

1 **Touch-screen-guided task reveals a prosocial choice tendency by chimpanzees (*Pan***
2 ***troglodytes*)**

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23 Abstract

24 Humans help others even without direct benefit for themselves. However, the nature of
25 altruistic (i.e. only the other benefits) and prosocial (i.e. self and other both benefit)
26 behaviors in our closest living relative, the chimpanzee, remains controversial. To address
27 this further, we developed a touch-screen-guided task that allowed us to ~~easily~~ increase
28 the number of trials for a thorough test of chimpanzees' prosocial and altruistic tendencies.
29 Mother-offspring dyads were tested in the same compartment; one was the actor while
30 the other was the recipient. In experiment 1, the actor chose among ~~3~~three options:
31 prosocial, selfish (only the actor benefited) and altruistic. To better understand the nature
32 of the chimpanzees' choices and to improve experimental control, we conducted two
33 additional experiments. Experiment 2 consisted of two-option choices interspersed with
34 three-option choices, and in experiment 3 the two-option choice were blocked across all
35 trials. The results of experiment 1 clearly showed that chimpanzees acted prosocially in
36 the touch-screen-guided task, choosing the prosocial option on an average of 79% of
37 choices. ~~Five~~5 out of ~~six~~6 chimpanzees showed the preference to act prosocially against
38 chance level. The preference for the prosocial option persisted when conditions were
39 changed in experiments 2 and 3. When only selfish and altruistic options were available
40 in experiments 2 and 3, chimpanzees preferred the selfish option. These results suggest
41 that 1) most individuals understood the nature of the task and modified their behav~~ior~~
42 according to the available options, 2) ~~five~~5 out of ~~the six~~6 chimpanzees chose to act
43 prosocially when they had the option to ~~and~~ 3) offspring counterbalanced between
44 altruistic and selfish, when given those two options~~s~~, perhaps to avoid suffering
45 repercussions from the mother.

46

47

49 Introduction

50 Humans are clearly a case in which social exchange increases the relative fitness
51 of individuals who engage in altruistic behaviors, enabling altruism to diffuse through
52 subsequent generations (Fehr & Fischbacher, 2003; Warneken & Tomasello, 2009).
53 Humans frequently help others without directly benefiting themselves (Fehr & Gächter,
54 2002; Fehr & Fischbacher, 2004). Prosocial behavior is described as any behavior that
55 includes actions intended to benefit another, such as helping, comforting, sharing
56 resources and cooperating (Batson & Powell, 2003). Altruism is a motivational concept
57 in which the actor does not consciously regard his self-interests (Hoffman, 1978; Batson
58 & Powell, 2003). Therefore, this behavior can benefit the recipient while entailing costs
59 to the actor, or in the absence of any obvious proximate reward (Batson & Powell, 2003;
60 de Waal, 2008). This concept contrasts with egoism (here referred to as selfish behavior),
61 which has the ultimate goal of increasing one's own welfare (Mueller, 1986).

62 How did prosocial behaviors evolve in humans? Comparative studies can provide
63 important perspectives for addressing this question. In recent decades multiple studies
64 have explored prosocial and altruistic behaviors in nonhuman primate species (de Waal
65 et al., 2008; Lakshminarayanan & Santos, 2008; Cronin, Schroeder & Snowdon, 2010;
66 Skerry, Sheskin & Santos, 2011; Horner et al., 2011a; Takimoto & Fujita, 2011; Suchak
67 & de Waal, 2012; Kim et al., 2015). To understand the mechanisms that underlie prosocial
68 and altruistic behavior, the chimpanzee is a good model for the following three major
69 reasons: 1) ~~T~~hey share a recent common ancestry with humans, which makes them ~~the~~
70 ~~best~~besta good comparative model for studying the evolution of human behavior (McGrew,
71 2010); 2) some observational studies have reported prosocial behavior in chimpanzees
72 (Nishida & Hosaka, 1996; Watts, 1998; Langergraber, Mitani & Vigilant, 2007;

73 Crockford et al., 2012); and 3) empirical evidence shows that chimpanzees understand
74 other individuals' intentions (Hare, Call & Tomasello, 2001, Yamamoto, Humle &
75 Tanaka, 2012).

76 Chimpanzees' cooperative and prosocial tendencies have been studied in a range
77 of settings (Hirata, 2009). However, the issue of prosociality remains controversial, as
78 some studies have failed to show such tendencies (Silk et al., 2005; Jensen et al., 2006;
79 Vonk et al., 2008) and other reported prosocial tendencies only slightly above chance
80 level (Warneken et al., 2007; Horner et al., 2011a; Melis, Schneider & Tomasello, 2011;
81 Melis et al., 2011; Claidière et al., 2015). Two main experimental paradigms have been
82 used to test prosociality in non-human primates (Horner et al., 2011a), namely using ~~→~~
83 assistance tests ~~→ (GAT)~~ in which the subject has to choose between helping, by providing
84 instrumental help, or not helping the recipient; ~~→~~ and Prosocial choices tests (PCT) ~~→~~ in
85 which the subject has to choose between a prosocial (allowing subject and recipient to be
86 rewarded) or selfish option (only the subject is rewarded). Some PCT studies have failed
87 to show a clear prosocial preferences in chimpanzees (Silk et al., 2005; Jensen et al.,
88 2006), arguably due to methodological constraints. Even with improved paradigms results
89 are unclear (60% prosocial) (Horner et al., 2011a) and open to challenge (Skoyles, 2011),
90 given the frequent selection (40%) of selfish tokens, when a choice between selfish and
91 prosocial tokens was presented by the experimenter. However, authors have argued that
92 organisms do not choose categorically but rather sample the choices from time to time,
93 which may result in a high proportion of selfish choices (Horner et al., 2011b).

94 We developed a touch-screen-guided task to re-examine the existence of prosocial
95 and altruistic behaviors, as well as the factors modulating their choices, using a new
96 paradigm. We tested three mother-offspring pairs of chimpanzees, who had experience
97 with various computer-controlled experiments (Matsuzawa, 2003; Matsuzawa, 2006;

98 Martin et al., 2014). Unlike most of the prosociality studies (but see: House et al.; 2014;
99 Suchak et al., 2014; Claidière et al., 2015), we tested the actor and recipient individuals
100 in the same compartment and we used a touch-screen-guided procedure that allowed us
101 to increase the number of trials per individual. A prosocial option was defined as the
102 chimpanzee playing the role of actor choosing to reward both actor and recipient. An
103 altruistic option was defined as the act of providing reward only to the recipient. A selfish
104 option was defined as the actor choosing to reward only himself. We ran three
105 experiments to examine how prosocial, selfish and altruistic tendencies were modulated
106 across different conditions. In ~~the~~ experiment 1, chimpanzees were requested to choose
107 among prosocial (P), selfish (S) and altruistic (A) options. In the experiments ~~2~~ and 3 they
108 were given two of the three options. Experiment 2 consisted of choosing between two out
109 of three choices that were presented randomly across the trials. Experiment 3 consisted
110 of ~~three~~ sessions, each one with two out three choices (for example, one session only
111 with prosocial and altruistic options, another with altruistic and selfish, and another with
112 prosocial and selfish) blocked across the trials. The following predictions were
113 formulated for each experiment: experiment 1) chimpanzees show a prosocial tendency
114 if they choose the prosocial option significantly more above other options and this
115 tendency increase across the trials; experiment 2) chimpanzees understand the meaning
116 of the keys if, a) they keep their prosocial preference and b) when given a choice between
117 two out of three the options, they show a preference for one of the options; experiment 3)
118 once presented with ~~two~~ out of ~~the three~~ options constantly across the trials, individuals
119 may counterbalance their choices to avoid repercussions from other individuals.

120

121 General Methods

122 Participants

123 Six chimpanzees (*Pan troglodytes*): one juvenile male (Ayumu, 12 years old), two
124 juvenile females (Cleo and Pal, around 12 years of age) and three adult females (Ai,
125 Chloe, and Pan, all around 30 years of age) participated as mother-offspring pairs.
126 Because of their mother-offspring relationship individuals had to be tested in the same
127 compartment: Ai with Ayumu (Am), Chloe (Ch) with Cleo (Cl), Pan (Pn) with Pal (Pl)
128 (Fig. 1). The chimpanzees live in groups of six and seven individuals in indoor-outdoor
129 enclosures at the Primate Research Institute, Kyoto University. The outdoor enclosure
130 (770m²) is environmentally enriched with artificial streams containing fish and more than
131 400 species of plants, in addition to ropes and climbing structures up to 15m high, and
132 has direct access to indoor quarters. All subjects had previously participated in various
133 computer-controlled perceptual–cognitive experiments (Matsuzawa, 2003; Matsuzawa,
134 2006; Adachi, 2014) including some in similar social settings (Martin, Biro &
135 Matsuzawa, 2011; Martin et al., 2014).

136

137 Apparatus

138 We used two 17-inch LCD touch panel displays (1280 x 1024 pixels) controlled
139 by custom-written software under Visual Basic 2010 (Microsoft Corporation, Redmond,
140 Washington, USA). Chimpanzees sat in one experimental chamber (approximately 2.5 m
141 wide, 2.5 m deep, 2.1 m high), while the experimenters sat outside the booth, separated
142 from the chimpanzees by transparent acrylic panels (Fig. 1). The displays were placed
143 into the acrylic panels. The appropriate distance between the active subject and its display
144 was 40 to 50 cm. Options appeared on the screen in sizes of about 3 to 4 degrees of visual
145 angle. The subjects responded by touching the options on the display surface with a
146 finger. A transparent acrylic panel fitted with an opening allowed manual contact with

147 the display while protecting it from damage. A food tray was installed below each display,
148 for delivering food rewards via a universal feeder (Bio Medica BUF-310P50). Displays
149 and feeders were automatically controlled by the same program that controlled the display
150 of the stimuli.

151

152 Stimuli

153 To initiate the task, a circular button was presented as stimuli in the bottom of the
154 actor's screen. After pressing the start key, three grayscale 3-D shape options (cube,
155 cylinder and sphere) horizontally aligned with equal spacing on the computer monitor of
156 one of the two chimpanzees (Fig. 2). Each symbol represented each given option:
157 altruistic, prosocial and selfish. To facilitate the association of the options with their
158 corresponding function, the position of the stimuli was fixed for each participant but
159 counterbalanced across participants. In experiment 1, the three options were presented
160 simultaneously on the actor's screen. In experiments 2 and 3, two out of the three options
161 were presented. In experiment 2, two-option choice trials (two out of three options) were
162 interspersed with three-option choice trials (as in experiment 1). In the two-option choice
163 trials, the combination of options was randomly assigned across the individuals. In
164 experiment 3, one of the three possible combinations of two options was constant across
165 the block of trials. Therefore, we ran [three](#) different sessions, each one with two options
166 (out of the three) available across trials (Table 1). The monitor of the second chimpanzee
167 showed a mid-grey blank screen throughout the sessions.

168

169 Procedure

170 Training and learning phase

171 In the training phase, the individuals were trained to discriminate three different
172 sounds corresponding to the three different outcomes (prosocial, selfish and altruistic).
173 The sounds used in this experiment were unfamiliar to chimpanzees, so they would not
174 associate with the regular rewarding sound used with other touchscreen tasks. In the
175 training phase, the individuals were tested alone. The actor was placed in in front of
176 his/her monitor, and the recipient was separated in the other compartment of the booth.
177 We did n^ot request the actor to touch the screen in this phase. The actor had access to
178 both feeders, including the recipient feeder. The actor could easily hear the sound and
179 pick up the reward on the recipient feeder. This way, we encouraginged the individuals
180 to understand that both feeders were providing food. We randomly chose which sounds
181 to play paired with the location of the outcome. We ran 200 trials for each individual.

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182 In the learning phases, we trained the chimpanzees to associate the assigned shape
183 with their respective function. Both chimpanzees were now placed in the same
184 compartment, in front of their respective monitors (Fig. 1). We ran 3 sessions, in which
185 each—only one of the three stimulies was presented for 24 trials: 24 trials with the
186 presentation of the cube, 24 trials with the sphere and 24 trials with the cylinder. Shapes'
187 functions were randomly assigned across the subjects.

188

189 Experimental phase

190 In the experimental phase, chimpanzees were tested in actor-recipient pairs, in
191 the same compartment of the experimental booth (Fig. 1), approximately 0.40 m apart.
192 One degree of gaze angle corresponded to approximately 0.7 cm on the screen at a
193 viewing distance of 40 cm. One chimpanzee was the actor while the other was the
194 recipient; role was randomly assigned across sessions. Each trial was initiated by the actor
195 pressing a green button on the middle bottom of screen. The actor made a choice by

196 touching one of the three options presented on the screen. A food reward (an apple piece,
197 ~~with~~ approximately 1 cm³) was given according to the assignments of the options and
198 their functions. The three options consisted in rewarding only the ~~author~~actor (selfish
199 (S)), both participants (prosocial (P)) ~~and~~or only the recipient (altruistic (A)). Feeder
200 activation was accompanied by two distinctive buzzer sounds with slight temporal delay
201 to indicate clearly which feeder was giving the reward. Throughout the procedure the
202 recipient sat in front of a grey screen. After the completion of the experiment (by the end
203 of the third session) the chimpanzees changed positions: the actor moved to the recipient's
204 place and vice-versa. Each pair received three sessions for each role, totaling six sessions
205 per day.

206 In the experiment 1, we ran ~~three~~³ sessions of 48 trials (144 trials in total) for each
207 actor. The actor could choose among ~~three~~³ options on the screen: P, S and A (Fig. 2). In
208 ~~a second round of testing, i.e.~~ experiment 2, option assignments and locations on the
209 screen were as in experiment 1, except that we also reduced the number of options from
210 three to two: ~~selfish and prosocial and selfish (P-S)~~, selfish and altruistic (A-S), or
211 prosocial and altruistic (P-A) (Table 1). We ran 32 trials of each combination, giving a
212 total of 96 trials for each subject. These two-option trials were randomly interspersed with
213 three-option trials at a ratio of 1:5, to ensure that chimpanzees could associate this new
214 condition with the previous one, as the conditions have been conducted in different days.
215 However, because our focus was on the two-option trials, we only analysed those trials
216 in this study. By reducing the options in some of the trials, we turned the social event
217 into a more critical decision-making situation than in experiment 1 (~~three-~~buttonoption-
218 choices) and, hence, ~~acutely~~ increased the social pressure between partners and possible
219 repercussions toward the active partner.

220 In experiment 3, to further explore the dynamics of the two-option task and
221 increase the social pressure between the partners, we provided each of the two option
222 choices in blocks of 48 trials in a counterbalanced order across participants (Table 1).
223 Experiment 3 involved presentations of two options at the same time and consisted of 96
224 trials presented in two sessions for each combination of two trial types: P-S, A-S, P-
225 A.

226 All experiments were carried out in accordance with the 2002 version of the
227 Guidelines for the Care and Use of Laboratory Primates by the Primate Research Institute,
228 Kyoto University. The experimental protocol was approved by the Animal Welfare and
229 Care Committee of the same institute (protocol# 2012-090).

230

231

232 Data analysis

233 Data analysis was performed using R 3.3.1 (R Core Team 2015) in R-studio
234 0.99.463 (R Studio 2015). For individual testing, we used Chi-square tests for the three-
235 choice experiment (experiment 1) and binomial tests for the two-choice experiment,
236 (experiment 2 and 3), to examine subjects' performance against chance level. We rejected
237 the null hypothesis if $P < 0.05$. Additionally, we use the function `geom_smooth`, method
238 = "loess" from the package "ggplot2" to fit a line using linear smoothing for the figures
239 corresponding to each experiment. The curve given by the `geom_smooth` function
240 produces an estimate of the conditional mean function. The shaded band represents a
241 pointwise 95% confidence interval on the fitted values (given by the line).

242

243 Results

244 Experiment 1

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245 Individual's responses showed ~~Five~~ out of the six individuals chose the prosocial
246 option above chance level (Chi-squared, Table 2). One ~~out~~ of the six individuals (Pn)
247 showed the opposite trend ~~by and~~ preferentially choosing ~~the~~ the selfish option more often
248 than prosocial, and ~~this~~ tendency increased across the trials.

249 —Figure 3A shows an increasing overall preference for the prosocial option over
250 all 144 trials for five out of six individuals, while the preference for the selfish and
251 altruistic options decreased over the trials. The selfish individual, Pn was plotted
252 separately (Fig. 3B) to show her preference of the selfish ~~key option~~ over the prosocial
253 and altruistic options across trials.

254 Experiment 1 reveals an exploratory phase, in which, in the beginning individuals
255 (except for Cl) were choosing the three options at similar proportions (first bin of 8 trials,
256 Fig. 3A) until they started showing a preference for the prosocial option with the increase
257 of trials.

258

259 Experiment 2

260 Individual's responses showed ~~Four~~ out of the six individuals chose the prosocial
261 option above chance level (Fig. 4A). ~~The male offspring (Am)~~ did not choose the
262 prosocial option above chance level in this experiment (Binomial test, Table 3). ~~For four~~
263 ~~out of six individuals, the preference to choose the prosocial option was kept over the~~
264 ~~trials (Fig. 4A). For~~ and the selfish subject, Pn, kept choosing the selfish option more than
265 the prosocial option as she did in experiment 1, thereby deviating from the pattern shown
266 by the other participants (Fig. 4B). In this experiment, the proportion of prosocial choices,
267 for three out of six individuals (Am, Ch and Pn), decreased in this experiment, compared
268 to experiment 1 (Am, Ch and Pn). The probability of mothers choosing the selfish option
269 over the altruistic and prosocial options increased in experiment 2 compared to

270 experiment 1 (Fig. 5). ~~An exploratory phase was not observed in this experiment~~ Unlike
271 ~~in experiment 1, the chimpanzees' choices did not vary over trials~~ suggesting that
272 individuals may have remembered the symbol assignments from the previous experiment.

273

274 Experiment 3

275 Similar to experiment 1, the individual's responses showed that five of the six
276 individuals chose the prosocial option above chance level (Binomial test, Table 4).
277 Similar to experiment 2, the proportion of choosing the prosocial key was kept constant
278 across the trials, for five out of six individuals (Fig. 6A). Like in the experiments 1 and 2,
279 Pn stood out from other participants by choosing ~~preferably~~ the selfish option over the
280 prosocial option (Fig. 6B). Overall, the proportion of prosocial choices over selfish
281 increased from the experiment 2 for three individuals (Ai, Am and Ch).

282 Mothers showed a greater tendency than their offspring to choose the selfish
283 option over the altruistic option (Fig. 5A). The probability of choosing the altruistic
284 option also increased in experiment 3, with the exception of the male offspring (Am),
285 who showed a similar pattern to mothers (Table 4). Similar to experiment 2, an
286 exploratory phase was not observed.

287

288 Discussion

289 Overall, we found that prosocial behavior predominated over selfish and altruistic
290 behaviors (experiment 1). Prosocial responding was slightly more frequent when the
291 alternative was altruistic responding (experiments 2 and 3) compared to selfish, and all
292 individuals show a clear preference for behaving prosocially over the altruistic option. In
293 the early trials of experiment 1, chimpanzees chose among the three options at close to
294 the chance level (~~exploratory phase~~); however, their options ~~remained~~ stabilized with

295 increasing experience of the outcome of each choice. In experiments 2 and 3 no such
296 exploratory ~~phase behavior~~ was observed, suggesting that most of the chimpanzees (with
297 exception of Cl) understood and remembered the outcome of their choices ~~from~~
298 ~~experiment 1~~. Cl always chose the prosocial option from the beginning ~~of experiment 1~~
299 and did not explore other outcomes ~~in the experiment 1~~. ~~Besides, she may have chosen~~
300 ~~randomly when the altruistic and the selfish options were given~~. Therefore, there is the
301 possibility that she may have just learned that ~~the~~ prosocial symbol was rewarding ~~to~~ her
302 ~~via simple associate learning~~ or ~~she may have~~ learned to avoid the other choices.

303 Four out of ~~the~~ six chimpanzees showed a tendency towards prosocial behavior,
304 supporting findings of previous experimental studies (Warneken et al., 2007; Horner et
305 al., 2011a; Melis et al., 2011) and evidence from observations in the wild (Nishida &
306 Hosaka, 1996; Watts, 1998; Duffy, Wrangham & Silk, 2007). A potential limitation of
307 the study by Horner et al. (2011a) concerns the low number of repetitions (30 trials). In
308 the present study, the proportion of prosocial ~~options choices made by the chimpanzees~~
309 at around 30 trials (~~here i.e.~~ 4 bins) was similar to that in Horner et al. (2011a). However,
310 by increasing the number of trials (by a factor of 4.8) we increased the overall prosocial
311 bias from an average of 60% in Horner et al. (2011a) to an average of 88 %, and to 100 %
312 for five out of six chimpanzees. During the first phase of trials in experiment 1,
313 chimpanzees chose more equitably among the three options (exploratory phase), before
314 eventually switching their preference for the prosocial option, a preference that persisted
315 until the end of testing. The prosocial-selfish rate found in previous studies (~~e.g.~~, Silk et
316 al., 2005; Jensen et al., 2006; Horner et al., 2011a) may be, therefore, a consequence of
317 ~~subjects receiving~~ fewer trials.

318 ~~In addition to experiencing more trials in the current experiment, it is also~~
319 possible that having the two individuals sharing the same compartment during the

320 experiment ~~increased the social pressure~~ motivated the chimpanzees to act more
321 prosocially because of fear of repercussions from the partner. Tennie, Jensen & Call
322 (2016) have showed that chimpanzees' willingness to help others may depend on the
323 experimental settings, therefore prosociality could arise as a by-product of the
324 experimental design. Further studies are required to better address this question, as we
325 could not control for the effect of sharing the same chamber in these experiments.

326 In contrast to our results, no modulation of prosocial behavior by relative social
327 rank was observed in Horner et al. (2011a). It can be argued that the lack of any rank-
328 related influence on prosocial behavior might be due to the physical separation of the two
329 actors in that study. ~~Having the two partners in the same experimental chamber, may have~~
330 ~~increased the social pressure and that might be a crucial difference; the fear of potential~~
331 ~~repercussions is likely to be strongly reduced if the two partners are physically separated,~~
332 ~~as in previous studies (Silk et al., 2005; Horner et al., 2011a).~~ The fear of potential
333 repercussions from the mothers could explain why the female offspring acted more
334 altruistically (given the selfish option) compared to their mothers, in ~~the~~ experiment 3.

335 One may argue that chimpanzees were choosing the prosocial option with the
336 intention of scrounging the reward from the partner, however we ~~haven't~~ did not observed
337 any scrounging behavior or attempt to steal the reward during the experiment. Moreover,
338 we ~~have also~~ did not observed any signs of frustration by the partner, when they were most
339 likely to occur, in the experiment 3, when given the choice between acting selfishly or
340 altruistically.

341 Some previous studies that failed to show~~s~~ or showed little evidence of~~s~~
342 prosociality appear more complex methodologically and may have required extra
343 cognitive effort compared to the task used in our study. Examples include using tokens
344 to exchange for food rewards with a human experimenter (e.g. Horner et al., 2011a), or

345 using a stick as a tool to dislodge food rewards (e.g. Vonk et al., 2008). In those cases,
346 actors behaved “prosocially” even in a ghost condition in which no conspecific was
347 present. Given the settings of our experiment, we could not run a condition with the
348 partner being absent. If we had run the ghost condition, the actor could try to maximize
349 the reward by choosing the prosocial option in the absence of a partner, thus spoiling the
350 association between the key and the reward outcome. If we had blocked the passage of
351 the recipient, we would have to run the experiment with both subjects separated from the
352 beginning, which was not our goal, as we wanted to test individuals in the same
353 compartment to increase social pressure. Therefore, to be able to run a ghost condition
354 we would have to change our settings from the start. Further experiments should take
355 these matters into account.

356 Although rank turned out to be an important factor in our study (with mothers
357 being the more dominant individuals), because we tested only mother-offspring pairs, we
358 could not examine the influence of kinship separate from rank. Considering the various
359 differences we found in the response patterns between the mothers and their respective
360 offspring, we cannot support the suggestion that chimpanzees return past favors (Gomes,
361 Mundry & Boesch, 2009; Gomes & Boesch, 2011). As stated in Horner et al. (2011a),
362 this lack of evidence might be related to the fact that cooperative behaviors such as
363 hunting (Boesch & Boesch, 1989; Boesch, 1994) patrolling and coalitions (Mitani,
364 Merriwether & Zhang, 2000) are more typical of male than female chimpanzees. We
365 tested five females and only one male; clearly, further studies are needed to address the
366 question of sex differences regarding prosocial tendencies.

367 One chimpanzee, Pn, showed a preference for the selfish option over altruistic and
368 prosocial options, and this tendency was maintained across experiments. Pn’s behavior in
369 combination with that of the two mothers from the other two pairs led to an overall

370 increase in the proportion of selfish vs. prosocial options. However, it should be noted
371 that not all mothers showed higher proportions than their offspring, also reflected in the
372 greater dissimilarity among individuals in P-S than P-A trials. Pn chose selfish when
373 selfish was an option, and prosocial when selfish was not an option; she never chose the
374 altruistic option. In a previous study, the same individual failed to help a partner in the
375 absence of any request, while all other individuals tested did so (Yamamoto, Humle &
376 Tanaka, 2012). There is one clear difference in the life history of Pn compared to other
377 participants: Pn was hand-raised by humans. If food is always provided by human
378 caretakers, there is no dependence on other chimpanzees, hence sharing food or begging
379 for food from other chimpanzees may be unnecessary. Previous studies showed the
380 opposite pattern, however when having a human as mediator (Warneken & Tomasello,
381 2006). Given our small sample size, this explanation is speculative. However, it raises the
382 interesting possibility that the tendencies to share food (prosocial) or provide food to other
383 (altruistic) are not genetically predetermined behavioral traits; instead, they could arise
384 from a gene-environment interaction (Plomin, DeFries & Loehlin, 1977). Further studies
385 are required to examine the effect of chimpanzee rearing history on prosocial and
386 altruistic tendencies. One offspring participant showed an increasing trend toward
387 choosing selfish over altruistic options (Am). This individual was an 11-year-old male
388 who at the time of the study was involved in competition with the alpha-male of the group.
389 This social circumstance might indicate a switching point for Am from offspring behavior
390 to more adult-like behavior.

391 In summary, while it is valid to question (Skoyles, 2011) a 60% advantage for
392 prosocial above selfish options (Horner et al., 2011a), we found prosocial responses at
393 much higher rates with increasing task experience. This factor could explain the
394 differences found in Horner et al. (2011a). Sampling alternative options to confirm the

395 game's contingencies (Horner et al., 2011a) did not occur. Notwithstanding the small
396 sample size, based on our results we suggest that the rank-relationship between partners,
397 in contrast to Horner et al. (2011a), and supporting other authors (Melis, Schneider &
398 Tomasello, 2011; Yamamoto, Humle & Tanaka, 2012) may modulate prosocial
399 tendencies: with increasing social pressure and hence fear of repercussions from their
400 mothers, female offspring showed altruistic behavior.

401 Overall, this study confirms that chimpanzees are not “indifferent to the welfare
402 of others” (Silk et al., 2005), however their choices reveal a balanced interplay of
403 rationally maximizing their own gains (Jensen, Call & Tomasello, 2007) while
404 circumventing repercussions from the partner (dDe Waal, 1982). Further, we provide a
405 new framework for examining social cognition in a computer-guided testing procedure,
406 allowing better identification of effect-modulating factors.

407

408 Conclusion

409 We provide a new framework for assessing prosociality in non-human primates,
410 through the utilization of a controlled computer apparatus. This improvement of the old
411 paradigm allows us to increase the number of trials and prevents the direct participation
412 of humans in the task that could be a distracter or bias in the chimpanzees' choices.
413 Additionally, the touchscreen methodology developed in the study helps controlling for
414 the effect of visible food along with the ability to increase trial numbers (Cronin 2012).

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415 Our study revealed a preferential tendency towards acting prosocially by on
416 chimpanzees when they are facing with two other options: being selfish or altruistic
417 by benefiting themselves or the other, respectively. Besides showing a prosocial tendency
418 on a three choice task (prosocial, selfish or altruistic) and on a two choice task (prosocial

419 ~~or selfish), we go further and explore other conditions that are relevant to understand the~~
420 ~~factors modulating chimpanzees' prosocial and altruistic choices.~~ Ultimately, we
421 hypothesize that the rearing history of chimpanzees and the rank-relationship between
422 partners influenced their positive or negative response towards prosociality.

423

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