Catcalls: exotic cats discriminate the voices of familiar caregivers

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Background. The ability to differentiate familiar from unfamiliar humans has been considered a product of domestication or early experience. Few studies have focused on voice recognition in *Felidae* despite the fact that this family presents the rare opportunity to compare domesticated species to their wild counterparts and to examine the role of human rearing. **Methods**. We tested whether non-domesticated *Felidae* species recognized familiar human voices by exposing them to audio playbacks of familiar and unfamiliar humans. In a pilot study, we presented seven cats of five species with playbacks of voices that varied in familiarity and use of the cats' names. In the main study, we presented 24 cats of 10 species with unfamiliar and then familiar voice playbacks using a habituation-dishabituation paradigm. We anticipated that human rearing and use of the cats' names would result in greater attention to the voices, as measured by the latency, intensity, and duration of responses regardless of subject sex and subfamily. **Results.** Cats responded more quickly and with greater intensity (e.g., full versus partial head turn, both ears moved versus one ear twitching) to the most familiar voice in both studies. They also responded for longer durations to the familiar voice compared to the unfamiliar voices in the main study. Use of the cats' name and rearing history did not significantly impact responding. These findings suggest that close human contact rather than domestication is associated with the ability to discriminate between human voices and that less social species may have socio-cognitive abilities akin to those of more gregarious species. With cats of all species being commonly housed in human care, it is important to know that they differentiate familiar from unfamiliar human voices.

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27 **Abstract**

28 **Background**. The ability to differentiate familiar from unfamiliar humans has been considered a

29 product of domestication or early experience. Few studies have focused on voice recognition in

30 *Felidae* despite the fact that this family presents the rare opportunity to compare domesticated

31 species to their wild counterparts and to examine the role of human rearing.

32 **Methods**. We tested whether non-domesticated *Felidae* species recognized familiar human

33 voices by exposing them to audio playbacks of familiar and unfamiliar humans. In a pilot study,

34 we presented seven cats of five species with playbacks of voices that varied in familiarity and

35 use of the cats' names. In the main study, we presented 24 cats of 10 species with unfamiliar and

36 then familiar voice playbacks using a habituation-dishabituation paradigm. We anticipated that

37 human rearing and use of the cats' names would result in greater attention to the voices, as

38 measured by the latency, intensity, and duration of responses regardless of subject sex and

39 subfamily.

40 **Results.** Cats responded more quickly and with greater intensity (e.g., full versus partial head

41 turn, both ears moved versus one ear twitching) to the most familiar voice in both studies. They

42 also responded for longer durations to the familiar voice compared to the unfamiliar voices in the

43 main study. Use of the cats' name and rearing history did not significantly impact responding.

44 These findings suggest that close human contact rather than domestication is associated with the

45 ability to discriminate between human voices and that less social species may have socio-

46 cognitive abilities akin to those of more gregarious species. With cats of all species being

47 commonly housed in human care, it is important to know that they differentiate familiar from

48 unfamiliar human voices.

49 **Keywords**: Felid, vocal discrimination, familiar human, rearing history

Introduction

51   The ability to recognize familiar and unfamiliar individuals plays a pivotal role in the

52   social lives of animals, and this is often accomplished through voice recognition. For example,

53   mother cats (*Felis catus*) recognize the cries of their kittens (Szenczwe et al., 2016), lions

54   (*Panthera leo)* identify members within and outside of their social groups (Gilfillan et al., 2016),

55   spotted hyenas (*Crocuta crocuta*) respond more strongly to the whoops of cubs to whom they are

56   related (Holekamp et al., 1999), and female great tit birds (*Parus major*) discriminate their

57   mate's call from neighbors' vocalizations (Blumenrath, Dabelsteen & Pedersen, 2007). Beyond

58   recognizing individual and familiar conspecifics, nonhuman primates (Candiotti, Zuberbühler, &

59   Lemasson, 2013) and birds (Dhondt, & Lambrechts, 1992) can identify individuals of

60   neighboring heterospecifics. With humans becoming a more commonly encountered

61   heterospecific, animals may develop the ability to discriminate human voices, and this may

62   depend upon the nature of exposure to humans. We tested whether members of various species

63   of non-domesticated cats with different rearing histories differentiated between familiar and

64   unfamiliar human voices.

65   Recognition of human vocal cues has been investigated in many domesticated species,

66   such as dogs (*Canis lupus familiaris)* (Adachi, Kuwahata, & Fujita, 2007), horses (*Equus*

67   *caballus)* (d'Ingeo et al., 2019), pigs *(Sus scrofa domesticus)* (Bensoussan et al., 2019), and cats

68   *(Felis catus)* (Saito & Shinozuka, 2013). The few studies that have examined non-domesticated

69   species focused on animals that are naturally gregarious, such as gorillas *(Gorilla gorilla*, Salmi

70   et al., 2021) and elephants (*Loxodonta africana*, McComb et al., 2014). In a review of human

71   vocal discrimination in nonhumans (Kriengwatana, Escudero, & Ten Cate, 2014), the only

72   relatively asocial species represented was the domestic cat (Saito & Shinozuka, 2013). There is

73   little investigation of vocal recognition in exotic cats despite their prevalence in human care. The

74   current study extends this research to 25 individuals of 10 non-domesticated felid species housed

75   in human care. The cat family, or *Felidae*, are of interest given their relatively asocial natural

76   history coupled with their close association with humans in modern society. They are a highly

77   diverse group consisting of 38 species (IUCN Red List, n.d.). The subfamily, Pantherinae,

78   consists of seven species: lions (*Panthera leo*), tigers (*Panthera tigris*), leopards (*Panthera*

79   *pardus*), jaguars (*Panthera onca*), snow leopards *(Panthera uncia),* and two species of clouded

80   leopard (*Neofelis nebulosa* and *Neofelis diardi)*. The subfamily, Felinae, which is responsible for

81   the evolutionary line that produced the modern domestic cat, includes the remaining 31 species

82   (Castello, Sliwa, & Kitchener, 2020). Members of both Pantherinae and Felinae are commonly

83   found in human care, housed in zoos, sanctuaries, nature preserves, and personal collections in

84   great numbers. In the current studies, we included members of four Pantherinae species (clouded

85   leopard, *Neofelis nebulosa*; snow leopard, lion, and tiger) and six Felinae species (cheetah,

86   *Acinonyx jubatus;* cougar, *Puma concolor* cory; fishing cat, *Prionailurus viverrinus*; Canadian

87   lynx, *Lynx canadensis;* sand cat, *Felis margarita* and serval, *Leptailurus serval*) allowing us to

88   address the potential breadth of the ability to recognize familiar heterospecific voices across non-

89   domesticated felid species.

90   Recognition of individuals along with other socio-cognitive abilities, such as the ability

91   to follow gaze and point cues, have been attributed to the process of domestication (Hare et al.,

92   2002; Topál et al., 2005). However, megachiropteran bats (*Pteropus*) were able to follow point

93   signals to locate hidden food items only when socialized with humans from an early age (Hall et

94   al., 2011), suggesting that socialization with humans might be as important as domestication (if

95   not more so) in facilitating an understanding of human communicative behaviors. Saito and

96   Shinozuka (2013) demonstrated that domestic cats respond differently to their owner's voice

97   compared to the voices of unfamiliar humans. If wild cats share with domestic cats the ability to

98   differentiate human voices, this would suggest that this ability is not dependent on domestication

99   or human rearing (henceforth, hand-reared). A single study conducted with wild cats (Leroux et

100 al., 2018) found that a group of eight hand-reared male cheetahs (*Acinonyx jubatus*)

101 discriminated between the voices of familiar and unfamiliar humans, as indicated by greater

102 visual attention and more rapid response to familiar human voices compared to unfamiliar

103 human voices. If social ecology is critical for the development of individual vocal recognition,

104 lions may show stronger discrimination of familiar voices compared to other species, as they are

105 the only wild cat known to live in large social groups (M. Sunquist & F. Sunquist, 2002). Here,

106 we examine our results with lions both included and excluded from analyses to examine the

107 impact of group-living on heterospecific recognition.

108   Because the single finding of human voice discrimination in non-domestic cats comes

109 from a group of hand-reared cheetahs, it is important to determine whether the finding is

110 dependent upon human rearing. Hand-reared cats may exhibit important differences from

111 mother-reared cats. For example, Mellen (1992) found differences in responses to familiar and

112 unfamiliar humans such as heightened aggression and fear, as well as less interest in social

113 interaction to unfamiliar (relative to familiar) humans in human-reared compared with mother-

114 reared kittens. Mellen's results have informed husbandry and rearing techniques in zoos,

115 encouraging mother-rearing whenever possible. Whereas the preference for most species and

116 facilities is that offspring are mother-reared (Hampson & Schwitzer, 2016), there are some

117 circumstances that require human intervention (e.g., maternal neglect, wild orphans, infanticide,

118   or large litters that are physically taxing on the mother, Hines, n.d.). Thus, we were able to

119   examine the role of hand-rearing compared to mother-rearing in response to human voices.

120   A secondary question was whether cats might respond to the sound of their names

121   without regard for the identity of the caller. Saito et al. (2019) found that domestic cats

122   responded more to their names than to other words but whether exotic cats are more responsive

123   to commands or greetings when their names are spoken is unknown. The animals housed in

124   managed care frequently work closely with their human caretakers, as a necessary aspect of their

125   daily husbandry. Animal caretakers commonly use verbal cues when working with the animals,

126   especially during training and when calling the animals by their names. These animals also may

127   interact to some degree with the public regularly, so that they hear many different voices and

128   words, including their own names if those are known to the public. There is much debate in the

129   captive animal industry as to whether names of animals should be posted publicly for visitors to

130   know (personal obs). The giving of a name to an animal is a form of anthropomorphism, in

131   which humans might unconsciously assign characteristics and be more sympathetic to a named

132   animal than to an unnamed animal (Chartrand, Fitzsimons, & Fitzsimons, 2008). The constant

133   repetition of a behavioral cue, such as the calling of a name, without a subsequent reinforcer may

134   desensitize the animal to that cue, which could lead to complications in training and frustration

135   for the animal (Miltenberger, 2015). If the cats are responsive to their names regardless of

136   whether they are spoken to by a familiar or unfamiliar voice, it might be beneficial to prevent

137   members of the public from knowing and calling the cats' names. At the same time, such a

138   finding may demonstrate that cats will be more responsive to communication from their keepers

139   if their names are used.

140   The purpose of this study was to examine recognition of familiar human voices in

141   captively-managed exotic cats excluding the domestic cat, *F. catus*, as well as any hybrids of the

142   domestic cat, such as savannah (*Felis catus × Leptailurus serval*) and bengal cats (*Felis catus x*

143   *Prionailurus bengalensis)*. We conducted two studies using slightly different playback

144   procedures. In a pilot study, we presented a small group of captive cats with six 3-trial sessions

145   including playbacks of unfamiliar, less familiar, and more familiar caregiver voices either using

146   their name or not. We were interested in whether any effects of familiarity were restricted to

147   humans with which the cats had particularly close relationships. To include more cats from

148   various facilities in the main study, we minimized the number of required sessions by shifting to

149   the dishabituation paradigm used by Saito and Shinozuka (2013) and focused on only the most

150   familiar caregiver's voice. This method allowed us to witness a stronger response to the familiar

151   voice when directly contrasted with unfamiliar voices within the same sessions. Within session

152   comparisons limit the influence of extraneous factors that vary across test sessions. In our main

153   study, cats were presented with a series of audio playbacks of three different unfamiliar humans

154   speaking the same phrase, then a playback of a familiar voice and, finally, a fourth unfamiliar

155   voice. Typically, in this paradigm, subjects habituate to the sound of strangers' voices, but show

156   a rebound effect in attention and responsiveness during the familiar voice playback, that then

157   dissipates with a subsequent unfamiliar voice (Saito & Shinozuka, 2013). Such a pattern suggests

158   recognition and discrimination of the familiar voice from among other voices. For our purposes,

159   we did not consider it necessary that the cats habituated to the unfamiliar voices so long as they

160   showed a pronounced response to the familiar voice that differed from that to the unfamiliar

161   voices, because the cats were tested in public facilities where we could not completely control

162   other sounds, including voices, during testing. We hypothesized that cats would show greater

163 attention as measured by faster latencies to respond and greater intensity and duration of

164 responses following the familiar voice relative to the unfamiliar voices. Behavioral responses

165 such as head, ear, and body orientation, movement towards or away from the sound, and

166 vocalizations were considered cumulatively rather than separately as was done by Saito and

167 Shinozuka (2013), due to the rarity of any single behavior. We compared responses to the five

168 vocal cues in sessions in which the subjects' names were or were not spoken, and examined the

169 predictive factors of sex, subfamily (*Pantherinae* versus *Felinae*), and rearing history (hand-

170 reared vs. mother-reared). We predicted an interaction between rearing history and familiarity in

171 that cats that were hand-reared would respond faster, more intensely and for longer to voices

172 they were familiar with compared to cats that had been mother-reared. Lastly, we predicted that

173 cats would respond faster, more intensely and for longer when the cues included their names,

174 compared to the cues with no name spoken, and that the use of a name would interact with

175 familiarity to predict the intensity of responses, such that the cats would show a stronger

176 response to their name only when spoken by a familiar speaker. Inclusion of sex and subfamily

177 were for exploratory purposes as we did not have specific hypotheses regarding these factors.

178 **Materials and Methods**

179 *Ethics Statement*

180 The experiments reported here were reviewed and approved by Oakland University's

181 IACUC (Protocol # 2021-1155).

182 *Subjects*

183 Seven individuals of five species (tiger, *P. tigris; cheetah, A. jubatus; serval, L. serval;*

184 *puma, P. concolor; lynx, L. canadensis*) housed at Zoo Miami in Florida and the Creature

185   Conservancy in Ann Arbor, MI. participated in a pilot study. All but one of these cats, plus 18

186   additional cats representing ten species subsequently participated in the main study

187   (approximately 3-6 months later). Information about each subject's subfamily (Pantherinae or

188   Felinae), sex, and rearing history (hand-reared or mother-reared) are reported in Table 1. Rearing

189   history was categorized as hand reared (reared exclusively by humans starting at no later than

190   four months of age, which is the start of the weaning period for most large exotic cats; Jhala &

191   Sadhu, 2017) or mother-reared (raised exclusively by their mother, or co-raised with the mother

192   and humans, from birth to at least four months of age). We did not differentiate between

193   subspecies; that is, Malayan tigers (*P. tigris tigris)* and Sumatran tigers (*P. tigris sumatrae)* were

194   classified as tigers.

195   ***Materials***

196   Audio recordings of each voice were taken using a Zoom h1n Handy recorder and played

197   back for the subjects using an Ultimate Ears BOOM 3 Bluetooth speaker. Observations were

198   recorded using a GoPro Hero 10. Data were coded and analyzed by naïve coders using freely

199   available BORIS v.8.20. software (Friard & Gamba, 2016). All testing occurred at the cat's

200   home facility, in their regular habitat. The researcher performed all playback sessions, as well as

201   recorded all observations, from outside of the enclosure.

202   In the pilot study, each cat was exposed to three different voices speaking two different

203   cue types. Thus, each human speaker provided six different recordings, three of them speaking

204   the name absent (NA) cue, and three of them speaking the name present (NP) cue. A total of 18

205   recordings were collected for each cat to ensure that the cats never heard the exact same

206   recording more than once to control for habituation. The speakers, matched for sex, were

207   categorized as Most Familiar (MF), Less Familiar (LF), and Unfamiliar (UF). In the main study,

208   each cat was exposed to five different voices (four UF and one MF voice) speaking the same two

209   cue types (NA, NP). Thus, each speaker provided two different recordings, one for the NP

210   condition, and one for the NA condition. The MF speaker was someone that the cat was very

211   familiar with, such as the cat's primary keeper or trainer. If the facility did not assign primary

212   trainers or keepers, then we used the voice of the person who had worked with the cat for the

213   longest period of time. The LF speaker was someone that the cat had heard before, but had

214   minimal structured interaction with. This person was either a member of staff that did not work

215   with the cat, an intern, or a volunteer. The LF speaker could not have actively participated in

216   training or care of the cat, which included but was not limited to, feeding, directly providing

217   enrichment, or participating in husbandry tasks such as veterinary care. The UF speakers were

218   four different sex-matched people that the cat had never encountered or heard before. These

219   recordings were provided by individuals that had not been to the facility the cat currently resided

220   at or had resided at in the past.

221   The NA cue was a short phrase that the cat was familiar with, "Good morning, how are

222   you doing today?". This phrase was selected from the results of a poll from exotic cat keepers on

223   zookeeping Facebook pages, in which they submitted a phrase they speak regularly to the cats in

224   their care but that was not associated with food rewards. Some variation of the used phrase was

225   found to be the most common occurrence across facilities. The NP cue matched the NA cue, but

226   the cat's name was said in the phrase, e.g., "Good morning, Harper, how are you doing today?".

227   In instances where the cat had multiple names, such as registered names, house names, or public

228   names, the name that was used was the one that the animal care staff used most frequently. We

229   deliberately used a phrase that we knew was familiar to all cats given that we could not be aware

230   of the cats' exposure to less common phrases, and because this might be the strongest test of

231   whether the cats differentiated familiar voices from unfamiliar voices speaking familiar phrases.

232   All recordings were made in a quiet room with no additional voices in the background.

233   The recordings were less than 5 seconds long. The speakers were controlled for sex, volume, and

234   neutral tone of voice, matching the MF voice within 1 dB and 2 Hz. In the main study, Audacity

235   v.3.4.2 audio editing software was used to create a single file for each session of playbacks with

236   the order of the UF voices randomized for each subject to control for reactions to specific voices

237   occurring in the same temporal position across sessions.

238   ***Procedure***

239   A wireless speaker was set up outside of the enclosure in the visitor area, and was no closer than

240   three feet away from the primary containment barrier. The researcher and observation recording

241   equipment were also outside of the enclosure in visitor space (Figure 1). Prior to each trial, the

242   cat must have been on exhibit for at least 15 minutes and must have been awake. The time

243   allotment was to avoid potential distraction or inattention due to examining the space for food or

244   enrichment items. Each subject was provided an acclimation period with the researcher and the

245   equipment. Sessions did not start until the subject(s) had shown no interest or attention to the

246   recording equipment or researcher for at least two minutes. All trials were performed in the

247   absence of visitors, either before or after operating hours, during lulls in visitation, or on days the

248   facility was not open to the public. Eight cats were housed in pairs; lions, snow leopards and

249   cougars in Cincinnati, and cheetahs in Miami. Playback sessions were presented to these four

250   pairs with both names being spoken in the name condition. Coders were instructed to code the

251   behavior of each easily recognizable individual separately. They were told the position of each

252   subject at the start of the session so that they could track the target individual. The subjects were

253 actively monitored for the duration of each session for stress behaviors, such as repeated

254 aggressive reactions, pacing, or other signs of distress. No abnormal behaviors indicating stress

255 due to the playback sessions were observed in any of the subjects.

256   In the pilot study, each cat participated in six 3-trial playback sessions, with each session

257 consisting of one playback from each speaker (MF, LF, UF). Whether playbacks included the

258 cats' name was randomly determined for each session. Each speaker's voice was presented three

259 times in each name condition across the course of the study. Each three-trial session lasted for 28

260 minutes total; three minutes of baseline prior to each playback, and three minutes of observation

261 following the end of each playback with a minimum of five minutes between each trial (e.g., 3

262 min observation – Playback 1 – 3 min observation +5 min ITI – 3 min observation – Playback 2

263 – 3 min observation + 5 min ITI – 3 min observation – Playback 3 – 3 min observation). If more

264 than one session was conducted for the same subject in a day, each session occurred at least one

265 hour following the previous session, and no more than three sessions were conducted in a single

266 day.

267   We conducted the main study approximately 3-6 months following the pilot study

268 (depending upon the institution). In the main study, we used the habituation-dishabituation

269 paradigm (Saito & Shinozuka, 2013). The playbacks for each session were in the order of

270 unfamiliar voice 1, unfamiliar voice 2, unfamiliar voice 3, most familiar voice, unfamiliar voice

271 4 with 30 seconds of interstimulus silence between each voice. Unfamiliar voices were

272 randomized in order between NA and NP sessions. Each cat participated in two playback

273 sessions (one NA and one NP with order randomized across subjects). Sessions lasted no more

274 than 3.5 minutes.

275   Behaviors were coded from video recordings of each session by two naïve coders. The

276   behaviors coded were those inferred to indicate interest or attention to the location of the

277   playback, such as change in gaze direction (a change in the direction of the eyes without

278   movement of the head) , ear and head movement (notable movement of the ears, either one or

279   both, and the head that could not be accounted for by other behaviors such as grooming),

280   locomotion towards or away from the sound (intentional locomotion that was initiated following

281   the playback), or response vocalizations (social vocalizations such as chuffs, hisses, growls, or

282   chirps, immediately following the playback). Behaviors were recorded for three minutes before

283   the playback, during the playback and for three minutes following the end of each playback. Pre-

284   trial recording allowed the establishment of baseline behaviors for the cat prior to the

285   introduction of the cue. Recording for an extended period after the playback also gave us the

286   ability to code for latency (how long after the recording did the reaction take place), intensity

287   (how strong of a reaction was there), and follow up behaviors. A lack of response was recorded

288   as a latency of 30 seconds, the amount of time between each playback, and a duration of 0

289   seconds.

290   Intensity was rated on a scale of 0-4 with 0 indicating no reaction, and 4 indicating a full

291   head turn and ear movement towards the speaker or locomotion towards the speaker.

292   Intermediate scores were assigned if there was a mild head movement or a single ear twitch.

293   Both positive and negative response behaviors were assessed, as per the Standardized Ethogram

294   for Felidae (Stanton, Sullivan, & Fazio, 2015). A negative behavior was defined as an aversive

295   reaction to the sound, and included movement away from the sound, aggressive movement

296   towards the sound (charging or bluff-charging), or aggressive vocalizations (hisses, roars,

297   growls), although the only negative behaviors recorded were species-typical hissing from two

298   serval subjects. To aid the accuracy of vocalization coding, coders were provided with auditory

299   examples of observed vocalizations, as well as their context. The auditory examples were

300   separate from the video recordings coded. The coders were trained on a test video to identify

301   possible behaviors that may be observed in each video, as well as to train them on the BORIS

302   software. Both coders were naive to any difference in the voice playbacks, only being informed

303   that there were three or five playbacks that would occur within a session (depending on the

304   study), and what words the playback would include for accurate identification.

Results

306   All analyses were conducted in IBM Statistical Package for the Social Sciences (SPSS) v. 28.

Pilot Study

Reliability

309   To assess the reliability of our behavioral coding, each video was coded by two coders.

310   Results were compared between a random selection of 25% of the sessions. We found excellent

311   agreement between the two coders for latency *(Pearson's r= .998 p= <.001), duration (r=.997,*

312   *p= <.001), and intensity (r=.900, p= <.001).*

Response to Playbacks

314   Data were examined and met the requirements for sphericity, skewness and kurtosis. A

315   repeated-measures ANOVA of latency to respond with name (absent, present) and familiarity

316   (unfamiliar, less familiar, most familiar) along with their interaction as within-subjects factors

317   revealed a significant interaction between familiarity and name ($F_{2,10} = 6.082$, $p = .019$, $\eta_p^2 =$

318   .549). To explore the interaction, we conducted separate ANOVAs for name present and absent

319   conditions. There was no significant main effect of familiarity when the cats' names were

320   spoken, ($F_{2,10}$ = 3.544, p = .069, η_p^2 = .451) but the effect was significant when the names were

321   not spoken ($F_{2,10}$ = 4.747, p = .030, η_p^2 = .442). Cats responded most quickly to the most

322   familiar voice in both name conditions; However, the pattern of results differed slightly (see

323   Figure 2). If the name was spoken, the cats responded more quickly to both familiar voices

324   compared to the unfamiliar voice, but if the name was not spoken, cats responded more quickly

325   to the most familiar and unfamiliar voices compared to the less familiar voice. If we conducted

326   the same analysis omitting the least familiar condition, we obtained a significant effect of

327   familiarity ($F_{1,5}$ = 7.895, p = .038, η_p^2 = .423), with no significant interaction with or main effect

328   of name. Cats responded significantly more quickly to familiar (M = 34.487s, SE = 13.191s)

329   versus unfamiliar voices (M = 92.808s, SE = 10.479s).

330   A repeated-measures ANOVA of intensity of response with name (absent, present) and

331   familiarity (unfamiliar, less familiar, most familiar) along with their interaction as within-

332   subjects factors revealed no significant effects. If we conducted the same analysis omitting the

333   least familiar condition, we obtained a significant effect of familiarity ($F_{1,5}$ = 6.958, p = .046,

334   η_p^2 = .582). Cats responded with greater intensity to the familiar (M = 1.527s, SE = .111s) versus

335   the unfamiliar voices (M = 1.124s, SE = .109s).

336   A repeated-measures ANOVA of duration of response with name (absent, present) and

337   familiarity (unfamiliar, less familiar, most familiar) along with their interaction as within-

338   subjects factors revealed no significant effects regardless of whether we included the least

339   familiar condition in the analysis.

340   ***Main Study***

341 ***Reliability***

342   To assess the reliability of our behavioral coding, each video was coded by two naïve

343 coders. Results were compared between a random selection of 30% of the sessions (half name

344 present and half name absent). We obtained an excellent level of agreement between the two

345 coders for latency *(Pearson's r= .968, p= <.001), duration (r=.913, p= <.001), and intensity*

346 *(r=.978, p= <.001).*

347 ***Response to Playbacks***

348   Data were analyzed using a mixed-model ANOVA for each of the outcomes of latency,

349 intensity, and duration of responses. The within-subject variables of name use (NA, NP) and

350 familiarity (playback trials 1-5), as well as the between-subject variables of rearing history

351 (mother-reared, hand-reared), sex, and subfamily were examined. We included all two-way

352 interactions involving the within-subjects variables of name and familiarity. We could not

353 examine species differences due to the small sample sizes within each species. Sphericity and

354 homogeneity assumptions were met for all outcomes. However, the data were not normally

355 distributed according to Shapiro-Wilks tests and examination of Q-Q plots. We elected not to

356 transform the data given that the data were not skewed and did not demonstrate kurtosis, and

357 given the concern that transformation can obscure the interpretation of the results. Lastly, non-

358 normality typically does not alter the validity of the results for F tests when homogeneity

359 conditions are met (Stevens, 2016). The complete results appear in Table 2.

360   For latency, a main effect was found for subfamily ($F_{1,20}$=9.112, *p*= .007, η_p^2= .790),

361 with subjects from Felinae responding more quickly (*M*=7.505s, *SD*=1.369s) than subjects from

362 Pantherinae (*M*=13.360s, *SD*=1.767s). A significant effect was also found for familiarity ($F_{4,}$

363    $_{80}$=3.691, p = .008, η_p^2 = .156) and name ($F_{1,20}$=4.571, p= .045, η_p^2 = .186). Simple contrasts

364   indicated that the cats responded significantly more quickly to the fourth playback trial (the

365   familiar voice) compared to each of the other trials (see Figure 3). Cats responded significantly

366   faster when the name was absent (M =8.465s, SE = 1.543s) versus present (M = 11.357s, SE =

367   1.688s). Omitting the data from the three lion subjects, there were still significant main effects of

368   familiarity ($F_{4,\,68}$ =4.788, p=.002, η_p^2 = .220), name ($F_{1,17}$=5.109, p=.037, η_p^2 = .231) and

369   subfamily ($F_{1,17}$=13.314, p=.002, η_p^2 = .439) in the same directions.

370   For intensity, a significant effect was found for familiarity ($F_{4,\,80}$=10.542, p= <.001, η_p^2

371   =.345). Simple contrasts indicated that the cats responded with significantly more intensity to the

372   fourth playback trial (the familiar voice) compared to each of the other trials (Figure 4). There

373   was also a significant main effect of subfamily ($F_{1,\,20}$=8.185, p=.010, η_p^2 = .290) with subjects

374   from Felinae responding more intensely (M=2.131, SD=.204) than subjects from Pantherinae

375   (M=1.308, SD=.215). There were no other significant effects or interactions for intensity.

376   Omitting the data from the three lion subjects, there were still significant main effects of

377   familiarity ($F_{4,\,68}$ = 9.273, p<.001, η_p^2 = .353) and subfamily ($F_{1,17}$=16.802, p<.001, η_p^2 = .497)

378   in the same directions.

379   For duration, a significant effect was found for familiarity ($F_{4,\,80}$ = 4.021, p = .005, η_p^2 =

380   .167). Simple contrasts indicated that the cats responded for significantly longer to the fourth

381   playback trial (the familiar voice) compared to each of the other trials (Figure 5). There were no

382   other significant effects or interactions for duration. Omitting the data from the three lion

383   subjects, there was still a significant main effect of familiarity ($F_{4,\,68}$=3.902, p=.007, η_p^2 = .187).

384   However, there was also a significant interaction of name by subfamily, ($F_{1,\,17}$=5.852, p=.027,

385   η_p^2 = .256). To examine this interaction, the analysis was re-run for each subfamily separately

386   without including subfamily as a factor. The main effect for name was not significant for either

387   subfamily so this result will not be discussed further.

Discussion

389   Across two studies, various species of non-domesticated cats showed evidence of

390   differentiating familiar human voices from unfamiliar voices, similar to what has been shown in

391   domestic cats (Saito & Shinozuka, 2013) and hand-reared cheetahs (Leroux et al., 2018). This is

392   the first time such an ability has been demonstrated in nine additional exotic cat species (Table

393   1), and the first time that early socialization and sex have been examined as possible contributors

394   to responsiveness to human voices in exotic cats. Overall, cats responded more quickly and with

395   greater intensity to familiar voices compared to unfamiliar voices regardless of sex, rearing and

396   whether their names were spoken. In the main study, cats also responded for significantly longer

397   to the familiar versus the unfamiliar voices. Evidence of the ability to differentiate familiar and

398   unfamiliar human voices was not driven by the inclusion of the single gregarious species of cat

399   as the significant effects of familiarity remained when we omitted data from our three lion

400   subjects. Whereas lions may be the only truly social species of cat, all cat species must interact

401   with other animals regularly; whether it be while hunting prey, raising young, finding a mate, or

402   competing for territory. No cat lives a completely asocial life so social behaviors may still be

403   beneficial. Elbroch and colleagues (2017) showed that even relatively asocial pumas (*Puma*

404   *concolor*) were impacted by changes in the composition of their nearest neighbors. Their social

405   interactions were explained better by reciprocity than by kinship, suggesting an ability to track

406   social behaviors not often attributed to cat species (Vonk, 2018). The present results add to the

407   growing literature suggesting that researchers have misattributed a lack of social cognition to

408 non-group-living species and highlights the need to extend studies of social cognition to less

409 commonly studied species.

410   Research with domesticated species had suggested that the ability to recognize individual

411 humans may be a consequence of domestication (Adachi, et al., 2007; Bensoussan et al., 2019;

412 d'Ingeo et al., 2019; Saito & Shinozuka, 2013), whereas studies with wild, yet highly social

413 species suggest that this ability stems from the selective pressures associated with living in social

414 groups (Kriengwatana et al., 2014). Exotic cats are neither domesticated nor highly social (other

415 than lions). Of the 25 cats tested, only three were lions. Most were housed individually, and more

416 than a third were raised by their mothers. Results from the only other study of this kind with

417 exotic cats (cheetahs, Leroux et al., 2018) suggested that early socialization may play a role in

418 the cats' abilities to discriminate human voices. The results from our main study, which are

419 consistent with those of Saito and Shinozuka (2013) using the same habituation-dishabituation

420 paradigm that those authors used with domestic cats, suggest a family-wide ability that is not

421 dependent on domestication or social living. The lack of significant effects of rearing history

422 suggests that this ability to discriminate human voices may depend upon regular rather than early

423 exposure to humans. It is important to note that all but two of our subjects were reared in

424 captivity (not wild born; the exceptions are two cougars at the Cincinnati Zoo) and that most of

425 the hand-reared cats had transitioned to protected contact, a management strategy in which

426 keepers can interact with animals only through a barrier, early in life. However, six of the hand-

427 reared cats remained in close human contact serving as ambassador cats to promote education at

428 the zoos where they were housed. Therefore, it is possible that effects are enhanced by continued

429 close contact with humans.

430   This is the first time the effects of the use of undomesticated cats' names, as spoken by

431   familiar and unfamiliar voices, has been examined. Contrary to findings that domestic cats

432   respond to their names (Saito et al., 2019), the use of the cats' names here had only a single

433   effect on latency, and in the opposite direction to what we predicted with cats responding

434   significantly more quickly when their name was not used. This finding that cats are not unduly

435   distracted by the use of their names by strangers may aid zoological facilities in their decisions

436   about whether to publicly post animal names. With one of the primary concerns being a

437   degradation of the name cue in training if it is repeated frequently by guests without reward, the

438   findings of this study suggest that cats may not be highly responsive to their names, but will be

439   responsive to speakers with whom they are familiar. With studies showing that knowing the

440   name of an animal, a form of anthropomorphism, makes people more sympathetic to the animal

441   (Chartrand, 2008), and more willing to engage in conservation efforts (Manfredo et al., 2020), it

442   may be beneficial for facilities housing exotic cats to post their names for visitors in an effort to

443   engage them further with the conservation mission of the facility.

444   Most importantly, cats demonstrated differential responding to the familiar voice

445   regardless of whether their name was spoken. Notably, all speakers spoke a familiar phrase but

446   the cats responded with greater speed, more intensity, and for longer durations only when this

447   familiar phrase was spoken by familiar voices. Although it is possible that they responded to

448   specific phrasing rather than recognition of the speaker per se (Kriengwatana et al., 2014), the

449   results nonetheless suggest that the cats recognize familiar voices speaking familiar phrases.

450   Future studies will need to determine whether cats also respond to familiar voices speaking

451   unfamiliar phrases.

452   **Limitations and Future Directions**

453   Most of our subjects were housed individually. However, eight cats were tested in pairs

454   so it is possible that some of these cats responded to their cage mate's response rather than to the

455   playback itself. Although this study included representation from many cat species, it was

456   limited by a small sample size within each species due to the relatively small population of

457   captive exotic cats available for testing, precluding an analysis of species differences. Members

458   of Felinae responded more quickly and with greater intensity compared to members of

459   Pantherinae but subfamily did not interact with familiarity. We have no immediate explanation

460   for the main effects of subfamily. Future studies will need to explore whether Felinae are

461   generally more reactive than Pantherinae, which are typically larger. Future studies might

462   examine whether time spent with cats, longevity of the human-cat relationship, and quality of the

463   training interactions predict responsiveness to familiar versus unfamiliar caregivers. Importantly,

464   the current results do not allow for the conclusion that cats can discriminate among individual

465   humans. They merely show that cats respond more strongly to the voices of familiar versus

466   unfamiliar humans in general. Future research is necessary to determine whether cats can

467   discriminate between familiar and unfamiliar human scents and visual features. Methods such as

468   cross-modal matching in which subjects are presented with stimuli from different modalities

469   (e.g., auditory, olfactory, and visual stimuli) representing the same or different individuals and

470   are expected to attend for longer to the mismatched stimuli compared to the matched stimuli

471   (e.g., Takagi et al., 2019) might demonstrate more conclusively whether cats discriminate among

472   individual humans.

473   **Conclusions**

474   This study contributes to the growing literature suggesting that adapting to a social

475   lifestyle and human domestication are not the only important factors in predicting social

476   cognitive abilities even when considering the ability to read human communicative cues

477   specifically. Exposure to humans may promote the development of abilities that researchers

478   would not be able to observe in the wild, such as the ability of cats to discriminate familiar

479   human voices. This study adds to the growing body of work showing that even non-domestic

480   cats are not indifferent to familiar humans and may help dispel the notion that cats are aloof.

481   ***Data Availability***

482   All data are available at https://osf.io/9vuk5/?view_only=5035dcfb065b4a7cbb23a419450eb0b7

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List of Subjects

1 **Table 1**

2 Subject Subfamily, Species Common Name, Sex, Rearing History, Facility and Study Involvement

Subject	Subfamily	Species	Sex	Rearing Style	Facility	Study Participation	Sessions - Pilot	Sessions - Main
Diesel	Felinae	Cheetah	M	HR	Zoo Miami	1 and 2	3	3
Koda	Felinae	Cheetah	M	HR	Zoo Miami	1 and 2	3	3
Nia	Felinae	Cheetah	F	HR	Cincinnati Zoo	2		2
Tommy	Felinae	Cheetah	M	HR	Cincinnati Zoo	2		2
Jean	Pantherinae	Clouded Leopard	F	HR	Zoo Miami	2		2
Harper	Felinae	Cougar	F	HR	Creature Conservancy	1 and 2	6	2
Tecumseh	Felinae	Cougar	M	HR	Cincinnati Zoo	2		4
Joey	Felinae	Cougar	M	HR	Cincinnati Zoo	2		4
Tallulah	Felinae	Fishing Cat	F	MR	Greensboro Science Center	2		3
Mako	Felinae	Fishing Cat	M	MR	Greensboro Science Center	2		3
Gordie	Felinae	Lynx	M	HR	Creature Conservancy	1 and 2	5	2
Amirah	Pantherinae	Lion	F	MR	Zoo Miami	2		4
Imani	Pantherinae	Lion	F	HR	Cincinnati Zoo	2		2
John	Pantherinae	Lion	M	MR	Cincinnati Zoo	2		2
Layla	Felinae	Sand Cat	F	MR	Greensboro Science Center	2		2
Kira	Felinae	Serval	F	HR	Greensboro Science Center	2		3
Major	Felinae	Serval	M	HR	Zoo Miami	1 and 2	4	2
Scout	Felinae	Serval	M	HR	Zoo Miami	1 and 2	4	2
Tut	Felinae	Serval	M	HR	Greensboro Science Center	2		3
Nubo	Pantherinae	Snow Leopard	M	MR	Cincinnati Zoo	2		2
Renji	Pantherinae	Snow Leopard	F	HR	Cincinnati Zoo	2		2
Berani	Pantherinae	Tiger	M	MR	Zoo Miami	1	3	
Jin	Pantherinae	Tiger	F	MR	Cincinnati Zoo	2		3
Rocky	Pantherinae	Tiger	M	MR	Greensboro Science Center	2		2
Zero	Pantherinae	Tiger	M	HR	Cincinnati Zoo	2		3

5 *Note*. HR = human-reared, MR = mother-reared

Results from the main study.

1 Table 2

2 Results from the main study.

	Latency			Intensity			Duration		
	F	p	η_p^2	F	p	η_p^2	F	p	η_p^2
Subfamily	9.112	.007	.313	8.185	.010	.290	0.241	.629	.012
Sex	1.319	.264	.062	3.621	.072	.153	0.367	.552	.018
Rearing	1.032	.322	.049	1.532	.232	.071	0.129	.129	.111
Name	4.571	.045	.186	0.119	.734	.006	0.147	.706	.007
Familiarity	3.691	.008	.156	10.542	<.001	.345	4.021	.005	.167
Name by Familiarity	0.318	.865	.016	1.990	.104	.090	0.370	.829	.018
Rearing by Name	2.223	.152	.100	0.659	.426	.032	2.219	.152	.100
Rearing by Familiarity	1.192	.321	.056	1.494	.212	.070	0.409	.801	.020
Sex by Name	0.856	.366	.041	0.595	.449	.029	.000	.998	.000
Sex by Familiarity	1.578	.188	.073	1.358	.256	.064	0.249	.910	0.12
Subfamily by Name	0.02	.883	.001	0.764	.392	.037	3.067	.095	.133
Subfamily by Familiarity	1.661	.167	.077	1.026	.399	.049	0.228	.922	.011

Figure 1

Experimental Set-Up for Playback Trials and Observation
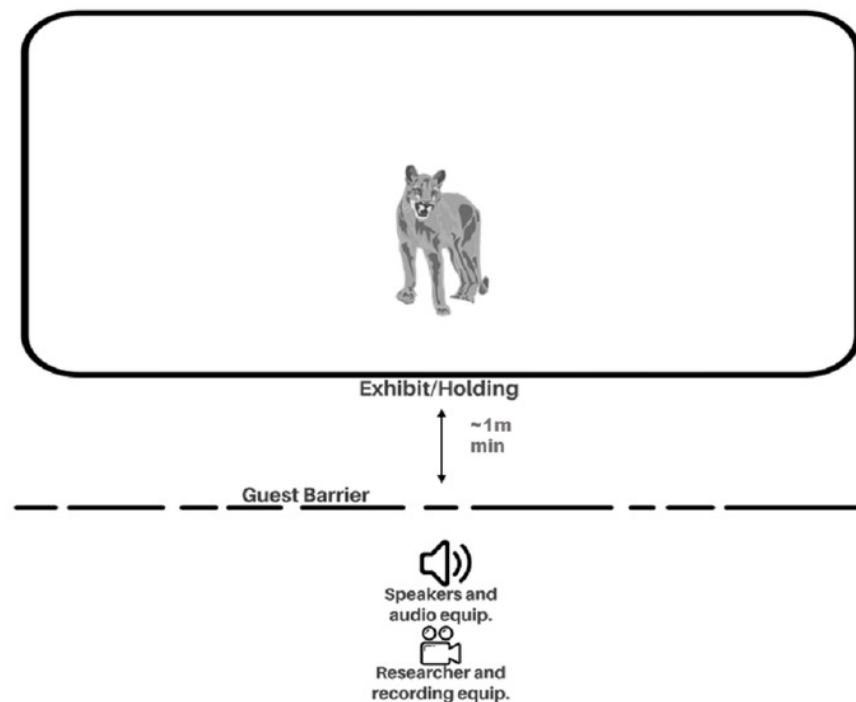
Figure 2

Latency to Respond to Playbacks in Study One
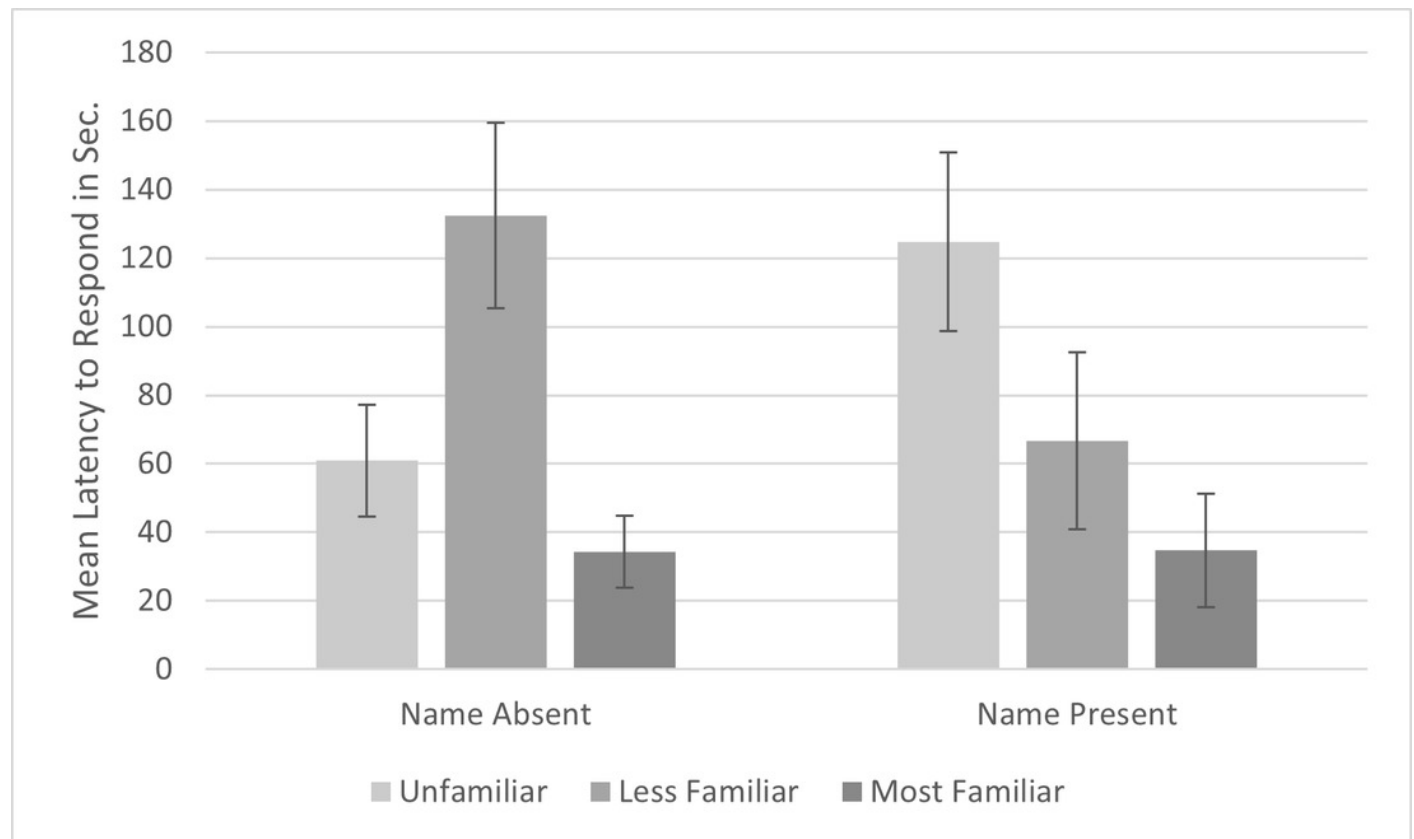
Figure 3

Latency to Respond to Playbacks in the Main Study

Note. Error bars indicate standard deviations.
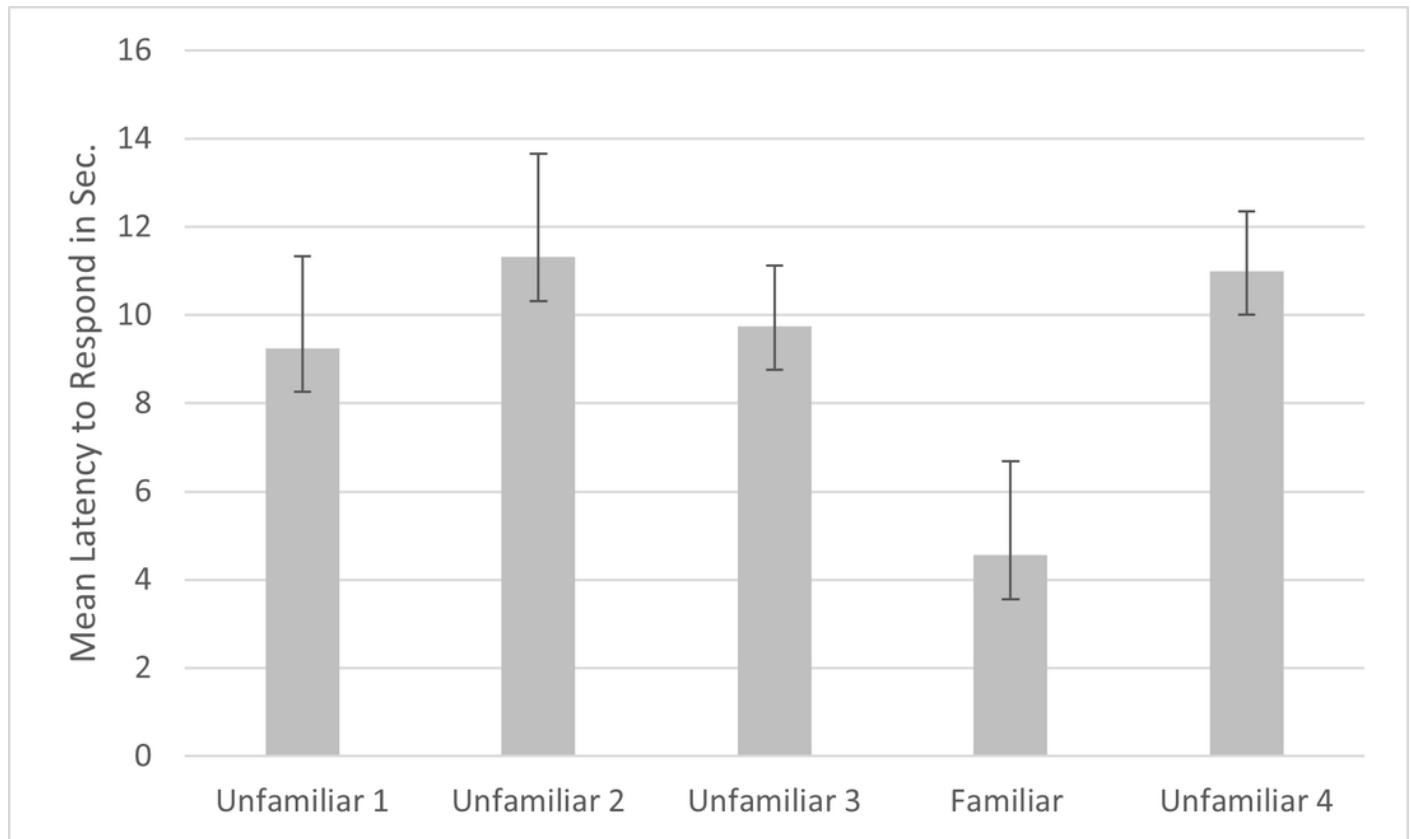
Figure 4

Intensity of Reaction as a Function of Playback Trial in the Main Study.

Note. Intensity was measured from 0 (no response) to 4 (full head turn or locomotion towards speaker) of the first reactionary behavior following each playback.
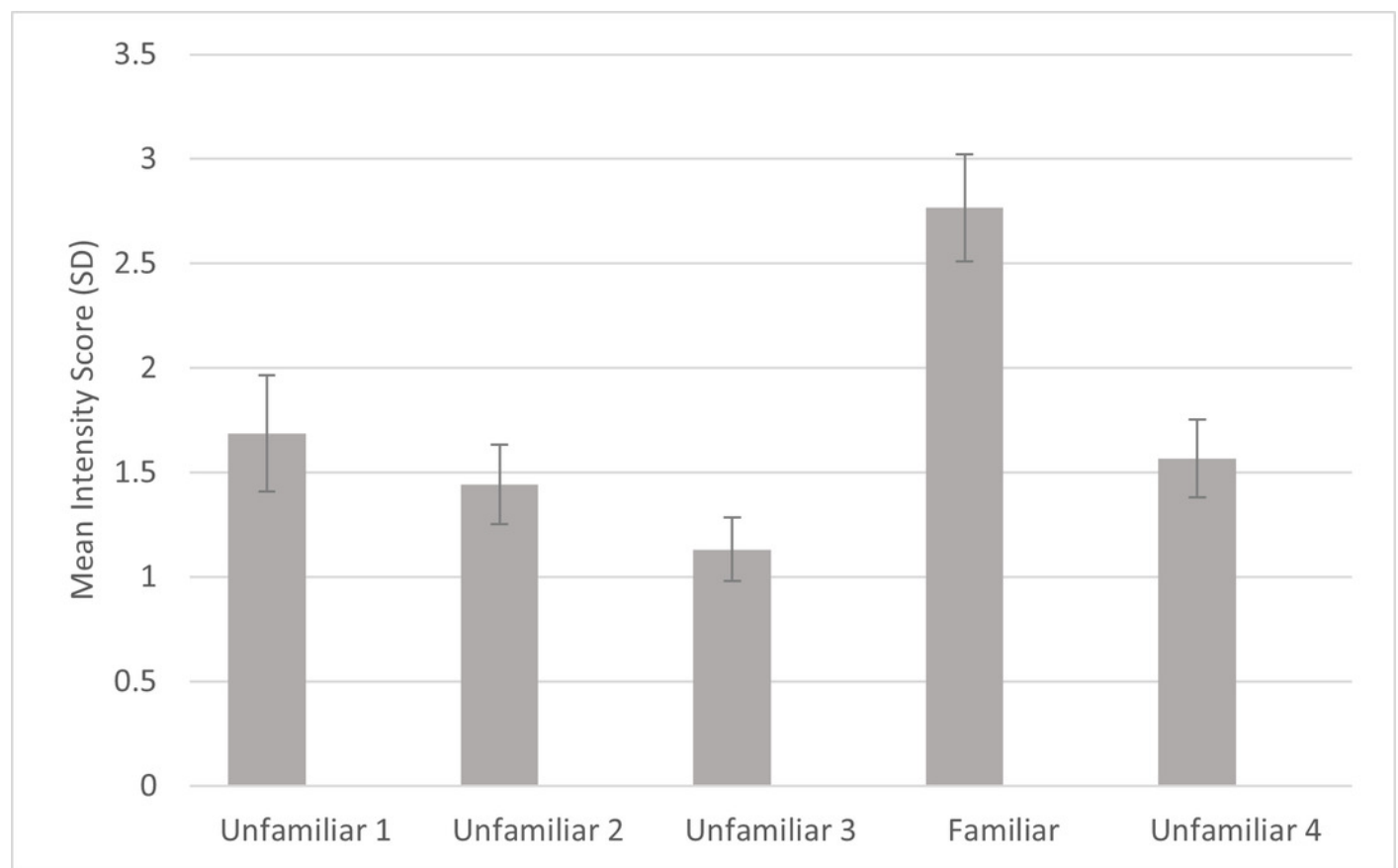
Figure 5

Duration of Behavior as a Function of Playback Trial