

1 **Food calls enhance visual discrimination learning in chimpanzees (*Pan troglodytes verus*)**

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Abstract

20 Social learning is of universal importance to animal life and communication is likely to foster
21 it. How do animals recognise when others produce actions that lead to relevant new
22 information? To address this, we exposed four chimpanzees to an arbitrary learning task, a
23 two-choice visual discrimination paradigm presented on a touch screen that led to food
24 rewards. In each trial, images were paired with one of four acoustic treatments: 1) relevant or
25 2) irrelevant chimpanzee calls ('rough grunts' to food; 'pant grunts' to a dominant
26 conspecific), 3) a mechanical noise (hammer knocking sounds) 4) silence. As we were
27 interested in the effect of food calls on learning speed as compared to control stimuli, each
28 chimpanzee was tested with the food call treatment, and one of the three control stimuli
29 (either the pant grunt, mechanical noise or silence condition). We found that learning was
30 significantly enhanced in the contextually correct 'rough grunt' condition, suggesting that
31 food calls may play a role in the cultural transmission of food preferences, by priming
32 individuals about a learning opportunity. We discuss these findings and propose that, at least
33 in chimpanzees, the enhancing effect of these vocalisations may be related to the way they
34 affect receivers' motivational/emotional and attentional systems.

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Keywords

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social learning, vocalisation, touch screen, emotion, motivational processes

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40 Introduction

41 Socially-induced learning is a widespread and evolutionarily adaptive phenomenon.
42 [Heyes \(1994\)](#) defined social learning more broadly as "... learning that is influenced by
43 observation of, or interaction with, another animal (typically a conspecific) or its products"
44 ([Heyes, 1994, p. 207](#)). Central to social learning theory is the extent to which social learning
45 processes in nonhuman animals resembles those found in humans, especially imitation and
46 teaching. However, social learning does not need to be restricted to copying actions, as has
47 been shown by years of research into socially-induced food preferences in rats for instance
48 ([Galef, 1996](#); [Galef & Henderson, 1972](#)). Indeed, social learning is thought to evolve whenever
49 attending to others is more beneficial than individual, trial-and-error learning, such as when
50 learning opportunities are rare (e.g., avoiding predation) or potential errors harmful such as
51 for noxious food ([Galef & Giraldeau, 2001](#); [Laland, 2004](#)). Thus, social learning may include
52 processes whereby monitoring the behaviour or products of others endow individuals with an
53 ability to recognise learning opportunities.

54 Some have argued that social living could favour the evolution of such perceptual,
55 attentional and motivational biases toward social information ([Heyes, 2012](#); [Leadbeater, 2015](#)).
56 For example, the 'natural pedagogy hypothesis' proposes that human infants are tuned to
57 ostensive communicative signals and that this in turn facilitates cultural transmission ([Csibra &
58 Gergely, 2011](#)). Tests of the natural pedagogy hypothesis in rhesus monkeys (*Macaca mulatta*)
59 and chimpanzees (*Pan troglodytes*) indicate that ostensive cues do not help focus the
60 receivers' attention on referents ([Bettle & Rosati, 2021](#); [Kano, et al., 2018](#)), unlike in human
61 infants ([Senju & Csibra, 2008](#)). However, there is nonetheless evidence from cotton-top
62 tamarins (*Saguinus oedipus*) that adults produce a distinct type of food vocalisation that is
63 directed at juveniles and which elicits approach and taking of the food offered ([Joyce &
64 Snowdon, 2007](#); [Roush & Snowdon, 2001](#)). Food avoidance also appears vocally-aided by

65 increases in alarm calls and decreases in food call production ([Snowdon & Boe, 2003](#)),
66 suggesting that communication can promote learning. There is further evidence in the
67 predator-avoidance domain that calls can foster learning ([Griffin, 2004](#)), as demonstrated in
68 blackbirds that socially learn to avoid other species, simply from perceiving others' mobbing
69 vocalisations ([Vieth, Curio, & Ernst, 1980](#)). Thus, while ostensive communication may not be
70 useful to primates (besides humans), communicative signals may still facilitate learning about
71 external events, by biasing receivers' attention and motivational drives.

72 One domain in which social learning is likely to be critical is in foraging, particularly
73 for generalist feeders ([Galef & Giraldeau, 2001](#)). East African chimpanzees, for instance,
74 consume fruits from around 80 different plant species, against a background of hundreds of
75 tree species, many of which are probably non-palatable or even noxious ([Whiten, 2017b](#)). In all
76 likelihood, individuals learn to discriminate palatable from non-palatable species by visual
77 cues and by observing which ones are consumed or avoided by other group members, but it is
78 currently unclear whether communication plays a role during this process.

79 Chimpanzees, like many other social species ([Clay, Smith, & Blumstein, 2012](#); [Marler,](#)
80 [2004](#)), produce an acoustically distinct vocalisation when finding food, the 'rough grunt'
81 ([Goodall, 1986](#)), with evidence that the call's acoustic structure varies with perceived food
82 quality, which listeners attend to for foraging decisions ([Slocombe & Zuberbühler, 2005, 2006](#)).
83 But chimpanzee food calls also have a strong social component ([Tagliabate, Reamer, Schapiro,](#)
84 [& Hopkins, 2012](#)), with individuals being more likely to call when socially bonded or dominant
85 individuals are nearby ([Kalan & Boesch, 2015](#); [Slocombe, et al., 2010](#)). A number of functional
86 hypotheses have been put forward, including food advertisement ([Schel, Townsend, Machanda,](#)
87 [Zuberbühler, & Slocombe, 2013](#)), feeding coordination ([Fedurek & Slocombe, 2013](#)) or conflict
88 mitigation ([Ischer, Zuberbühler, & Fedurek, 2020](#)). However, whether food calls play a role in

89 the cultural transmission of food preferences, by priming individuals about a learning
90 opportunity, has not been addressed so far.

91 Here, we tested whether food calls enhanced the learning performance of captive
92 chimpanzees, *P. t. verus*, in a visual discrimination task leading to food rewards, administered
93 on a touch screen. Before each trial, individuals were primed with contextually relevant or
94 irrelevant conspecific vocalisations, i.e., either ‘rough grunts’ (naturally given to palatable
95 foods) or acoustically similar ‘pant grunts’ (naturally given to more dominant individuals).
96 We also administered two additional control conditions, i.e., a mechanical sound or a silent
97 track. As we were interested in the effect of food calls on learning speed, each chimpanzee
98 was tested with the food call treatment and one of the three control conditions (pant grunts,
99 mechanical noise or silence). We assessed how many trials subjects required before reaching
100 a pre-determined learning criterion under the different priming conditions. If food calls
101 facilitate visual discrimination learning leading to food rewards, we predicted faster learning
102 compared to other social and non-social acoustic stimuli.

103

104

Methods

105 Study Site and Subjects

106 This study was conducted with chimpanzees housed at Basel Zoo, Switzerland.
107 During the study period (September 2017 – May 2018), the group consisted of three adult
108 males, six adult females and four juveniles and infants. All individuals were part of a cohesive
109 social group with access to four indoor (totalling 1,030m³) and two outdoor enclosures
110 (totalling 3,900m³). Individuals were fed a mix of fruit and vegetable diet, supplemented with
111 small amounts of proteins, distributed several times throughout the day. Enrichment included
112 different structural installations (varied substrates, swings, climbing structures, hiding places
113 and natural landscapes), opportunities to manipulate objects (boxes, balls, bags, barrels etc.)

114 and food-related challenges (uncommon foods and food puzzles). Social enrichment consisted
115 of training and structured play. The animals were never put under caloric or water restrictions
116 or isolated from the group, as isolation is restricted to medical emergencies.

117 Five of 10 group members had shown an interest in using the touch screen device
118 during the study period, while four of these five reached a level of proficiency sufficient to be
119 included in the experiment (see training procedure for details). They were the three males (10,
120 13, and 15 years old) and one juvenile female (four years old, added to the experiment last).
121 The oldest male was introduced to the group in 2013, while the other three individuals were
122 born at Basel Zoo. Training great apes to use touch-screens in environments where animals
123 are not separated for ethical reasons is an exceedingly time-consuming process, such that our
124 sample size is within the expected range ([for a review on the challenges of using touch-screens in](#)
125 [zoos see Egelkamp & Ross, 2019](#)). Arguably, data from subjects tested in socially unconstrained
126 conditions provide an important complement to a scientific literature largely generated by
127 research facilities where subjects are socially managed ([Baker, 2018](#)).

128

129 **Touch Screen Device and Set-up**

130 The touch screen device consisted of an Iiyama ProLite T1931SR monitor encased
131 within a transparent plexiglass frame (73x55x35cm), with a 16.5x32.5cm opening allowing
132 chimpanzees to insert their arms to reach the monitor, while protecting it from shocks and
133 frontal hits (see supplementary material S1 for pictures). The plexiglass frame was fixed onto
134 a fenced opening, in one of the indoor enclosures, while the centre of the monitor was 52cm
135 above the floor at approximately eye level for a sitting chimpanzee. A small opening centred
136 below the monitor and connecting to the outside of the enclosure via a tube allowed the
137 experimenter to give a reward for successful trials. The experimenter could monitor
138 chimpanzees' approaches via a webcam and also operated the laptop (either MacBook or

139 Dell), connected with a VGA cable to the touch screen. The experimental task was designed
140 in and presented via Matlab (MathWorks ®), using the Psychophysics Toolbox extensions
141 ([Brainard, 1997](#)). A Premio 8 speaker (T.A.G. Montpellier, France) placed directly behind the
142 touch screen, 60cm above floor level and out of sight of the chimpanzees, was used to
143 broadcast sound treatments and reinforcer tones during the discrimination task.

144

145 **Visual Stimulus Presentation**

146 We created a total of eight pairs of matching visual stimuli, such that each chimpanzee
147 received two unique sets to prevent individuals learning to solve the task by watching others
148 (as individuals were not separated). Stimuli were human-made objects, (presumably)
149 unfamiliar to the animals. Within each set, the visual stimuli were selected to be similar in
150 size, shape and colour (Figure 1), to limit any potential image preference bias (see
151 supplementary resource S2 for all picture sets). One picture of each set was randomly selected
152 as the rewarded stimulus (S+) while the second was unrewarded (S-).

153

154 **Audio Stimuli**

155 During each trial, subjects were primed with one of four acoustic stimuli, i.e., a series
156 of food calls (FC), pant grunts (PG), mechanical noises (MN) or silence (SL). The PG, MN
157 and SL conditions served as controls, to ensure that any effect due to the FC condition could
158 not be attributed to individual trial-and-error learning (SL), asocial noise stimulation (MN) or
159 irrelevant social cues (PG). Food calls and pant grunts were from identified captive and wild
160 chimpanzees with known context. We selected high quality recordings where at least four
161 distinct call elements were present (see supplementary materials S3 for audio files). We
162 obtained food call series from two adult males (one captive) and one wild, adult female. This
163 female also provided a pant grunt series emitted in response to an adult male's approach. All

164 recordings were from individuals unfamiliar to the test subjects, to avoid potential familiarity
 165 effects. We used hammer knocking sounds as the mechanical noise as these had spectro-
 166 temporal features that were somewhat similar to chimpanzee calls (Figure 2). As we were
 167 interested in the effect of food calls on learning speed as compared to control stimuli, each
 168 chimpanzee received a FC treatment, and one control stimulus, either a PG, MN or SL
 169 condition (Table 1). Chimpanzees were randomly allocated to each exemplar and control
 170 condition, except for the juvenile female who was allocated to the same FC/SL combination
 171 as Fahamu as she began the experiment after the other three individuals had completed their
 172 tasks and results indicated that further replication of this combination was warranted (see
 173 results section).

174

175 **Figure 2 about here.**

176

177 **Table 1**178 *Repartition of Treatment Conditions and Exemplar Stimuli for each Chimpanzee.*

Subject (Sex)	Test condition/ Sound origin	Control condition/ Sound origin
Colebe (M)	FC/ Male A (wild)	PG/ Female A (wild)
Fahamu (M)	FC/ Female A (wild)	SL/ Silent track
Kume (M)	FC/ Male B (captive)	MN/ Hammer knocks
Lazima (F)	FC/ Female A (wild)	SL/ Silent track

179

180 While recording techniques and equipment varied, we ensured maximal consistency
 181 across stimuli during post-processing. All recordings were wave files, to which we applied a
 182 high-pass filter (100Hz) to remove background noise and amplitude normalisation. Sound

183 tracks were created to be equal in duration (1.8s) and to contain four elements in each case.
184 Time intervals between elements varied as to mimic the natural temporal structure of one of
185 the original recordings, but this temporal pattern was kept identical across all sound tracks.
186 We additionally created a silent track of equal duration (no sound element), to ensure that
187 even during the silent condition, any potential effect due to speaker activation was controlled
188 for. All post-processing was performed in Audacity 2.2.2 (audacityteam.org).

189

190 **Touch Screen Training**

191 None of the chimpanzees had previous experience in touch screen-based experimental
192 research and thus required a basic training phase. Initial interaction with the device was
193 promoted by scattering food on and around the device and verbally encouraging individuals to
194 approach the set-up. Through progressively rewarding approach behaviours toward the set-up,
195 hand movements within the box and manual investigation of the screen, chimpanzees began
196 to hit the screen. The first task they learned was thus to hit the screen anywhere to obtain a
197 reward. Once they comfortably performed this task, we presented a blue square in the middle
198 of the screen, which they had to hit to obtain the food. As individuals became proficient in
199 this task (correctly hitting the square on the first touch on at least 80% of the trials within a
200 session), we progressively reduced the size of the square. We then introduced a variety of
201 images (e.g. landscapes, foods, abstract images) to habituate them to variations in visual
202 stimuli and began introducing trials, where the location of the square was randomly varied
203 each time. Individuals were judged sufficiently proficient in the use of the touch screen device
204 when they were able to hit a square target of 540 pixels or smaller, randomly located on the
205 screen in at least 80% of the trials over at least three consecutive training sessions. These
206 training sessions took place between September 2017 and February 2018. Sessions were
207 performed in the morning (0900-1100 hours) and afternoon (1300-1500 hours). Each

208 individual chimpanzee could interact with the touch screen for a maximum of 30 trials per
209 session, at which point the end of its session was signalled by the screen going red for 5s.
210 This procedure ensured that the maximal amount of food that they could receive was within
211 their normal daily intake and prevented conflicts and screen monopolization by more
212 dominant individuals.

213

214 **Task Procedure**

215 The task consisted of presenting two pictures of a given set, side by side, in the middle
216 of the screen. The playback of one of the four sound treatments (FC, PG, MN or SL) started
217 1.0s before and overlapped for 0.8s with the visual presentation. If the chimpanzees selected
218 the S+, we played a secondary positive reinforcer tone and provided a piece of fruit or nut
219 (either grape, blueberry or hazelnut) through a dedicated feeding tube. If the S- was selected,
220 we played a different secondary negative reinforcer tone and no reward was offered. Each
221 presentation trial was separated by an inter-trial interval of 5s. Tasks were divided into blocks
222 of 10 trials each, with a maximum of two blocks per day. Blocks always contained trials for
223 both treatment types in a 50/50 ratio, presented in a pseudo-random order, controlled so that
224 no more than two tests of the same treatment type occurred consecutively. This procedure
225 avoided any potential order effect in learning and controlled for any potential biasing effect
226 due to daily variations in individual performance or social environment. Each block within a
227 session was preceded by five ‘warm-up’ trials, where individuals just had to hit the training
228 square and the session concluded with an additional five such trials. This procedure ensured
229 that individuals’ initial excitation did not affect their performance on experimental tests and
230 that regardless of their success on test blocks, they received some rewards to keep their
231 motivation levels up.

232

233 For each test trial, we recorded the chimpanzee's choice as 'correct' or 'incorrect', the
234 side (right or left) of the S+ and the time taken to select an image from visual stimulus onset
235 ('reaction time'). For eight trials out of 1660 (<0.01%), the results failed to save, such that we
236 obtained the treatment type and choice from the associated webcam audio but could not
237 obtain reaction time or stimulus side data because of the angle of the webcam. We determined
238 that learning had occurred for a given treatment condition if the chimpanzee correctly selected
239 the S+ in a minimum of 15 tests within 20 consecutive trials, spanning two blocks (binomial
240 test $p < 0.05$). Once the chimpanzee reached the learning criterion for a treatment, we stopped
241 the trials for that condition. Instead, subsequent daily sessions only included trials of the
242 remaining treatment type, while keeping the same number of trials (i.e. two blocks of 10 trials
243 each) and were continued until the individual reached the learning criterion on that condition,
244 too. Tests took place between February and May 2018.

245

246 **Statistical Analyses**

247 We tested for side biases using binomial tests (proportion of choice on a given side out
248 of the total number of presentations on that side), for each individual separately. We also
249 investigated the likelihood that initial image preference could explain the pattern of results.
250 We calculated the individual and joint probabilities that individuals would have an initial
251 preference for S+ (regardless of its reward value) in either or both treatment conditions for
252 one, two or all chimpanzees.

253 After performing these control procedures, we were interested in whether individuals
254 showed better learning rates in the FC versus the control conditions. To test whether treatment
255 influenced learning speed, we used a paired t-test to compare the number of trials required to
256 reach criterion in each treatment. As long as the normality assumption is met (which was
257 confirmed using the Shapiro-Wilks test), there is no minimum sample size required for this

258 test. Then, to test whether chimpanzees were overall better in the food condition and made
259 fewer errors, we calculated the mean success rate (proportion of correct trials out of a block)
260 for each individual in each treatment and then used a paired t-test. To investigate how
261 treatment type (FC vs control conditions) influenced individuals' reaction times, we used
262 factorial ANOVA followed by Tukey HSD post hoc tests. Reaction times of the first two
263 block sessions only (to avoid unequal sample sizes) were log-transformed to meet the
264 normality and homoscedastic assumptions. The model included treatment type (FC vs control
265 conditions), chimpanzee identity as well as their interaction. As each chimpanzee received
266 different sound exemplars, including chimpanzee as a factor controlled for pseudo-replication.
267 We visually inspected diagnostic plots to check model assumptions. Statistical analyses and
268 plots were performed in R version 3.5.1, using the packages: ggplot2 ([Wickham, 2016](#)), plyr
269 ([Wickham, 2011](#)), ggsignif ([Ahlmann-Eltze, 2019](#)) and lme4 ([Bates, et al., 2015](#)).

270

271 **Ethical Note**

272 All procedures performed in this study were in accordance with the ethical standards
273 of Switzerland and Basel Zoo where the study was conducted (Kantonales Veterinäramt Basel
274 Stadt, permit number 2861).

275

276

Results

277 **Touch screen training**

278 In the preparatory phase, when chimpanzees were being trained on using the touch
279 screen, all individuals came to watch others manipulate the touch screen. Yet, after a few
280 weeks, only five individuals engaged repeatedly with the device and those individuals that
281 had not started interacting with the device, stopped paying attention and rarely came to watch.
282 Concurrently, we noticed the development of an order routine amongst those individuals

283 using the device, with the dominant chimpanzee (Kume) being typically the first to complete
 284 his session, followed by Fahamu, then by Colebe, and finally Lazima. Once this routine was
 285 established individuals essentially stopped paying much attention, displacing or attempting to
 286 steal food from each other and instead waited for their turn.

287

288 **Side Preferences**

289 We tested whether each individual showed evidence of a side bias by computing the
 290 number of times a side was chosen regardless of the side of the S+ (Table 2). Only Fahamu
 291 showed a significant side bias towards the right side, and this for both the FC and the SL
 292 condition. While we detected this side bias during the experiment and indeed, we stopped
 293 testing him after 300 tests in the FC condition, given our experimental aim, i.e., to investigate
 294 whether sound stimuli influenced learning speed, we did not introduce a correction procedure,
 295 as this would have impacted learning processes. Considering his strong side bias, we excluded
 296 him from further analyses, as clearly his responses were not affected by the experimental
 297 paradigm.

298

299 **Table 2**

300 *Distribution of Hits According to the Side, for each Condition and for each Chimpanzee.*

Chimpanzee	Colebe^a		Fahamu^a		Kume		Lazima	
<i>Condition</i>	<i>FC</i>	<i>PG</i>	<i>FC</i>	<i>SL</i>	<i>FC</i>	<i>MN</i>	<i>FC</i>	<i>SL</i>
<i>N hits left</i>	10	48	111	81	90	133	24	269
<i>N hits right</i>	8	38	188	138	90	137	16	271
<i>Probability</i>	0.55	0.56	0.37	0.37	0.5	0.49	0.6	0.5
<i>p-value</i>	0.81	0.33	<0.001	<0.001	1	0.85	0.27	0.96

301 *Note.* Distribution of hits according to the side (right or left) for each condition (FC=food call,
302 PG= pant-grunt, MN=asocial mechanical noise, SL=silence) and for each chimpanzee. Side
303 bias was tested using a binomial test.

304 ^a Missing side data for 6 (Colebe) and 2 (Fahamu) trials due to results failing to save.

305

306 **Image Preferences**

307 To prevent initial picture bias, we selected pictures of objects that were novel to the
308 subjects, resembled each other within a combination but were different across pairs (Figure
309 1). To rule out inherent preferences for some pictures, we calculated (for the remaining three
310 chimpanzees), the likelihood that the pattern of results obtained could be explained by a bias
311 in image preference caused by the pictures themselves and not their reward value. For each
312 individual, there could be three possible outcomes: there is a preference bias for S+, a
313 preference bias for S- or no preference bias for either pictures. Assuming that image
314 preference in one treatment was independent of the other treatment, for each individual there
315 was thus a $P(A) = 1/3$ (0.33) probability that S+ was initially preferred, for a given treatment.
316 For two individuals, the probability is thus $1/9$ (0.11) and for three individuals the probability
317 is $1/27$ (0.03). The jointed probability that this biased S+ combination occurred on both
318 treatment conditions is thus $P(A \cap B) = 1/9$ (0.11) for one individual, $1/81$ (0.01) for two
319 individuals and $1/729$ (0.001) for three individuals. These low probabilities suggest that it is
320 very unlikely that an initial image preference bias could have produced the results found in
321 this study.

322

323 **Learning Speed**

324 Ad hoc observations indicated that the first time subjects heard the playback stimuli
325 (particularly FC and PG), they reacted very strongly with, for example, Kume (FC)

326 attempting to go behind the device to identify the sound source, and Colebe (PG) moving
327 away and only coming back several minutes later. However, after only a few trials, they
328 habituated to the sounds and resumed working on the screen as they had done previously
329 during the training phase.

330 All three chimpanzees needed fewer trials to learn to discriminate S+ in the FC
331 condition compared to control treatments (PG, MN or SL, Figure 3a): Colebe (FC = 20 trials,
332 PG = 90 trials), Lazima (FC = 40, SL = 540), Kume (FC = 180, MN = 270). However, the
333 difference was not statistically significant (paired t-test: $t = -1.57$, $df = 2$, $p = 0.26$, 95% CI: -
334 822.88 - 382.88), which was to be expected given the large variance and low power = 0.28.
335 Yet, Cohen's $D = 0.91$ showed this difference to be large, confirming that it is the lack of
336 power rather than the absence of a difference that caused the non-significant result.

337

338 **Learning Accuracy**

339 When looking at whether chimpanzees, overall, made fewer errors in the FC treatment, we
340 found a significant difference (paired t-test: $t = 112.88$, $df = 2$, $p < 0.001$, 95% CI: 0.12 - 0.13,
341 Cohen's $D = 1.26$, Figure 3b), confirming that chimpanzees were better at learning the task in
342 the FC condition.

343

344 **Figure 3 about here.**

345

346 **Reaction Times**

347 Reaction times were not affected by the treatment type (ANOVA: $F_{1,109} = 0.49$, $P = 0.49$,
348 $\eta_p^2 = 0.004$) but varied among individuals (ANOVA: $F_{2,109} = 5.52$, $P = 0.005$, $\eta_p^2 = 0.09$), with no
349 significant interaction (ANOVA: $F_{2,105} = 0.3$, $P = 0.74$, $\eta_p^2 = 0.005$). Tukey post-hoc tests
350 revealed that Lazima was marginally faster than Kume ($P = 0.06$) and significantly faster than

351 Colebe ($P=0.005$), who did not differ from Kume ($P=0.6$, Figure 4). Removing four outliers
352 (values greater than three times the standard deviation), which were likely the result of
353 individuals being distracted from the task by social events, did not change the results.
354 Furthermore, visual inspection of reaction times across all sessions show no evidence of any
355 systematic treatment effect (see supplementary material S4).

356

357 **Figure 4 about here.**

358

Discussion

359 In this study, we exposed chimpanzees to an arbitrary visual discrimination task and
360 found that subjects learned faster and made fewer errors, when choices were primed with
361 conspecific food calls compared to acoustically similar greeting calls or control conditions.
362 Importantly, none of the acoustic signals that we used as primers were in any way directly
363 helpful to solve the discrimination problem. Nevertheless, we observed that one of them, the
364 food call, augmented subjects' learning performance nearly fourfold relative to baseline and
365 control conditions (Figure 3). In our study, subjects required on average 80 trials (± 71.2 SD)
366 to learn the task in the food call condition but nearly four times more (300 ± 185 SD) in the
367 control conditions, a rate comparable with other visual discrimination studies on chimpanzees
368 ([Fagot & Tomonaga, 2001: 216-720 trials](#); [Vonk, Jett, Mosteller, & Galvan, 2013: 360-1,240 trials](#)).
369 The learning rates in the control conditions were thus on par with data from other laboratories,
370 demonstrating the massively facilitated learning effect if subjects were primed with food
371 calls.

372 We acknowledge that our sample size was small, although not atypical for great ape
373 cognition studies ([Egelkamp & Ross, 2019](#)). Nevertheless, single-subject studies have been key
374 in animal cognition research ([Pepperberg, 2009](#); [Premack & Premack, 1983](#)), including zoo
375 research ([Slocombe & Zuberbühler, 2005](#)), as they provide evidence that the trait under study is

376 within the range of the species' cognitive abilities. Training chimpanzees to operate touch
377 screen devices is a time-consuming and difficult process, especially in zoo environments
378 where individuals are not individually separated from the rest of the group. This generates a
379 number of complexities, such as the fact that subjects may become distracted by ongoing
380 social events and/or lose the food rewards they gained after successful performance. This may
381 explain the faster reaction times of the juvenile individual as she would be more susceptible to
382 food stealing and displacement. Furthermore, we noted considerable individual differences in
383 learning performance. Firstly, one of four subjects completely failed to learn the task and
384 instead developed a side bias, a common animal strategy with such tasks e.g. ([Allritz, Call, &](#)
385 [Borkenau, 2016](#)). But even with the remaining three subjects there were considerable
386 individual differences with Colebe (low-ranking adult male), Lazima (low ranking juvenile)
387 and Kume (alpha male) requiring 2, 4 and 18 sessions, respectively, to learn the task. Age,
388 sex, social status and cognitive differences are all possible causes of these performance
389 differences ([Aplin, Sheldon, & Morand-Ferron, 2013](#); [Rosa, Nguyen, & Dubois, 2012](#); [Webster &](#)
390 [Laland, 2010](#)). In chimpanzees, low-ranking and younger individuals are more likely to rely on
391 social information than high-ranking and adult individuals ([Biro, et al., 2003](#); [Kendal, et al.,](#)
392 [2015](#)), a pattern also found in our data.

393 How fast the subject learned a novel and arbitrary association between a visual
394 stimulus and the availability of food varied between the food call and control conditions.
395 Thus, we propose that this may be a case of 'social priming', whereby the vocalisation primes
396 readiness to learn or informs individuals about a learning opportunity, resulting in faster
397 associative learning. Importantly, the manifold facilitative effect of food calls suggests that it
398 could have important evolutionary implications and requires an explanation from a functional
399 and a mechanistic perspective.

400 The fact that food calls, but not greeting calls or other acoustically conspicuous
401 sounds, enhanced learning may be part of an evolved capacity, which helps individuals to
402 identify palatable foods. Chimpanzees are generalist feeders that depend on seasonal fruits
403 and plants ([Goodall, 1986](#)), suggesting that individuals benefit in learning from others where
404 and when to find food and what to eat ([Galef & Giraldeau, 2001](#)). As mentioned, while there is
405 ample evidence that chimpanzees use social information to solve instrumental problems
406 ([Whiten, 2017a](#)), much less is known about how they acquire their foraging skills, which in
407 primates is largely based on visual discrimination, although potent behavioural conformity in
408 agreement with the ‘copy when uncertain’ strategy was shown in vervet monkeys,
409 *Cercopithecus aethiops* ([van de Waal, Borgeaud, & Whiten, 2013](#)). Our study suggests that it is
410 within chimpanzees’ cognitive abilities to be able to use others’ food calls to identify the
411 context as a learning opportunity, thus enhancing learning performance in visual
412 discrimination, an essential part of obtaining competencies in foraging. However, determining
413 the extent to which this capacity is functional in the wild will require naturalistic studies.

414 Importantly, this suggests that communicative signals, produced in contexts where
415 social learning outweighs individual trial-and-error learning, foster learning but by which
416 mechanisms? [Guilford and Dawkins \(1991\)](#) have proposed that some animal signals are more
417 efficient at facilitating learning processes than others, with evidence in visual and olfactory
418 domains ([Roper & Marples, 1997](#); [Speed, 2000](#)), most likely due to an evolved perceptual bias.
419 We find this an unlikely explanation for the present study. Chimpanzee food calls are graded
420 signals that vary in a large range of acoustic features ([Slocombe & Zuberbühler, 2006](#)) as well as
421 show potential socially-induced structural changes ([Watson, et al., 2015](#)) making it impossible
422 to relate a set of acoustic properties with learning efficacy. In addition, pant-grunts (the
423 control social calls), have very similar spectro-temporal features (Figure 2), further arguing
424 against an explanation based on acoustic surface features.

425 Another possibility is that the food calls attracted chimpanzees' attention to a relevant
426 learning opportunity, similarly to how black-capped chickadees, *Parus atricapillus*, are more
427 likely to learn to pierce a bottle cap when a conspecific is present but not interacting with the
428 item, than when there is no conspecific present ([Sherry & Galef, 1990](#)). However, this
429 explanation seems unlikely, first, because that provides no justification as to why only food
430 calls (and not greeting calls) would draw one's attention and, second, because the absence of
431 a difference in reaction time does not support the idea that these stimuli differentially affected
432 attention, at least in terms of decreasing the latency to interact with the task.

433 We find it more plausible that food calls represent a contextually appropriate signal, as
434 it predicts food, which corresponds with the desired outcome of the discrimination task for the
435 subjects, unlike the other acoustic primers. It is likely that in our experiment, chimpanzees
436 already had a pre-existing notion of food calls as predictors of food, resulting from a natural
437 appetitive conditioning process. Appetitive conditioning activates the reward system,
438 including the amygdala, which is known to play a role in attributing valence to a stimulus
439 ([Paton, Belova, Morrison, & Salzman, 2006](#)), emotional arousal ([Braesicke, et al., 2005](#)), and alter a
440 subject's attention and perception of the stimulus ([Holland & Gallagher, 1999](#); [Phelps & LeDoux,](#)
441 [2005](#)). When hearing playback of food calls, subjects may have experienced a positive
442 emotional state, temporally linked with the task, and this may have helped to enhance their
443 performance relative to baseline ([Heyes, 2012](#)). Indeed, in humans emotional states are known
444 to influence learning, with positive emotions improving performance ([Pekrun, 2006](#); [Um, Song,](#)
445 [& Plass, 2007](#)). In this view, food calls enhanced learning because they rendered subjects into a
446 positive emotional state which helped to solve the task faster.

447 What remains unclear from our study is whether food calls have a generalised
448 enhancement effect on any associative learning or whether the effect is limited to learning
449 visual tasks and/or tasks that lead to food rewards, i.e., contextually congruent situations. This

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615

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Figures Captions

617

Figure 1

619 *Examples of Pairs of Visual Stimuli Used in the Discrimination Task.*

620 *Note.* Paired visuals were selected to be similar in shape, size and colours and represented

621 human-made objects presumably unfamiliar to the subjects. One visual of each pair was

622 randomly selected as the S+.

623

Figure 2

625 *Spectrograms of Exemplar Acoustic Stimuli.*

626 *Note.* Spectrographic (window length=512, overlap=88%) representation for a food call series

627 (top panel), a pant-grunt series (middle panel) and hammer knocking sounds (bottom panel).

628

Figure 3

630 *Number of Trials Taken Before Reaching the Learning Criterion and Success Rate.*

631 *Note.* A) Absolute numbers of trials for the three chimpanzees that completed the task,

632 depending on the condition (FC=food call, PG= pant-grunt, MN=asocial mechanical noise,

633 SL=silence). B) Mean +/- SD success rate (proportion of correct trials per block) in the FC

634 and Control conditions (N=3).

635 *** Paired t-test $P < 0.001$.

636

Figure 4

638 *Differences in Reaction Times According to Conditions and Chimpanzees.*

639 *Note.* Mean +/- S.E. log-transformed reaction times, according to condition, either food call or

640 control (either pant-grunts, mechanical noises or silence) and chimpanzee.

641