback. CSD is a typical posture that females
58 perform when they accept male courtship, and researchers have utilized it as a reliable index of sexual
59 motivation in response to songs [21–23]. We also analyzed if song preference in our subjects could be
60 predicted by the similarity of the stimulus to the father's song.

61

62

63 **Methods**

64 **Animals**

65 We used 10 adult female Bengalese finches as subjects for the song preference test. They
66 were obtained from 8 different clutches in our laboratory colony. For breeding, 15 adult finches were
67 used (7 males and 8 females; one male was paired with 2 different females successively). The 15 adults
68 were either bred in our laboratory or purchased from a commercial breeder. The female subjects were
69 raised by both parents and housed with their families (parents and siblings) in a home cage (size: 30
70 cm wide × 24 cm deep × 33 cm high) until approximately 120 days post hatch (dph). Each home cage
71 was placed in a colony room but visually isolated from one another. The female subjects were kept in
72 a single-sex group cage (37 × 42 × 44 cm) after separation from the parents and male siblings (if any).
73 The number of birds kept in a group cage ranged from 6 to 14. All subjects were sexually mature at
74 the beginning of the experiment (mean age = 279 dph, range = 164-376 dph). No birds had experienced
75 breeding prior to the current study. For the preparation of song stimuli, 19 adult (> 180 dph) male
76 Bengalese finches were used, 7 of which were fathers of the subjects described above.

77 All birds were kept under a 14:10 h light:dark cycle with food and water provided ad libitum.
78 They were also fed oyster shell and greens once a week. The temperature and humidity were
79 maintained at around 25 °C and 60%, respectively. After finishing all the experiments, the subjects,
80 their parents, and the birds used for stimulus recordings continued to be housed in our colony for
81 additional research. All experimental procedures in this study were approved by the Institutional

82 Animal Care and Use Committee at the University of Tokyo (permission #27-9 and #2020-2).

83 **Song preference test**

84 Briefly, we designed a playback experiment to test if females perform more CSDs to their
85 father's song compared to unfamiliar conspecific songs. The overall schedule of the experiment is as
86 follows: the birds first received a hormone implant, then they were moved to the experimental
87 environment for acclimation and isolation from males, and finally they were tested with song playback
88 (Fig. 1(a)).

89

90 **Fig 1. Experimental schedule and stimuli.** (a) Overall schedule of the experiment. Each line above
91 the horizontal axis indicates the period in which birds were under that manipulation. The start of the
92 song playback test was set as day zero. (b) A schematic diagram of the stimulus presentation schedule
93 in a single test. Five songs, each composed of 6 renditions (6 rectangles in the figure) were played. (c)
94 A spectrogram of one rendition of the song stimulus is shown as an example.

95

96 **Hormone implantation surgery**

97 Female songbirds seldom perform CSDs in response to song playback alone in the
98 laboratory, but studies have shown that subcutaneous implantation of estradiol increases this behavior
99 [21]. Thus, we adopted this hormone implantation method in our experiment and confirmed that the

100 method did indeed increase CSDs in response to song playback (S1 File). Following a previous study
101 using the same bird species [22], we administered 17β -estradiol (E2758, Sigma Aldrich) in silastic
102 tubing with a 1.0 mm inner diameter (100-0N, Kaneka medical products) containing 8 mm of hormone
103 in powder form. During the surgery, a bird was manually restrained, and lidocaine (Xylocaine,
104 AstraZeneca) was applied onto the skin for local anaesthesia. A small incision was made in the skin
105 on the bird's back and a tube filled with hormone was inserted subcutaneously. The test period started
106 6 – 10 days after the surgery (Fig. 1(a)). After finishing all the tests, local anaesthesia was again
107 applied to the bird's back and the hormone tube was excised. From the day of implantation, we
108 continued to monitor the physical condition of the birds every day until a few days after the tube
109 removal.

110 **Preparation and presentation of song stimuli**

111 In the song preference tests, we presented 5 different conspecific songs to each subject: the
112 father's song and 4 unfamiliar songs. Females had never been exposed to these 4 unfamiliar songs
113 prior to the experiment. We presented the song of one subject's father to 2 or 3 other subjects (that
114 hatched in a different clutch) to exclude the possibility that a particular characteristic of a given song
115 generally attracts females, independent of experience.

116 To prepare stimuli, we recorded songs from adult male Bengalese finches in a soundproof
117 chamber through a microphone (PRO35, Audio-technica) fixed at the top of the cage. The signal from

118 the microphone was amplified (QuadMic, RME) and digitized (Delta66, M-AUDIO) at 16 bits with a
119 44.1 kHz sampling rate. All recordings were undirected songs, as each bird was kept alone in the
120 chamber during recording. For each male singer, we randomly selected 6 renditions of songs that were
121 recorded without any background noise (Fig. 1(c)). The duration of a single song rendition was 7.04
122 ± 0.64 (mean $\pm s.d.$) seconds. The sound waveform was first band-pass filtered at 0.5 – 10 kHz. We
123 normalized the sound amplitude by the standard deviation of the waveform. For each singer, a song
124 was composed of 6 song renditions presented with a 700-ms interval between each rendition (thus
125 approximately 45 seconds in total, Fig. 1(b)). The order of the 6 renditions within a song was
126 randomized each time. Song stimuli were played back from a loudspeaker (MM-SPL2N2, SANWA
127 Supply) positioned next to the test cage. The equivalent continuous A-weighted sound pressure level
128 was measured at a point in the test cage that was 22.5 cm away from the speaker and adjusted to
129 approximately 67 dB using a sound level meter (NL-27, Rion).

130 **Environment and procedure for song preference tests**

131 Preference tests were conducted in a test cage ($30 \times 24 \times 33$ cm) placed in a sound
132 attenuation room ($163 \times 163 \times 215$ cm). The light:dark cycle, temperature, and humidity of the testing
133 environment was the same as in the colony room. Subjects were moved to the test cage in a group of
134 either 3 or 4 birds (10 birds were divided into 3 groups) at least 3 days prior to the first test. The
135 purpose of this was to acclimate the birds to the testing environment as well as to isolate them from

136 the males both socially and acoustically. The cage mates stayed together in the test cage during the
137 whole testing period. However, just before and during a test, birds other than the test subject were
138 moved to another soundproof chamber. A subject was isolated in the test cage 30 - 60 minutes before
139 the start of song playback until the end of the test. All cage mates were returned to the test cage as
140 soon as the test was finished.

141 In a single test, 5 songs (each consisting of 6 renditions) were played back in a random order
142 (Fig. 1(b)). The inter-stimulus-interval was a random value ranging from 40 to 45 seconds. Thus, the
143 duration of one test was approximately 450 seconds. Since some birds did not perform any CSDs in a
144 test, the following criterion was set. We defined a valid test as one in which the subject expressed at
145 least one CSD (in other words, a test was regarded invalid if she did not express any CSDs). We
146 continued testing each female until 5 valid tests were obtained for that individual. One out of the 10
147 birds failed to meet the criterion due to health issues. We ceased testing that bird after 4 valid tests.
148 The total number of tests required to reach the criterion varied between individuals (mean = 6.3 tests
149 range = 5-9 tests). Each bird was tested once every 2 days to avoid habituation to stimuli. Thus, the
150 test period for a subject lasted for 10-18 days, depending on the number of tests required. All the tests
151 were conducted in the morning (7:00AM – 12:00PM).

152 **Recording and quantification of behavior**

153 A web camera (BSW200MBK, Buffalo) recorded the movement and posture of subjects

154 during the tests. The frame rate and sampling rate for video and audio recordings were 16 Hz and 44.1
155 kHz, respectively. The experimenter analysed the videos with the sound muted and had no access to
156 any information regarding stimulus presentation order until the end of analysis, in order to minimize
157 the effect of observer bias in behavioral quantification. For each stimulus in each test, we recorded the
158 occurrence of CSDs performed during the song presentation period. A typical CSD could be
159 recognized relatively easily: the bird usually tilted her head and chest down, with her tail feather raised
160 and quivering [24], as already described in other literature [22,25]. Across individuals, there were
161 variations in the number of CSD bouts performed, the duration of bouts, and the posture displayed
162 during CSDs. However, it was technically difficult to quantitatively code the response based on these
163 features. Thus, we analyzed their response based on whether or not a bird performed CSDs in a trial
164 (a song presentation in a test). For the analysis, data from all tests (both valid and invalid) in all subjects
165 was used. The response rate for each stimulus was calculated as the number of tests in which a bird
166 showed CSDs to that song divided by the total number of tests. We used this rate for description and
167 figure illustration purposes but used the actual number of tests showing CSDs in the GLMM analysis
168 detailed below.

169 **Evaluation of song similarity**

170 If the development of female song preference depends on auditory experience with the
171 father's song, it can be expected that a bird's response to a given song is predicted by the similarity

172 between that song and the father's song. To test this possibility, for each unfamiliar song stimulus, we
173 calculated the acoustical and temporal similarity to the father's song and analysed if these similarity
174 indices predicted CSD frequency. For the evaluation of acoustical similarity, we applied the similarity
175 measurement function (with asymmetric and time-courses mode) in Sound Analysis Pro 2011 [26] to
176 the wave file data of song stimuli used in our song preference tests. For the similarity calculation, each
177 song rendition was divided into 3 segments (duration of a segment = 2.00 ± 0.11 (mean \pm *s.d.*)
178 seconds). Thus, the total number of files per stimulus was 18 (3 segments \times 6 renditions). For every
179 combination of segments between an unfamiliar song and the father's song ($18 \times 18 = 324$
180 combinations), the similarity value was computed and the mean value across these combinations was
181 used as a representative value. To evaluate temporal similarity, we measured the song tempo, which
182 is defined as the number of syllables divided by the duration from the first syllable onset to the last
183 syllable offset. The mean song tempo of 6 renditions was used for each song. We then calculated the
184 tempo difference (absolute value) between a given unfamiliar song and the father's song.

185 **Statistical analyses**

186 To statistically test if females showed more CSDs to the father's song compared to
187 unfamiliar songs, we fitted a generalized linear mixed model (GLMM) to a dataset [27] of all tests
188 from all subjects. In the model, the dependent variable was the occurrence of CSDs in a given trial.
189 The bird's response was binarily coded as 0/1 (not performed/performed), respectively. The type of

190 song stimulus (unfamiliar/father's coded as 0/1) and song presentation order within a test (1-5) were
191 the fixed effects of independent variables. Subject ID (10 levels), stimulus ID (19 levels), and test
192 numbers (9 levels) were also included as random effects. The binomial distribution with a logit link
193 function was specified to represent the probability distribution.

194 We next analyzed the possible effect of song similarity in the prediction of female response
195 using a GLMM. In this analysis, we used trials of unfamiliar song playbacks from 7 birds that
196 responded to at least 1 unfamiliar song [27]. The total number of trials was 176. The response rate to
197 unfamiliar songs was low, and birds only responded in 17 trials. We fitted a model to test if acoustical
198 and/or temporal similarity to the father's song predicts female response to unfamiliar songs. The
199 dependent variable was the occurrence of CSDs coded as 0/1 (not performed/performed), and binomial
200 distribution with logit link function was specified. The SAP % similarity value, absolute value of the
201 tempo difference, and song presentation order were the fixed effects of independent variables. Subject
202 ID (7 levels), stimulus ID (17 levels), and test numbers (8 levels) were included as random effects.

203 GLMM estimation and statistical tests were conducted using R version 4.0.2 [28]. We used
204 lme4 [29] and lmerTest [30] packages for GLMM analysis. In all the GLMM analysis, models were
205 fitted using maximum likelihood estimation (Laplace approximation). For estimating the coefficients
206 and their standard errors, z -value (Wald statistics) and p -value were calculated and reported in the
207 results. For plotting data and fitting logistic regression curves, a Python-based package (SciPy version

208 0.19.0) was used.

209

210

211 **Results**

212 We first examined if female Bengalese finches performed more CSDs in response to
213 playback of the father's song compared to unfamiliar conspecific songs. In all of the subjects we tested,
214 the father's song elicited more frequent responses compared to the 4 other songs. The mean response
215 rate to the father's song and the second-preferred unfamiliar song was 0.790 ± 0.209 and 0.223 ± 0.193
216 (mean \pm *s.d.*), respectively (Fig. 2). The results of GLMM estimation indicated that the type of song
217 stimulus (unfamiliar/father's) was the strongest predictor of the birds' response ($\beta \pm$ *s.e.* = $4.499 \pm$
218 0.544 , $z = 8.278$, $p < 0.001$; Table 1). The presentation order within a test also significantly affected
219 the birds' response, although the estimated effect was relatively smaller than that of the song type (β
220 \pm *s.e.* = -0.346 ± 0.151 , $z = -2.297$, $p = 0.022$).

221

222 **Fig 2. Females performed more CSDs to their father's song.** Response rate of CSDs to each
223 stimulus ($n = 10$). Five songs are aligned in descending order of response rate. Dots connected with
224 broken lines show individual data, while bars indicate the population mean.

225

226 **Table 1. Effect of song type on females' response**

Independent variables	Estimates		<i>z</i> -value	<i>p</i> -value
Fixed effects	coefficient	<i>s.e.</i>		
Intercept	-1.957	0.598		
song type (unfam/father = 0/1)	4.499	0.544	8.278	< 0.001
presentation order (1-5)	-0.346	0.151	-2.297	0.022
Random effects	variance	<i>s.d.</i>		
subject ID (10 levels)	1.002	1.001		
stimulus ID (19 levels)	0.000	0.000		
test number (9 levels)	0.234	0.484		

227 Estimated parameters of the GLMM are shown. Independent variables with a *p*-value less than 0.05
 228 are indicated in boldface.

229

230 We next conducted a post hoc analysis on whether similarity of a song stimulus to the
 231 father's song predicted responses in the 7 birds that expressed CSDs to both song types (Fig. 3).
 232 Among the independent variables included in the GLMM, presentation order within a test was the
 233 strongest predictor of the response (Table 2). As with the result in Table 1, a song was more likely to
 234 elicit CSDs when it was presented earlier in a test (Fig. 3 (c)). Although there was a tendency for
 235 unfamiliar songs to elicit more frequent CSDs when these songs had greater similarity to the father's
 236 song (higher SAP % similarity, lower tempo difference, Fig. 3(a), (b)), this result was not statistically
 237 significant (Table 2). The overall results imply that female Bengalese finches in our study did
 238 recognize their father's song as an attractive courtship signal, but we cannot not conclude whether

239 their mate choice is affected by song features that are shared with their father's song.

240

241 **Fig 3. Analysis of song similarity.** CSD response was plotted against the **(a)** acoustical similarity
242 (SAP % similarity), **(b)** temporal similarity (absolute value of tempo difference) of a given unfamiliar
243 song to the father's song, or **(c)** presentation order within a test (1-5). In all the panels, 0 and 1 on the
244 vertical axis means 'not performed' or 'performed', respectively. Each data point corresponds to one
245 trial. Thus, there are 176 data points from 7 birds in total (17 points are plotted on 'performed'). The
246 lines and surrounding bands are the logistic regression curve with 95% confidential interval computed
247 by bootstrapping method (iteration $n = 1000$).

248

249 **Table 2. Effect of song similarity on females' response to unfamiliar songs**

Independent variables	Estimates		<i>z</i> -value	<i>p</i> -value
Fixed effects	coefficient	<i>s.e.</i>		
Intercept	-3.369	2.195		
SAP % similarity	0.068	0.039	1.745	0.081
tempo difference	-0.196	0.293	-0.667	0.504
presentation order (1-5)	-0.684	0.242	-2.828	0.005
Random effects	variance	<i>s.d.</i>		
subject ID (7 levels)	0.291	0.540		
stimulus ID (17 levels)	0.000	0.001		
test number (8 levels)	0.288	0.536		

250 Estimated parameters of the GLMM are shown. Independent variables with a *p*-value less than 0.05

251 are indicated in boldface.

252

253

254 **Discussion**

255 Previous studies in Bengalese finches and zebra finches have found that female birds
256 develop a long-lasting preference for their father's song [10–15]. From a functional viewpoint,
257 however, it was not clear if such a preference is an expression of sexual motivation in females. In the
258 current study, we tested whether female Bengalese finches are sexually attracted to their father's song
259 by measuring CSDs in response to song playbacks. We found that birds showed greater frequency of
260 CSDs to the father's song than to other unfamiliar conspecific songs (Fig. 2), which suggests that
261 females are sexually motivated when exposed to the father's song.

262 The song preference observed in our study might be regarded as an expression of sexual
263 imprinting on the father's song. This possibility has already been referred to in an early study of captive
264 zebra finches, although there has not been a conclusive experimental demonstration of this to date
265 [10]. Likewise, field research in Darwin's finches (*Geospiza*) reported female mate preference
266 consistent with sexual imprinting on the father's song [31]. However, the effect of experience with the
267 father's song on later mate preference, if any, may depend on the species. In canaries (*Serinus canaria*),
268 for example, adult females rather disfavor their foster father's song, which likely helps the species

269 avoid inbreeding [20]. On the other hand, it can be speculated that learning the father's song as a
270 sexually attractive signal may help other species avoid outbreeding or hybridization [32–35]. Whether
271 females of a species favor or disfavor incestuous signals might depend on the dispersal patterns and
272 breeding ecology of that species [16,36,37].

273 To examine if female Bengalese finches are sexually imprinted on their father's song,
274 however, more precise control of rearing conditions is necessary. For example, our experimental
275 design could not exclude the possibility that song preference was somehow inherited from parents to
276 daughters, as we used female finches that were cared for by their genetic parents. In addition, because
277 the subjects were housed with parents for a relatively long time (until about 120 dph), it is also possible
278 that such a long-time interaction with the father led to a particularly robust response selectivity to
279 conspecific songs. To avoid these confounding factors and better understand the process of preference
280 development, cross-fostering experiments and/or manipulation of the period of exposure to (foster)
281 father's song will be necessary in the future. Moreover, although we found that songs with higher
282 similarity to the father's song elicited more CSDs, this tendency was not statistically significant. In
283 testing the effect of similarity on female response to unfamiliar songs, the small number of trials
284 available for analysis was a limitation (Fig. 3). Manipulation of stimuli based on song similarity or a
285 particular song feature, rather than a post-hoc analysis as in this study, may enable a more detailed
286 analysis on the effect of auditory experience on song perception.

287 Regardless of the developmental mechanism of preference for the father's song, our results
288 together with previous findings [14,15] imply the importance of considering individual variations in
289 female song preference in the Bengalese finch. In previous studies on this species, researchers have
290 explored acoustical and temporal song characteristics that are preferred across individuals [14,38–40].
291 For example, in a call-back assay experiment where song tempo or pitch were manipulated, the authors
292 found that the majority of females preferred faster songs while changes in pitch were not a good
293 predictor of female response [38]. There are other studies that are especially relevant to the
294 characteristics of Bengalese finch song and its evolutionary process. The Bengalese finch is a
295 domesticated strain of its wild ancestor, the white-rumped munia (*Lonchura striata*), and the transition
296 probability of Bengalese finch song elements is known to be more complex than that of munias [41,42].
297 Thus, it is hypothesized that sexual selection contributed to an increase in sequential complexity across
298 generations. If this is the case, one would predict that that females should possess a preference for
299 such complexity [42]. However, the results of studies have been mixed: although some females did
300 show greater responses to more complex songs (measured by operant conditioning or nest building
301 behavior), there were individual variations in the preference for or sensitivity to the sequential
302 complexity of song [14,39,40]. Individual differences in song preference were also reported in another
303 study [22], but it was not known what factor(s) might explain such variation. Our results here suggest
304 that developmental song experience may account for this issue. Among different studies that used

305 different behavioral indices, there is general agreement that as a population, female birds tended to
306 prefer their father's song [14,15]. We propose that consideration of the early-life social environment
307 of females is important in re-interpreting previous findings and designing new experiments.

308

309

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316 **References**

- 317 1. Catchpole CK, Slater PJB. Bird Song. Cambridge: Cambridge University Press; 2008.
- 318 2. Searcy WA, Yasukawa K. Song and female choice. In: Kroodsma DE, Miller HE, editors.
319 Ecology and evolution of acoustic communication in birds. Cornell University Press; 1996. p.
320 454–73.
- 321 3. Clayton NS, Pröve E. Song discrimination in female zebra finches and bengalese finches. Anim
322 Behav. 1989;38(2):352–4.

- 323 4. Nagle L, Kreutzer M, Vallet E. Adult female canaries respond to male song by calling. *Ethology*.
324 2002;108(5):463–72.
- 325 5. Schmidt KL, McCallum ES, MacDougall-Shackleton EA, MacDougall-Shackleton SA. Early-life
326 stress affects the behavioural and neural response of female song sparrows to conspecific song.
327 *Anim Behav*. 2013;85(4):825–37.
- 328 6. Braaten RF, Reynolds K. Auditory preference for conspecific song in isolation-reared zebra
329 finches. *Anim Behav*. 1999;58(1):105–11.
- 330 7. Lauay C, Gerlach NM, Adkins-Regan E, DeVoogd TJ. Female zebra finches require early song
331 exposure to prefer high-quality song as adults. *Anim Behav*. 2004;68(6):1249–55.
- 332 8. Clayton NS. Subspecies recognition and song learning in zebra finches. *Anim Behav*.
333 1990;40(6):1009–17.
- 334 9. Chen Y, Clark O, Woolley SC. Courtship song preferences in female zebra finches are shaped by
335 developmental auditory experience. *Proc R Soc B Biol Sci*. 2017;284(1855):18–20.
- 336 10. Miller DB. Long-term recognition of father’s song by female zebra finches. *Nature*.
337 1979;280(5721):389–91.
- 338 11. Clayton NS. Song discrimination learning in zebra finches. *Anim Behav*. 1988;36(4):1016–24.
- 339 12. Riebel K. Early exposure leads to repeatable preferences for male song in female zebra finches.
340 *Proc R Soc B Biol Sci*. 2000;267(1461):2553–8.

- 341 13. Riebel K, Smallegange IM, Terpstra NJ, Bolhuis JJ. Sexual equality in zebra finch song
342 preference: Evidence for a dissociation between song recognition and production learning. *Proc R*
343 *Soc B Biol Sci.* 2002;269(1492):729–33.
- 344 14. Kato Y, Hasegawa T, Okanoya K. Song preference of female Bengalese finches as measured by
345 operant conditioning. *J Ethol.* 2010;28(3):447–53.
- 346 15. Fujii TG, Ikebuchi M, Okanoya K. Sex differences in the development and expression of a
347 preference for familiar vocal signals in songbirds. *PLoS One.* 2021;16(1):e0243811.
- 348 16. Charlesworth D, Charlesworth B. Inbreeding depression and its evolutionary consequences. *Annu*
349 *Rev Ecol Syst.* 1987;18:237–68.
- 350 17. Pusey A, Wolf M. Inbreeding avoidance in animals. *Trends Ecol Evol.* 1996;11(5):201–6.
- 351 18. Epinat G, Lenormand T. The evolution of assortative mating and selfing with in- and outbreeding
352 depression. *Evolution.* 2009;63(8):2047–60.
- 353 19. Riehl C, Stern CA. How cooperatively breeding birds identify relatives and avoid incest: New
354 insights into dispersal and kin recognition. *BioEssays.* 2015;37(12):1303–8.
- 355 20. Trosch M, Müller W, Eens M, Iserbyt A. Genes, environments and their interaction: song and
356 mate choice in canaries. *Anim Behav.* 2017;126:261–9.
- 357 21. Searcy WA. Measuring responses of female birds to male song. In: McGregor PK, editor.
358 *Playback and studies of animal communication.* New York: Plenum Press; 1992. p. 175–89.

- 359 22. Dunning JL, Pant S, Bass A, Coburn Z, Prather JF. Mate choice in adult female Bengalese
360 finches: females express consistent preferences for individual males and prefer female-directed
361 song performances. *PLoS One*. 2014;9(2):e89438.
- 362 23. Anderson RC. Operant conditioning and copulation solicitation display assays reveal a stable
363 preference for local song by female swamp sparrows *Melospiza georgiana*. *Behav Ecol Sociobiol*.
364 2009;64(2):215–23.
- 365 24. Fujii TG, Okanoya K. Supplementary movies for “Female Bengalese finches recognize their
366 father’s song as sexually attractive”. *figshare*. 2021. (doi: 10.6084/m9.figshare.14677650)
- 367 25. O’Loughlen AL, Beecher MD. Sexual preferences for mate song types in female song sparrows.
368 *Anim Behav*. 1997;53(4):835–41.
- 369 26. Tchernichovski O, Nottebohm F, Ho CE, Pesaran B, Mitra PP. A procedure for an automated
370 measurement of song similarity. *Anim Behav*. 2000;59(6):1167–76.
- 371 27. Fujii TG, Okanoya K. Supplementary dataset for “Female Bengalese finches recognize their
372 father’s song as sexually attractive”. *figshare*. 2021. (doi: 10.6084/m9.figshare.14677572)
- 373 28. R Core Team. R: A language and environment for statistical computing. *R Found Stat Comput*.
374 2018
- 375 29. Bates D, Mächler M, Bolker BM, Walker SC. Fitting linear mixed-effects models using lme4. *J*
376 *Stat Softw*. 2015;67(1):1–48.

- 377 30. Kuznetsova A, Brockhoff PB, Christensen RHB. lmerTest package: tests in linear mixed effects
378 models. *J Stat Softw.* 2017;82(13):1–26.
- 379 31. Grant BR, Grant PR. Songs of Darwin’s finches diverge when a new species enters the
380 community. *Proc Natl Acad Sci U S A.* 2010;107(47):20156–63.
- 381 32. Luo Z, Hu M, Hong M, Li C, Gu Q, Gu Z, et al. Outbreeding avoidance as probable driver of
382 mate choice in the Asiatic toad. *J Zool.* 2015;295(3):223–31.
- 383 33. Bateson P. Sexual imprinting and optimal outbreeding. *Nature.* 1978;273(5664):659–60.
- 384 34. Slagsvold T, Hansen BT, Johannessen LE, Lifjeld JT. Mate choice and imprinting in birds studied
385 by cross-fostering in the wild. *Proc R Soc London Ser B Biol Sci.* 2002;269(1499):1449–55.
- 386 35. Irwin DE, Price T. Sexual imprinting, learning and speciation. *Heredity (Edinb).* 1999;82(4):347–
387 54.
- 388 36. Mulard H, Danchin E, Talbot SL, Ramey AM, Hatch SA, White JF, et al. Evidence that pairing
389 with genetically similar mates is maladaptive in a monogamous bird. *BMC Evol Biol.*
390 2009;9(1):147.
- 391 37. Szulkin M, Sheldon BC. Dispersal as a means of inbreeding avoidance in a wild bird population.
392 *Proc R Soc B Biol Sci.* 2008;275(1635):703–11.
- 393 38. Dunning JL, Pant S, Murphy K, Prather JF. Female finches prefer courtship signals indicating
394 male vigor and neuromuscular ability. *PLoS One.* 2020;15(1):e0226580.

- 395 39. Morisaka T, Katahira K, Okanoya K. Variability in preference for conspecific songs with
396 syntactical complexity in female Bengalese Finches: towards an understanding of song evolution.
397 Ornithol Sci. 2008;7(1):75–84.
- 398 40. Okanoya K, Takashima A. Auditory preference of the female as a factor directing the evolution of
399 Bengalese finch songs. Trans Tech Comm Psychol Physiol Acoust. 1997;27:1–6.
- 400 41. Honda E, Okanoya K. Acoustical and syntactical comparisons between songs of the white-backed
401 munia (*Lonchura striata*) and its domesticated strain, the Bengalese finch (*Lonchura striata var.*
402 *domestica*). Zoolog Sci. 1999;16(2):319–26.
- 403 42. Okanoya K. Song syntax in Bengalese finches: Proximate and ultimate analyses. Adv Study
404 Behav. 2004;34:297–346.
- 405

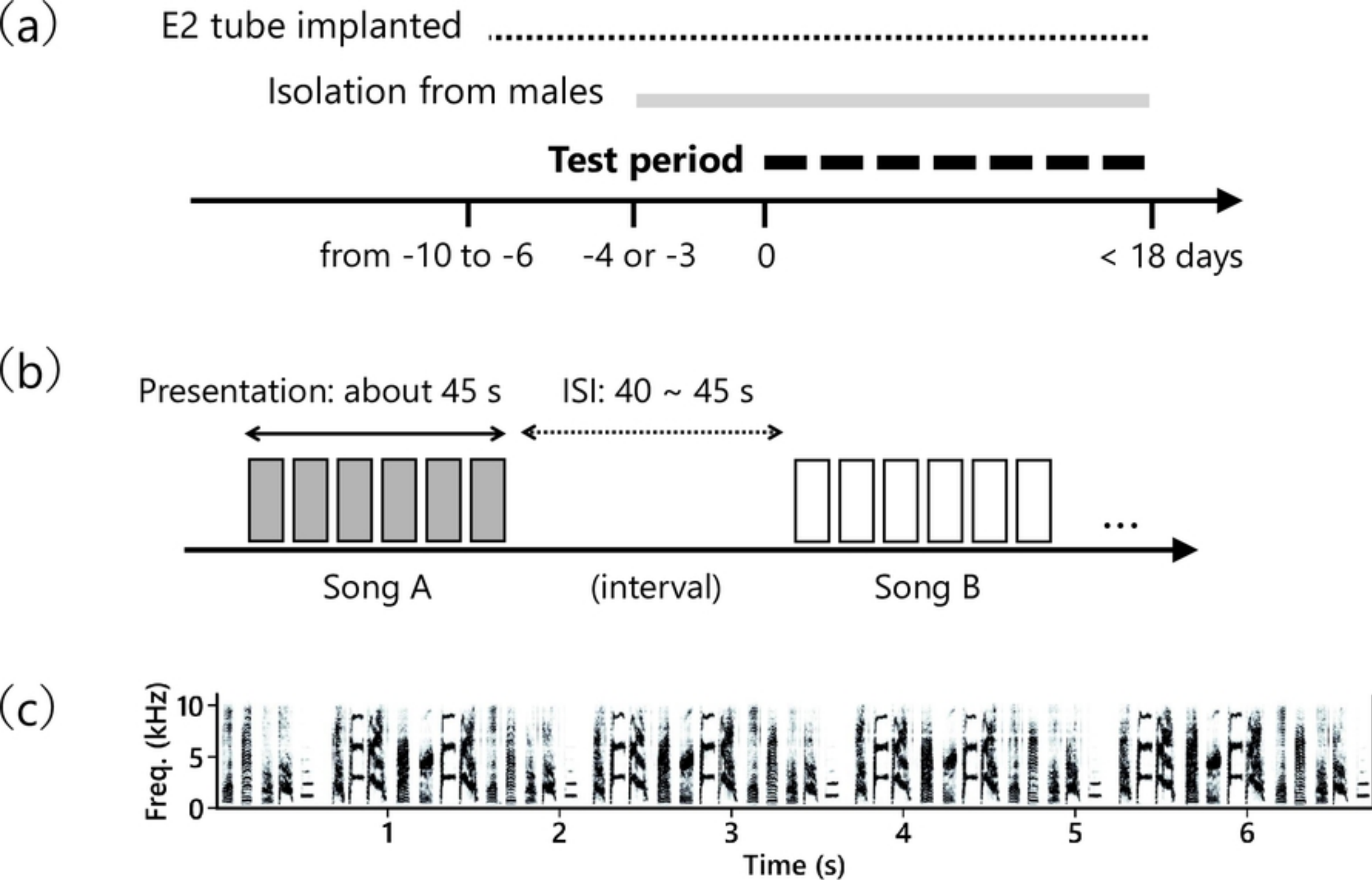


Figure 1

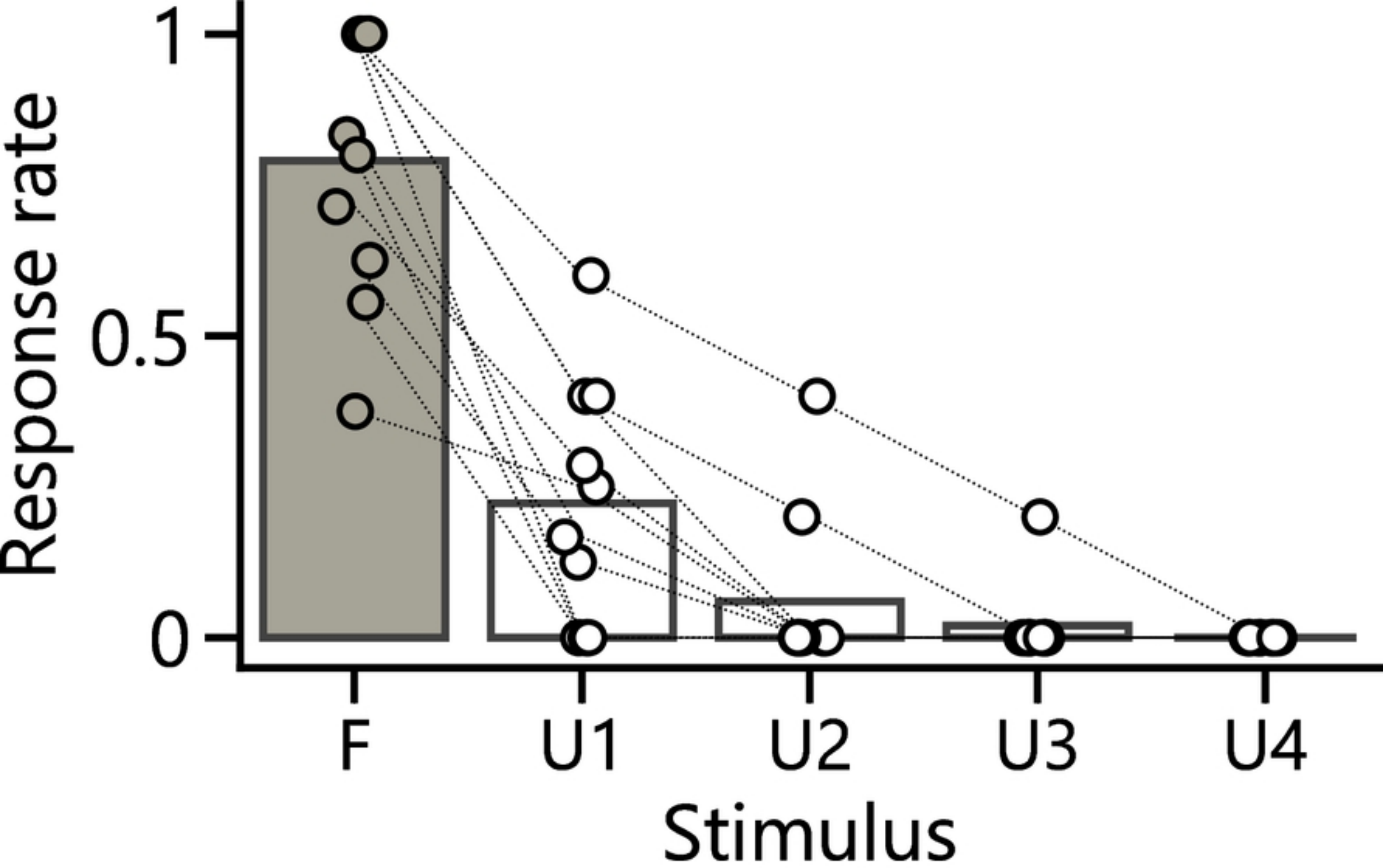


Figure2

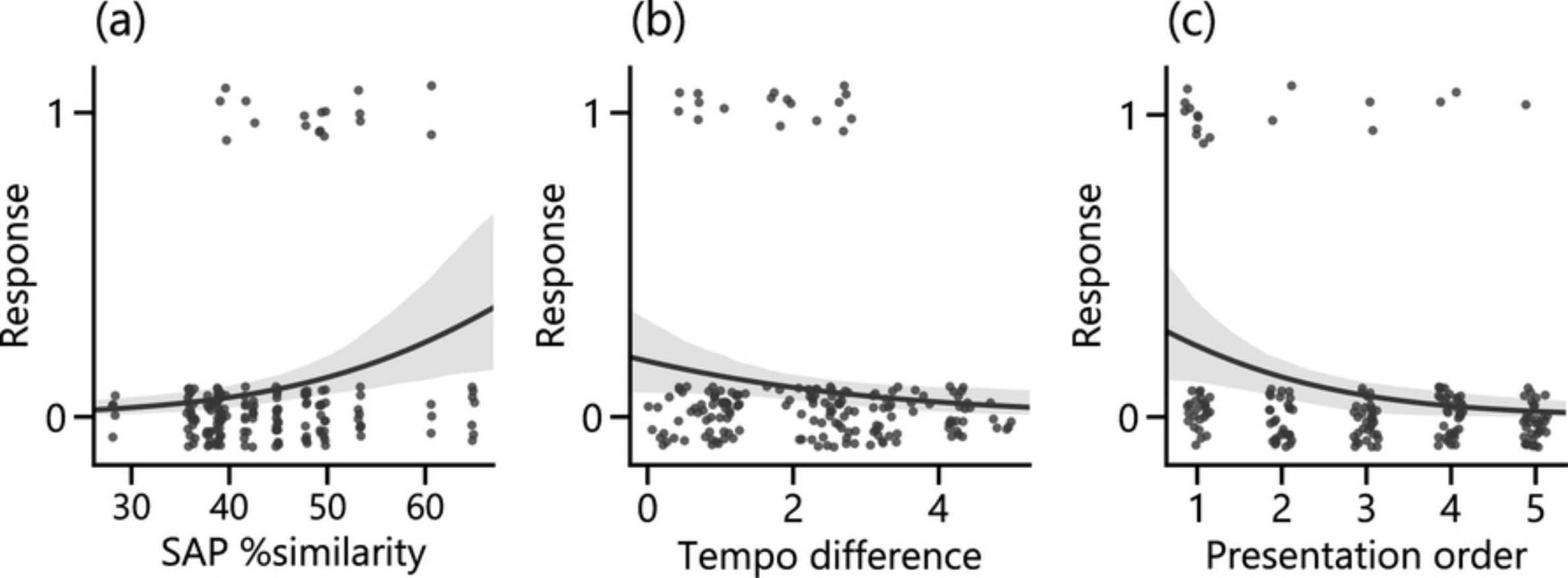


Figure3