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Evaluating mood changes in response to anthropogenic noise with a response-slowng
task in three species of zoo-housed primates

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Abstract

In the zoo environment anthropogenic noise is common as sound levels fluctuate due to visitors, construction, habitat design, and special events. In this study, changes in the mood of three species of zoo-housed primates in response to a loud annual event were evaluated with the response-slowing paradigm. In this paradigm, animals experiencing anxiety slow responses on simple cognitive tasks when emotional content is displayed. Following a previously validated approach, we measured latencies to touch potentially threatening (conspecific faces with directed gaze) and non-threatening (conspecific faces with averted gaze) images overlaid on a grey square, relative to neutral control images (grey squares only) on a touchscreen. In Experiment 1, four Japanese macaques (*Macaca fuscata*) were tested in two conditions: during a baseline (non-stressful) period and opportunistically during three days during which loud jets frequently flew overhead. Results indicated a significant effect of condition, with an increase in latency to touch images of conspecific faces relative to control images during the days of the loud event. In Experiment 2, chimpanzees (*Pan troglodytes*, n = 4) and western lowland gorillas (*Gorilla gorilla gorilla*, n=2) were tested during the same loud event following a similar methodology. The results revealed subtle changes across conditions, however, this was likely driven by the apes increasing their response speed to face stimuli relative to control stimuli over time (habituation). These findings suggest that the macaques, but not the apes, underwent detectable affective changes during the loud event. With additional development, this relatively simple paradigm may be an effective and feasible way to evaluate real-time changes in the mood of zoo-housed animals.

44 *Keywords:* response slowing, zoo, mood, affect, *Macaca fuscata*, *Gorilla gorilla*, *Pan*
45 *troglodytes*, noise

46 Anthropogenic noise can influence animal behavior, physiology and well-being
47 through effects on the auditory system, interference with sounds important to survival
48 and reproduction, and generation of startle or fear-related responses (Blickley &
49 Patricelli, 2010; Wright et al., 2007). Anthropogenic noises are often more frequent,
50 louder, and less predictable than natural (non-anthropogenic) acoustic stimuli (Kight
51 & Swaddle, 2011). In the zoo environment anthropogenic noise is common, as sound
52 levels may increase due to visitors, construction, habitat design, and special events.
53 Past studies have evaluated how various sources of noise in the zoo environment
54 influence behavioral and physiological indicators of welfare in a variety of species
55 (e.g., Birke, 2002; Chosy, Wilson, & Santymire, 2014; Davey, 2007; Kight &
56 Swaddle, 2011; Orban, Soltis, Perkins, & Mellen, 2017; Quadros, Goulart, Passos,
57 Vecci, & Young, 2014).

58 There is growing consensus that one of the essential contributors to an
59 animal's welfare state is their subjective, or affective experience (Dawkins, 2015;
60 McGuire, Vonk, Fuller, & Allard, 2017; Mellor, 2015; Whitham & Wielebnowski,
61 2013). However, to date there has been no research directly investigating the
62 relationship between anthropogenic noise and affective state in zoo-housed animals.
63 Several approaches to evaluating affective states that rely on judgement biases have
64 emerged in recent years (reviewed in Bethell, 2015), and most require extensive
65 training of the animals involved (Deakin, Browne, Hodge, Paul, & Mendl, 2016;
66 Harding, Paul, & Mendl, 2004; Mendl, Burman, Parker, & Paul, 2009; but see
67 Brydges & Hall, 2017). However, one recently-developed paradigm, the "response-
68 slowing paradigm," does not require extensive training and, therefore, is more feasible
69 for use in a zoo environment (Bethell, Holmes, MacLarnon, & Semple, 2016). The
70 response-slowing paradigm is grounded in human psychological research, and

71 specifically, the discovery that people experiencing anxiety show an impairment
72 (slower response time) on simple cognitive tasks when emotionally threatening
73 content is displayed, compared to non-anxious individuals (reviewed in Bar-Haim,
74 Lamy, Pergamin, Bakermans-Kranenburg, & Van Ijzendoorn, 2007; Mogg &
75 Bradley, 2016).

76 Bethell et al. (2016) demonstrated that the response-slowing paradigm can be
77 used to detect anxious mood in laboratory-housed rhesus macaques (*Macaca mulatta*)
78 who had recently undergone veterinary exams. The authors trained the macaques to
79 touch a plain grey square presented on a touchscreen monitor and then measured
80 changes in latency to touch the square when emotional content (images of
81 conspecifics directing gaze at the subject) was added to the square. Direct gaze is a
82 threatening communicative signal for macaques (Maestriperi, 1997), therefore, the
83 authors presumed that the squares containing conspecific direct gaze images had
84 negative emotional valence. Relative to their performance on control trials, the
85 monkeys were slower to touch the direct gaze face when they had recently undergone
86 a presumably stressful veterinary procedure, compared to less-stressful, baseline
87 periods. The authors found no such slowing effect following the veterinary exam for
88 images containing averted (submissive) gaze faces. Together, these findings suggest
89 that response latencies to touch single images presented on a touchscreen may provide
90 a measure of changes in affective state without the need for extensive training. In the
91 following experiments we adapted these methods for use with macaques in a zoo
92 setting (Experiment 1) and then applied a similar methodology for use with other
93 primate species in zoos (chimpanzees and western lowland gorillas) (Experiment 2).

94

95

Experiment 1

96

97 In Experiment 1, we applied the response-slowing paradigm to test whether
98 zoo-housed Japanese macaques (*Macaca fuscata*) experience changes in affect
99 corresponding with a noisy, annual public event, the Chicago Air and Water Show.
100 This event spans three days and is characterized by loud, low-flying jets intermittently
101 passing directly over the macaques' habitat. Previous work has shown that loud noises
102 such as heavy machinery and vehicles, over which macaques have no control, lead to
103 increases in plasma cortisol, aggression, and other behavioral indicators of stress
104 (Hanson, Larson, & Snowdon, 1976). We hypothesized that the monkeys would
105 experience anxious mood during the days of the Air and Water Show and show an
106 impairment (slower response time) on a simple cognitive task when emotionally
107 threatening content is displayed, compared to a baseline period.

108 **Method**

109 **Subjects.** Four Japanese macaques (one male and two females, 9-10 years old,
110 and one male, 1-year old), who were members of a troop of 12 housed at Lincoln Park
111 Zoo (Chicago, USA), voluntarily participated in this study.

112 **Materials and Testing Environment.** The full troop was comprised of three
113 adult males, five adult females, one juvenile male and three infant females. The troop
114 inhabited a large naturalistic outdoor habitat of 685 m² equipped with natural and
115 artificial trees, bushes, large rocks, a pool, grass and mulch during days with
116 additional indoor space (348 m²) available during nights and times of low
117 temperatures or inclement weather. Fresh produce and monkey chow were scattered
118 daily throughout their habitat and monkeys had access to water *ad libitum*.

119 Testing took place in one of two touchscreen computer booths integrated into
120 the monkeys' outdoor habitat (Figure 1). Stimuli were presented on a 22" Viewsonic

121 TD2240 touch-sensitive monitor connected to a personal computer in the adjacent
122 researcher area. A stimulus consisting of a grey rectangular frame measuring 10.2 x
123 12.7 cm (width x height on screen) served as the control stimulus. Test stimuli
124 consisted of color photographs of Japanese macaques obtained from the Internet (non-
125 copyrighted images from www.flickr.com and Google image search). Pictures were
126 selected for neutral expressions directing gaze toward the camera (12 pictures and
127 their mirror image resulting in 24 stimuli) or averting their gaze from the camera (12
128 pictures and their mirror image resulting in 24 stimuli). In Adobe Photoshop CS4,
129 images were trimmed so that only the macaque's head was visible and superimposed
130 onto the grey stimulus used for control trials (resulting in control and test images of
131 equal size). Luminosity and contrast energy were obtained for each image and there
132 were no significant differences in either measure between directed and averted stimuli
133 sets (two-sample t-test, luminosity $t(22) = 0.484, p = 0.69$; contrast $t(22) = 0.136, p =$
134 0.89).

135 **Procedure.** All participation was voluntary; the macaques could enter or exit
136 the booth through a hinged hanging door at any time during the test sessions that took
137 place weekdays between 11:20 AM and 1:00 PM. Sessions were paused when more
138 than one monkey was present in the booth to avoid aggression and allow clear
139 identification of the participant.

140 Prior to participation in this study, monkeys were trained to touch a single dot
141 when it appeared on the screen in order to receive a food reward (using Zenrichment
142 ApeTouch software). This training began in March 2015. PsychoPy version 1.83.04
143 (Peirce, 2009) was used to program and run the present experiment (Psychopy
144 software is free; experiment code available upon request).

145 Following the methods of Bethell et al. (2016), on each trial, monkeys were

146 presented with one image: either the control stimulus (grey square), a grey square
147 containing a direct-gaze stimulus, or a grey square containing an averted-gaze
148 stimulus. The trial types (control, direct gaze, averted gaze) were presented in a ratio
149 of 1:2:2 in a random order such that the control stimulus was shown on average half
150 as frequently as the other trial types. On direct-gaze and averted-gaze trials, exemplars
151 were selected randomly without replacement from the 24 available stimuli of each
152 type. The image was vertically centered on a black screen and randomized and
153 counterbalanced between a central, left and right position (Figure 2). We chose the
154 1:2:2 ratio to follow the validated methods of Bethell et al. (2016). Different locations
155 were used to safeguard against position biases. The maximum trial length that a single
156 image was on the screen was 60 s and the inter-trial interval was 8 s, during which
157 time a black screen was shown. If a monkey left the booth mid-trial, the aborted trial
158 was excluded from analyses.

159 The identification of the participating monkey was manually entered into the
160 software prior to their first trial upon each booth entry. Monkeys were rewarded for
161 touching the stimulus with approximately 1/8th of a peanut and a secondary
162 reinforcement tone. Rewards were delivered manually on a 100% reinforcement
163 schedule via a PVC tube that extended from the experimenter area into the
164 touchscreen booths (Figure 1). Response latencies (time elapsed between presentation
165 of stimulus and touch) were recorded automatically by the computer. Given that
166 participation was voluntary and monkeys were free to enter and exit the booth, there
167 was no set number of trials per day, but a 50-trial maximum per day per subject was
168 imposed, after which no additional trials appeared on the screen.

169 Subjects were tested during a baseline condition and during three days of the

170 2016 Chicago Air and Water Show (A&W) during which loud, low-flying jets passed
171 over the habitat between seven and 80 times each day between the hours of 10:00 AM
172 and 4:00 PM. The monkeys had been exposed to the jet noise only once previously
173 (2015) during which time we observed fleeing, defecating and hiding, leading us to
174 plan to test changes in affect during the 2016 A&W. During the A&W test sessions,
175 monkeys did not voluntarily participate at the exact times that jets flew overhead, as
176 they tended to gather and seek cover in their habitat during those moments. For three
177 of the four subjects the baseline condition preceded A&W and for one subject the
178 baseline period followed A&W. The number of baseline days experienced by each
179 monkey varied based on their rate of voluntary participation, as we stopped baseline
180 data collection for an individual once 200 trials were obtained (range 5-7 days). There
181 was a minimum of one month (31 days) between baseline data collection and A&W
182 data collection. The identity of the researcher was constant across conditions.

183 This study was approved by the Lincoln Park Zoo Research Committee, the
184 governing body for all animal research at the institution. No modifications were made
185 to standard animal care routines and the A&W was outside the control of Lincoln
186 Park Zoo. This research adhered to legal requirements in the United States of America
187 and to the American Society of Primatologists' Principles for the Ethical Treatment of
188 Nonhuman Primates.

189 **Statistical Analysis.** Analyses were conducted in R version 3.3.1 (R Core
190 Team, 2014). Histograms of response latencies were visualized and latency data were
191 trimmed so that responses greater or less than 2.5 standard deviations from each
192 participant's mean were excluded in order to remove outliers (Ratcliff, 1993). Data
193 were also analysed with trims of 2.0 and 3.0 SD and results did not differ from those
194 reported below. The histogram revealed a positive skew in the distribution, therefore,

195 data were normalized using a \log_{10} transformation. Reaction time ratio scores for each
196 subject were calculated for direct gaze and averted gaze trials following Bethell et al.
197 (2016). Specifically, the reaction time ratio (RTRatio) for each gaze trial was
198 calculated as \log_{10} latency gaze trial/mean \log_{10} latency control trial, where the
199 denominator was calculated separately for each monkey in each condition to account
200 for differences in response speeds that may be due to attention or arousal. RTRatios
201 >1 reveal slowing of responses toward faces relative to control trials (i.e., the grey
202 square), while ratio scores <1 reveal speeding of responses toward faces relative to
203 control trials.

204 Data were analysed using a linear mixed effects model that included subject
205 and unique image ID as random effects and condition (baseline vs A&W), trial type
206 (directed gaze vs averted gaze), and the interaction between condition and trial type as
207 fixed effects to predict the dependent variable RTRatio. We also included by-subject
208 random slopes for the effect of RTRatio (Barr, Levy, Scheepers & Tily, 2013).
209 Likelihood ratio tests using the anova function and chi-square distribution were used
210 to compare the full model with null models excluding each variable of interest
211 (condition, trial type, and their interaction). The assumptions of linearity and the
212 absence of heteroscedasticity were examined through plotting residuals, the
213 assumption of normality through visualisation of a Q-Q plot, and the absence of
214 collinearity of predictors was assumed from model design. Mixed-effects models
215 were run using the lme4 package (Bates, Maechler & Bolker, 2014).

216 **Results**

217 Each monkey participated in 5-7 baseline test days (completing 200 trials,
218 with the exception of one monkey who completed only 100 trials due to computer
219 error), and 1-2 days during A&W (completing 23, 27, 55 or 100 trials). No monkey

220 reached the maximum trial length (60 s) on any trial. There was no evidence of
221 habituation over sequential trials during the baseline period (Pearson correlation, trial
222 number and logRT, separately by subject and excluding control trials, all $p > 0.10$).
223 The full-null model comparison examining the effect of condition (baseline vs A&W)
224 was significant ($\chi^2_1 = 9.32, p = 0.03$), and the full-null model comparison examining
225 the effect of trial type (averted vs directed) was not significant ($\chi^2_1 = 2.33, p = 0.13$).
226 Full-null model comparisons revealed no significant interaction between condition
227 and trial type ($\chi^2_1 = 0.05, p = 0.83$). Complete model results are available in the
228 Supplemental Information. RTRatios were greater during A&W (mean RTRatio =
229 1.57) than at baseline (mean RTRatio = 0.98), revealing slowing of responses on
230 experimental trials relative to control trials (Figure 3).

231 **Discussion**

232 In Experiment 1, Japanese macaques demonstrated an increase in their latency
233 to touch stimuli containing images of conspecific faces relative to control stimuli
234 lacking conspecific faces during the days of a loud event. These findings suggest that
235 the macaques experienced changes in affect during the Air and Water Show. We also
236 predicted that the macaques would respond differently to the directed and averted
237 faces, presuming the first would be emotionally threatening and, therefore, elicit a
238 response-slowing effect while the latter would not. However, in Experiment 1 the
239 comparison between directed and averted faces was not significant. Furthermore, we
240 are limited in our ability to consider expected changes in response times over time
241 given that only one of the four subjects experienced a post-test baseline period. In
242 Experiment 2, we expand the scope of the study to assess response slowing in
243 response to the same loud event in zoo-housed chimpanzees (*Pan troglodytes*) and
244 gorillas (*Gorilla gorilla gorilla*).

245

246

Experiment 2

247

248 **Method**

249 **Subjects.** Four chimpanzees (one male and three females, range 18-33 years
250 old) and two western lowland gorillas (one female and one male, aged 21 and 28
251 years) housed at Lincoln Park Zoo in mixed-sex social groups of six and seven,
252 respectively, voluntarily participated in this study. The apes who participated in this
253 study were the same apes that regularly participate in the Lincoln Park Zoo
254 touchscreen research program.

255 **Materials and Testing Environment.** The gorillas and chimpanzees were
256 housed in naturalistic indoor and outdoor exhibits. Access to the outdoor yard was
257 temperature dependent (>5 degrees C) and during the course of the study all apes had
258 outdoor access at varying times. Indoor spaces ranged from 72 m² to 124 m² in size;
259 adjacent outdoor yards ranged in size from 116 m² to 1127 m². Exhibits incorporated
260 climbing structures, deep-mulch bedding, and additional off-exhibit holding areas.
261 Fresh produce and chow were scattered daily throughout their habitat and apes had
262 access to water *ad libitum*.

263 Apes were tested on touchscreen monitors attached to a mobile cart adjusted to
264 the height of each animal. During testing, the touchscreen was flush against the mesh
265 (5.1 cm x 5.1 cm) along the perimeter of their indoor habitat (Figure 4). For one
266 female gorilla, social group members were stationed by keepers in several locations
267 simultaneously to allow her to work uninterrupted by conspecifics for approximately
268 five minutes. All other apes were tested freely in their social group without
269 conspecific stationing as they were not interrupted by others. As with the macaques

270 tested in Experiment 1, stimuli were presented on a 22" Viewsonic TD2240 touch-
271 sensitive monitor connected to a personal computer in the adjacent researcher area.

272 Experiment 2 was run using ApeTouch Zenrichment software and the stimuli
273 size measured 7 cm x 7 cm on the screen. As in Experiment 1, a grey square served as
274 the control stimulus. Test stimuli consisted of color photographs of chimpanzees or
275 western lowland gorillas unknown to the subjects, obtained from the Internet and
276 selected and processed following the same criteria as Experiment 1. Subjects were
277 shown only stimuli created from faces of conspecifics. Luminosity and contrast
278 energy were obtained for each image and there were no significant differences in
279 either measure between directed and averted stimuli sets (two-sample t-test,
280 luminosity $t(46) = 1.33, p = 0.20$; contrast $t(46) = 1.37, p = 0.18$).

281 **Procedure.** Sessions took place between 13:30 and 15:30 and were voluntary;
282 apes could walk away from the touchscreen at any time. If they did so, the current
283 trial was discarded. Prior to participation in this study, the apes had participated in
284 several touchscreen studies evaluating serial learning and food preferences (e.g., Ross,
285 2009; Egelkamp, Hopper, Cronin, Jacobson, & Ross, 2016).

286 The stimuli were presented following the same methods as Experiment 1, with
287 the exception that the location of the image could appear in any location on the screen
288 rather than 3 pre-set locations, again randomizing locations to safeguard against
289 position biases and maintain interest. The maximum trial length was 60 s and the
290 inter-trial interval was 8 s, during which time a black screen was shown. If an ape
291 walked away from the touchscreen mid-trial, the aborted trial was excluded from
292 analyses.

293 The identification of the participating ape was manually entered into the
294 software prior to their first trial. Apes were rewarded for touching the stimulus with a

295 single blueberry and a secondary reinforcement tone on a 100% reinforcement
296 schedule via a PVC tube. As in Experiment 1, participation was voluntary with a 50-
297 trial maximum per day per subject imposed, after which no additional trials appeared
298 on the screen.

299 Subjects were tested during the 2017 Chicago Air and Water Show (A&W)
300 and two baseline periods, one beginning 30 days prior to the onset of A&W and one
301 beginning 18 days after A&W testing was complete. The identity of the researcher
302 was constant across conditions. Baseline data collection for an individual ceased once
303 200 trials were obtained, and apes completed each baseline period in five (minimum)
304 to 10 (maximum) days. Data were collected on three days during the Air & Water
305 Show. All apes participated on all three days except for one gorilla who participated
306 on only two days. All apes had been exposed to the jet noise annually since they
307 arrived at Lincoln Park Zoo in 2004.

308 In 2017 we also obtained sound recordings to assess decibel levels on zoo
309 grounds during the Air & Water Show. Using a sound level meter (SongMeter Model
310 SM2+, Wildlife Acoustics), we recorded 10-minute audio samples sequentially and
311 continuously between the hours of 1000 and 1600 during the three days of Air &
312 Water testing. We extracted the maximum dBA level per sample using the software
313 Praat (Boersma & Weenink, 2017). For comparison, we repeated sound pressure level
314 sampling during three days of the second baseline phase.

315 This study was approved by the Lincoln Park Zoo Research Committee, the
316 governing body for all animal research at the institution. No modifications were made
317 to standard animal care routines and the A&W was outside the control of Lincoln
318 Park Zoo. This research adhered to legal requirements in the United States of America

319 and to the American Society of Primatologists' Principles for the Ethical Treatment of
320 Nonhuman Primates.

321 **Statistical Analysis.** Analyses were conducted following the same methods as
322 Experiment 1, with the exception that there were three levels of condition (pre-
323 baseline, A&W, post-baseline). Given the small sample per species, chimpanzee and
324 gorilla responses were collapsed for analyses (*sensu* Howard, Wagner, Woodward,
325 Ross, & Hopper, 2017).

326 **Results**

327 Each ape voluntarily completed 200 trials during the pre-baseline (pre-BL)
328 and post-baseline (post-BL) periods, with the exception of one female gorilla who
329 completed 191 pre-BL trials and 160 post-BL trials. Apes completed between 57 and
330 150 trials during A&W (one ape completed 57, one completed 65, one completed 116,
331 and three completed 150). No ape reached the maximum trial length on any trial.

332 The full-null model comparison examining the effect of condition (pre-
333 baseline, A&W, post-baseline) revealed marginal significance ($\chi^2_1 = 5.61, p < 0.06$).
334 The direction of the coefficients indicates that the direction of RTRatio change across
335 conditions followed a chronological decrease from pre-baseline to A&W to post-
336 baseline (reference category = Air & Water, pre-baseline $\beta = 0.004$, SEM = 0.004,
337 post-baseline $\beta = -0.005$, SEM = 0.004; Figure 5). The full-null model comparison
338 examining the effect of trial type (averted vs directed) was not significant ($\chi^2_1 = 2.33$,
339 $p = 0.13$). Full-null model comparisons revealed no significant interaction between
340 condition and trial type ($\chi^2_1 = 2.69, p = 0.26$). Taken together, the results indicate that
341 the apes exhibited a slowing in their latency to touch faces relative to controls over
342 subsequent conditions and did not treat directed and averted faces differently (Figure
343 5). Complete model results are available in the Supplemental Information.

344 Visual inspection of the spectrograms produced during the 2017 Air & Water
345 Show reviewed in conjunction with fly-over times documented by researchers
346 indicated that most flyovers were identifiable in the spectrograms by brief spikes
347 exceeding 90 dBA. During the 2017 A&W show, results revealed that 14.6% of audio
348 samples registered sound pressure levels above 90 dBA (max dBA recorded = 93.5).
349 In contrast, only 1.0% of audio samples registered sound pressure levels above 90 dB
350 during the matched control period.

351 **Discussion**

352 In Experiment 2 we measured whether zoo-housed chimpanzees and gorillas
353 showed a response-slowing effect on a touchscreen task during the days of a loud
354 event to evaluate changes in mood. We obtained sound pressure levels to better
355 characterize the event, and found that levels regularly exceeded 90 dBA producing
356 short, unpredictable bouts of loud noise overhead. The experimental design expanded
357 upon the design of Experiment 1 with all subjects tested in two baseline periods, one
358 preceding and one following the loud event. We predicted that if the event negatively
359 impacted the apes' mood, we would observe a response slowing effect during the Air
360 and Water Show condition relative to both baseline conditions. However, when
361 examining the trend toward a significant effect of condition, responses generally
362 increased in speed relative to control trials over time. Similar to the macaques, the
363 apes did not respond differentially to directed and averted faces. The implications of
364 these findings are discussed together with the results of the Japanese macaques in the
365 General Discussion.

366

367 **General Discussion**

368 This study evaluated changes in affect resulting from anthropogenic noise in a
369 zoo environment. The response-slowing touchscreen task used here suggests that zoo-
370 housed Japanese macaques' underwent changes in mood during a loud annual event,
371 the Chicago Air & Water Show. This interpretation follows from the finding that,
372 during the days of the event, the latency to touch conspecific images, relative to
373 control images, slowed compared to a baseline period. A second experiment was
374 conducted to test whether the mood of chimpanzees and gorillas was affected by the
375 same loud event the following year. The results for the apes were more ambiguous.
376 There was a trend toward significant differences in response latencies to faces
377 compared to controls between baseline days and A&W Show days, but overall, the
378 apes responded to the face stimuli with increasing speed over subsequent conditions,
379 suggesting potential habituation to the stimuli. The full model results, including odds
380 ratios indicating the magnitude and direction of differences, are available in the
381 Supplemental Information.

382 We tentatively conclude the Japanese macaques experienced a change in affect
383 in response to the loud jets passing overhead whereas the apes did not. The difference
384 in affective response may stem from differences in habitat design and testing location,
385 as the macaques spend the majority of their daytime outdoors and touchscreen tests
386 took place in the periphery of their outdoor habitat. In contrast, the apes choose to
387 spend the majority of their time indoors (Kurtycz, Wagner, & Ross, 2014) and their
388 touchscreen tests also took place inside. The sound level recordings reflect the noise
389 level on zoo grounds outside, and by being inside the apes may have been shielded
390 from some of the noise of the A&W Show. Alternatively or additionally, the
391 difference between macaques and apes may have arisen from different histories of
392 exposure to the noisy event. Specifically, the macaques were tested during their

393 second year of exposure having arrived at the zoo in 2014, whereas the apes had been
394 exposed for 13 consecutive years. The apes may simply have habituated to the noise
395 or learned that it did not pose a threat.

396 It is also possible that the emotionally threatening stimuli used in this study
397 (direct gaze faces) were not perceived as emotionally threatening by the apes. We
398 tested both sexes of chimpanzees and gorillas with stimuli obtained from conspecifics
399 of both sexes, and it may be females directing gaze toward males is not a biologically
400 relevant stressor in species with male dominance and extreme sexual dimorphism.
401 Unfortunately our ape sample is not large enough to consider whether there is an
402 interaction between the subject's sex and the sex of the conspecific stimuli. It is also
403 likely that there are individual differences contributing to the results obtained here,
404 and teasing out how personality or temperament influences responses to social stimuli
405 is an important future direction. Related, there may have been self-selection among
406 the subjects in that the subset of touchscreen trained animals who voluntarily
407 participated during the Air and Water Show may have been willing to do so because
408 they experienced less stress than groupmates (see Morton, Lee, & Buchanan-Smith,
409 2013; Polgar, Wood, & Haskell, 2017). However that would only have led us to
410 underestimate the impact on mood for Japanese macaques. Finally, it is possible that
411 the difference between the macaques and apes may have arisen due to different
412 evolved predator responses. Macaques are under more threat from aerial predators
413 than apes (Iida, 1999), and noises from above the habitats may elicit a stronger stress
414 response from the macaques than apes. While we speculate about the potential
415 explanations for the differences between the macaques and the apes, we remain
416 cautious in our conclusion of species differences given that the response-slowing
417 paradigm has not yet been validated for apes as it has for macaques.

418 The pattern of response slowing that emerged when we introduced a second
419 baseline period in Experiment 2 suggests that habituation to face stimuli is a
420 possibility that may limit the utility of this paradigm. This limitation may be
421 especially pronounced given the frequent presentation of the face stimuli in the
422 present design. However, habituation cannot explain the pattern of results obtained for
423 the Japanese macaques given that three of the four subjects were tested in a baseline
424 period that *preceded* the Air and Water Show, yet the responses to face stimuli *slowed*
425 during the Air and Water Show. Moving forward, determining ideal ratios for
426 displaying face and control stimuli that generate a sufficient amount of repeated
427 samples from individuals to provide enough statistical power to test hypotheses about
428 changes in mood, while simultaneously minimizing habituation, will be essential to
429 creating a useful method. Researchers may also consider the possibility of changing
430 face stimuli throughout the experiment to minimize the potential for habituation,
431 although this strategy would come at the cost of introducing an additional source of
432 variation across conditions.

433 The response-slowing paradigm is motivated by the finding that emotional
434 content slows response times on simple tasks for humans experiencing anxiety.
435 However, the relationship between anxiety and biases in cognitive and attentional
436 processes is complex with several potential mechanisms at play (Mogg & Bradley,
437 2016). The pattern of results observed here for Japanese macaques, and for rhesus
438 macaques in Bethell et al. (2016), is consistent with a number of (non-mutually
439 exclusive) interpretations involving attention to threat and a subtle cognitive freeze
440 response. Under stressful conditions, animals may invest additional resources to
441 maintain a state of high social vigilance (Ebitz, Watson, & Platt, 2013). In the
442 response-slowing paradigm, the monkeys may be responding slower under stress

443 because their attention is more strongly captured by the conspecific faces (e.g.,
444 Bethell et al., 2012; Bradley, Mogg, & Miller, 2000; Garner, Mogg, & Bradley,
445 2006). An alternative explanation is an enhanced freeze response to conspecific faces
446 in macaques during the presumably stressful Air and Water Show (Bethell et al.,
447 2016). In order to experimentally test whether heightened vigilance is in fact the
448 mechanism responsible for the slowing, future work could disentangle the behavioral
449 response (touching the image) from the removal of the threatening stimuli
450 (disappearance of the image). Alternatively, adapting spatial cueing tasks (e.g., Kalin,
451 Shelton, Rickman, & Davidson, 1998; Parr, Modi, Siebert, & Young, 2013) in which
452 the spatial location of threatening stimuli is either consistent or inconsistent with the
453 location of a required response (e.g., a screen touch) to be used under stressful and
454 non-stressful conditions could be a fruitful way forward, as this approach would
455 measure which stimuli attract attentional investment.

456 Although we found an effect of condition that indicates monkeys responded
457 differently during A&W compared to baseline, and these findings were standardized
458 by condition-specific response speeds to control trials to account for variability across
459 conditions due to arousal or practice, we did not find a difference in response slowing
460 between averted and directed faces in either experiment. This pattern of results differs
461 from those of Bethell et al. (2016) that showed slowing in response to directed but not
462 averted faces in veterinary-stressed rhesus macaques. There are many potential
463 explanations for this difference including differences in the sex of subjects and stimuli
464 (Bethell et al., 2016 used all males for both), differences in laboratory and zoo
465 housing conditions, and potential differences in baseline levels of anxiety.
466 Furthermore, we may have lacked the statistical power necessary to detect a
467 difference between directed and averted faces or the distinction between directed and

468 averted faces may have been less pronounced in our study. There may also be species
469 or individual age or personality differences influencing our findings (Adams et al.,
470 2015; Wright et al., 2007). However, if the lack of a significant interaction represents
471 that the primates truly respond similarly to direct and averted faces, then either both
472 image types are being interpreted as threatening or the primates are not affected by
473 whether the image content is threatening as we assume in this paradigm. If the latter
474 interpretation is true, we still maintain that something about the macaques' affective
475 state has likely changed between the baseline and noise conditions given that their
476 responses to social versus non-social stimuli changed. What this reveals about the
477 state of the animal remains to be determined with future work aimed at unpacking the
478 mechanisms underlying the effect.

479 This study investigated the impact of noisy, unpredictable, repeated events on
480 the mood of zoo-housed Japanese macaques, chimpanzees and gorillas. The results
481 suggested a negative impact of the events on the mood of the Japanese macaques
482 through a change in the macaques' behavior on a response-slowing task consistent
483 with an anxious state. Whether other loud events that are common to zoo
484 environments, such as special events for donors or concerts, have an effect on the
485 mood of zoo animals remains to be determined. This report also demonstrates the
486 feasibility of voluntary cognitive testing in three primate species without isolating
487 subjects from their social group, which can increase the feasibility and validity of
488 cognitive testing (Cronin, Jacobson, Bonnie & Hopper, 2017). With further
489 development, the response-slowing paradigm used here may be an effective and
490 feasible way to evaluate real-time changes in the mood of zoo-housed animals under a
491 variety of circumstances.

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600 **Figures**

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602 Figure 1. Touchscreen computer booths integrated into the Japanese macaque habitat
603 at the Lincoln Park Zoo.

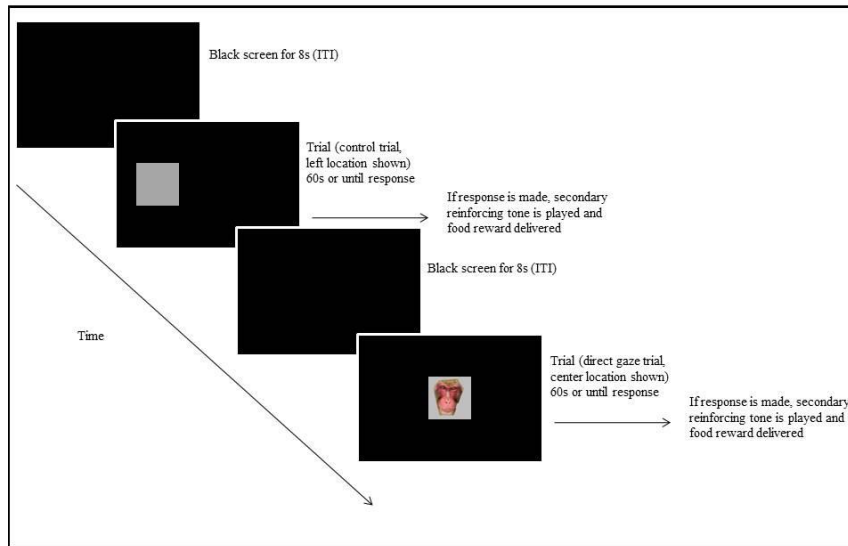
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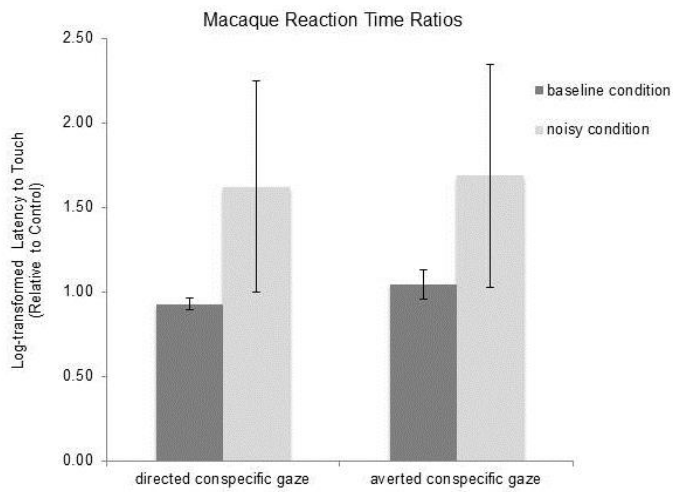
606 Figure 2. Example of the experimental procedure.

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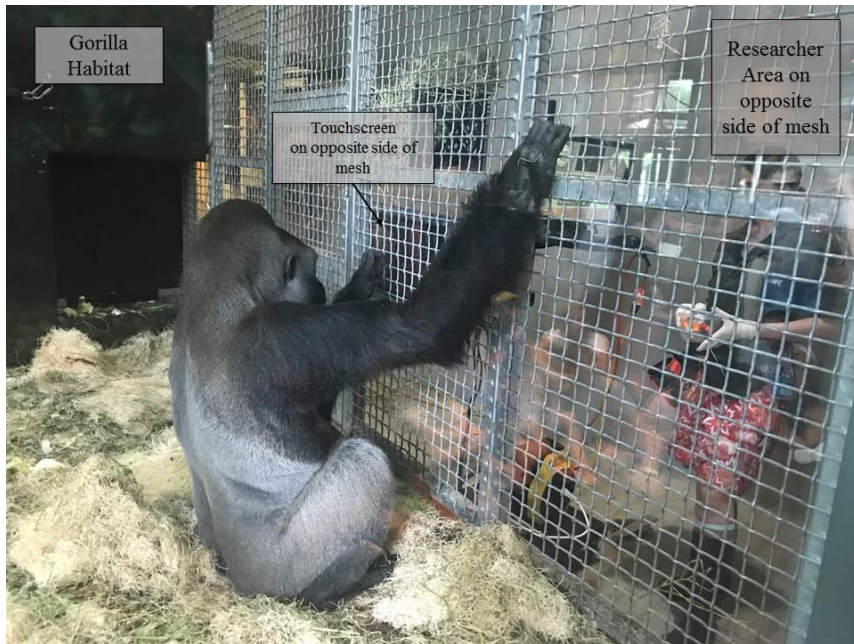
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609 Figure 3. Mean Reaction Time Ratios (\pm s.e.m.) for Japanese macaques across
610 baseline and noisy conditions for both trial types. The reaction time ratios are
611 standardized by the latency to touch control images in each condition, therefore,
612 values >1 indicate that subjects touched conspecific images more slowly than control
613 images, and values <1 indicate that subjects touched conspecific images more quickly
614 than control images.
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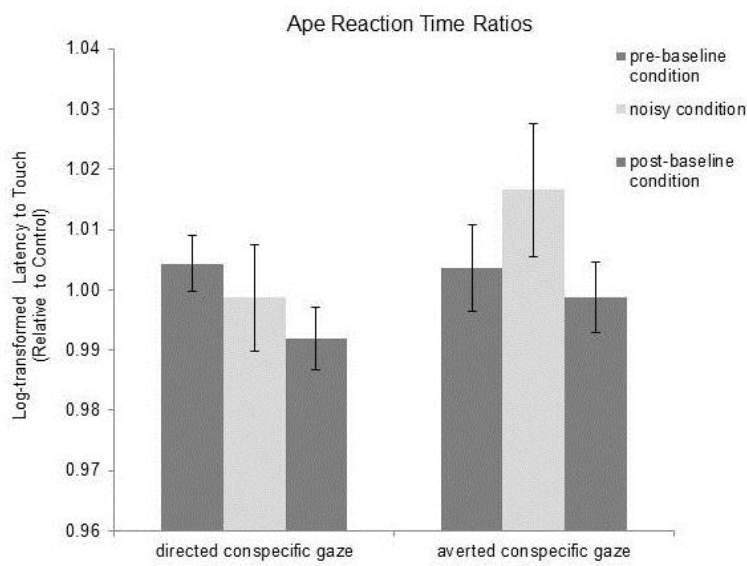
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619 Figure 4. Touchscreen computer session taking place in gorilla habitat at Lincoln Park
620 Zoo.
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625 Figure 5. Mean Reaction Time Ratios (\pm s.e.m.) for chimpanzees and gorillas across
626 conditions for both trial types. The reaction time ratios are standardized by the latency
627 to touch control images in each condition, therefore, values >1 indicate that subjects
628 touched conspecific images more slowly than control images, and values <1 indicate
629 that subjects touched conspecific images more quickly than control images.



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