

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

Renata S. Mendonça^{1,2†*}, Christoph D. Dahl^{3†}, Susana Carvalho^{2,4,5,6}, Tetsuro Matsuzawa^{1,7}, Ikuma Adachi⁸

¹ Primate Research Institute, Kyoto University, Section Language and Intelligence, 41-2 Kanrin, Inuyama, Aichi, 484-8506, Japan

² Centre for Functional Ecology - Science for People & the Planet, Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal

³ Institute of Biology, University of Neuchâtel, Department of Comparative Cognition, Rue Emile-Argand 11 2000 Neuchâtel, Switzerland

⁴ Primate Models for Behavioural Evolution Lab, Institute of Cognitive and Evolutionary Anthropology, University of Oxford, OX2 6PN, United Kingdom

⁵ Interdisciplinary Centre for Archaeology and Evolution of Human Behaviour (ICArEHB), University of Algarve, Gambelas, Faro, Portugal

⁶ Gorongosa National Park, Sofala, Mozambique

⁷ Institute for Advanced Studies, Kyoto University, Yoshida Ushinomiya-cho, Sakyo Kyoto, 606-8501, Japan

⁸ Primate Research Institute, Kyoto University, Center for International Collaboration and Advanced Studies in Primatology, 41-2 Kanrin, Inuyama, Aichi, 484-8506, Japan

*Correspondence to: Renata S. Mendonça (renatadasilva.mendonca@gmail.com)

†These authors contributed equally.

Abstract

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

48

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~~They share a recent common ancestry with humans, which makes them ~~the~~
70 ~~best~~ a 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;

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

Chimpanzees' cooperative and prosocial tendencies have been studied in a range of settings (Hirata, 2009). However, the issue of prosociality remains controversial, as some studies have failed to show such tendencies (Silk et al., 2005; Jensen et al., 2006; Vonk et al., 2008) and other reported prosocial tendencies only slightly above chance level (Warneken et al., 2007; Horner et al., 2011a; Melis, Schneider & Tomasello, 2011; Melis et al., 2011; Claidière et al., 2015). Two main experimental paradigms have been used to test prosociality in non-human primates (Horner et al., 2011a), namely using ~~the~~ ~~+~~ assistance tests ~~the~~ ~~(GAT)~~ in which the subject has to choose between helping, by providing instrumental help, or not helping the recipient; ~~2)~~ ~~and~~ ~~P~~ prosocial choices tests (PCT) ~~the~~ in which the subject has to choose between a prosocial (allowing subject and recipient to be rewarded) or selfish option (only the subject is rewarded). Some PCT studies have failed to show a clear prosocial preferences in chimpanzees (Silk et al., 2005; Jensen et al., 2006), arguably due to methodological constraints. Even with improved paradigms results are unclear (60% prosocial) (Horner et al., 2011a) and open to challenge (Skoyles, 2011), given the frequent selection (40%) of selfish tokens, when a choice between selfish and prosocial tokens was presented by the experimenter. However, authors have argued that organisms do not choose categorically but rather sample the choices from time to time, which may result in a high proportion of selfish choices (Horner et al., 2011b).

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

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

General Methods

Participants

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

Apparatus

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

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

Stimuli

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

Procedure

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 front of
176 his/her monitor, and the recipient was separated in the other compartment of the booth.
177 We did not 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 encouraged 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.

Formatted: Font color: Auto

Formatted: Font color: Auto

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 ~~stimuli~~ 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

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

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

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

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

Data analysis

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

Results

Experiment 1

Formatted: Font color: Auto

Formatted: Font color: Auto

Individual's responses showed ~~five~~ five out of ~~the~~ six individuals chose the prosocial option above chance level (Chi-squared, Table 2). One ~~out of the~~ six individuals (~~Pn~~) showed the opposite trend ~~by and~~ preferentially choos~~ing~~ the selfish option more often than prosocial, and th~~is~~e tendency increased across the trials.

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

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

Experiment 2

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

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

Experiment 3

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

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

Discussion

Overall, we found that prosocial behavior predominated over selfish and altruistic
behaviors (experiment 1). Prosocial responding was slightly more frequent when the
alternative was altruistic responding (experiments 2 and 3) compared to selfish, and all
individuals show a clear preference for behaving prosocially over the altruistic option. In
the early trials of experiment 1, chimpanzees chose among the three options at close to
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 CI) understood and remembered the outcome of their choices from
298 experiment 1. CI 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

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

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

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

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

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

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

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

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

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

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

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

Conclusion

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

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

Formatted: Font color: Auto

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

Acknowledgments

We thank Dr. James R. Anderson for his editing of the manuscript, and Dr. Masaki Tomonaga and the staff of the Language and Intelligence Section for their help and useful comments. We also thank the Center for Human Evolution ~~Modeling~~Modelling Research at the Primate Research Institute for daily care of the chimpanzees.

References

- Adachi I. 2014. Spontaneous Spatial Mapping of Learned Sequence in Chimpanzees: Evidence for a SNARC-Like Effect. *PLoS ONE* 9:e90373. doi: 10.1371/journal.pone.0090373.
- Batson CD, Powell AA. 2003. Altruism and Prosocial Behavior. In: Weiner IB, Freedheim DK, Schinka JA, Velicer WF, eds. *Handbook of psychology*. Wiley, New York: Wiley, 282-316.
- Boesch C .1994. Cooperative hunting in wild chimpanzees. *Animal Behaviour* 48:653-667. doi: 10.1006/anbe.1994.1285.
- Boesch C, Boesch H. 1989. Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal Physical Anthropology* 78:547-573. doi: 10.1002/ajpa.1330780410.

442 Claidière N, Whiten A, Mareno MC, Messer EJE, Brosnan SF, Hopper LM, Lambeth SP,
 443 Schapiro SJ, McGuigan N. 2015. Selective and contagious prosocial resource
 444 donation in capuchin monkeys, chimpanzees and humans. *Scientific Reports*
 445 5:7631. doi: 10.1038/srep07631.

446 Crockford C, Wittig RM, Mundry R, Zuberbühler K. 2012. Wild Chimpanzees Inform
 447 Ignorant Group Members of Danger. *Current Biology* 22:142-146. doi:
 448 10.1016/j.cub.2011.11.053.

449 Cronin KA, Schroeder KKE, Snowdon CT. 2010. Prosocial behaviour emerges
 450 independent of reciprocity in cottontop tamarins. *Proceedings of the Royal Society*
 451 *of London. Series B, Biological Sciences*. doi: 10.1098/rspb.2010.0879.

452 de Waal F. 1989. *Chimpanzee politics: Power and sex among apes*. Baltimore: Johns
 453 Hopkins University Press.

454 de Waal FBM. 2008. Putting the Altruism Back into Altruism: The Evolution of Empathy.
 455 *Annual Review of Psychology* 59:279-300. doi:
 456 10.1146/annurev.psych.59.103006.093625.

457 Duffy KG, Wrangham RW, Silk JB. 2007. Male chimpanzees exchange political support
 458 for mating opportunities. *Current Biology* 17:R586-R587.

459 Fehr E, Fischbacher U. 2003. The nature of human altruism. *Nature* 425:785-791.

460 Fehr E, Fischbacher U. 2004. Third-party punishment and social norms. *Evolution and*
 461 *Human Behavior* 25:63-87. doi: 10.1016/S1090-5138(04)00005-4.

462 Fehr E, Gächter S. 2002. Altruistic punishment in humans. *Nature* 415:137-140.

463 Gomes CM, Boesch C. 2011. Reciprocity and trades in wild West African chimpanzees.
 464 *Behavioral Ecology and Sociobiology* 65:2183-2196. doi: 10.1007/s00265-011-
 465 1227-x.

466 Gomes CM, Mundry R, Boesch C. 2009. Long-term reciprocation of grooming in wild
 467 West African chimpanzees. *Proceedings of the Royal Society of London. Series B,*
 468 *Biological Sciences* 276:699-706. doi: 10.1098/rspb.2008.1324.

469 Hare B, Call J, Tomasello M. 2001. Do chimpanzees know what conspecifics know?
 470 *Animal Behaviour* 61:139-11. doi: 10.1006/anbe.2000.1518.

471 Hirata S. 2009. Chimpanzee social intelligence: selfishness, altruism, and the mother-
 472 infant bond. *Primates* 50:3-11. doi: 10.1007/s10329-008-0122-1.

473 Hoffman ML. 1978. Psychological and Biological Perspectives on Altruism.
 474 *International Journal of Behavioral Development* 1:323-339. doi:
 475 10.1177/016502547800100403.

476 Horner V, Carter JD, Suchak M, de Waal FBM. 2011a. Spontaneous prosocial choice by
 477 chimpanzees. *Proceedings of the National Academy of Sciences* 108:13847-13851.
 478 doi: 10.1073/pnas.1111088108.

479 Horner V, Carter JD, Suchak M, de Waal FB. 2011b. Reply to Skoyles: Misplaced
 480 assumptions of perfect human prosociality. *Proceedings of the National Academy*
 481 *of Sciences* 108:E836-E836.

482 House BR, Silk JB, Lambeth SP, Schapiro SJ. 2014. Task design influences prosociality
 483 in captive chimpanzees (*Pan troglodytes*). *PLOS ONE* 9:e103422.

484 Jensen K, Call J, Tomasello M. 2007. Chimpanzees Are Rational Maximizers in an
 485 Ultimatum Game. *Science* 318:107-109. doi: 10.1126/science.1145850.

486 Jensen K, Hare B, Call J, Tomasello M. 2006. What's in it for me? Self-regard precludes
 487 altruism and spite in chimpanzees. *Proceedings of the Royal Society B: Biological*
 488 *Sciences* 273:1013-1021. doi: 10.1098/rspb.2005.3417.

489 Kim Y, Martinez L, Choe JC, Lee DJ, Tomonaga M. 2015. Orangutans (*Pongo* spp.) do
 490 not spontaneously share benefits with familiar conspecifics in a choice paradigm.
 491 *Primates* 56:193-200. doi: 10.1007/s10329-015-0460-8.

492 Lakshminarayanan VR, Santos LR. 2008. Capuchin monkeys are sensitive to others'
 493 welfare. *Current Biology* 18:R999-R1000. doi: 10.1016/j.cub.2008.08.057.

494 Langergraber KE, Mitani JC, Vigilant L. 2007. The limited impact of kinship on
 495 cooperation in wild chimpanzees. *Proceedings of the National Academy of*
 496 *Sciences* 104:7786-7790.

497 Martin, CF, R Bhui, P Bossaerts, T Matsuzawa, and C Camerer. 2014. Chimpanzee
 498 choice rates in competitive games match equilibrium game theory predictions.
 499 *Scientific Reports* doi: 10.1038/srep05182.

500 Martin CF, Biro D, Matsuzawa T. 2011. Chimpanzees' use of conspecific cues in
 501 matching-to-sample tasks: public information use in a fully automated testing
 502 environment. *Animal Cognition* 14:893-902. doi: 10.1007/s10071-011-0424-3.

503 Matsuzawa T. 2003. The Ai project: historical and ecological contexts. *Animal Cognition*
 504 6:199-211.

505 Matsuzawa T. 2006. Sociocognitive development in chimpanzees: a synthesis of
 506 laboratory work and Fieldwork. In: Matsuzawa T, Tomonaga M, Tanaka M, eds.
 507 *Cognitive development in chimpanzees*. Tokyo:Springer, pp 3-33.

508 McGrew WC. 2010. In search of the last common ancestor: New findings on wild
 509 chimpanzees. *Philosophical Transactions of the Royal Society B* 365: 3267-3276.

510 Melis AP, Schneider A-C, Tomasello M. 2011. Chimpanzees, *Pan troglodytes*, share
 511 food in the same way after collaborative and individual food acquisition. *Animal*
 512 *Behaviour*. doi: 10.1016/j.anbehav.2011.05.024.

513 Melis AP, Warneken F, Jensen K, Schneider A-C, Call J, Tomasello M. 2011.
 514 Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of*
 515 *the Royal Society B: Biological Sciences* 278:1405-1413. doi:
 516 10.1098/rspb.2010.1735.

517

518 Mitani JC, Merriwether DA, Zhang C. 2000. Male affiliation, cooperation and kinship in
 519 wild chimpanzees. *Animal Behaviour* 59:885-893. doi: 10.1006/anbe.1999.1389.

520 Mueller DC. 1986. Rational egoism versus adaptive egoism as fundamental postulate for
 521 a descriptive theory of human behavior. *Public Choice* 51:3-23. doi:
 522 10.1007/BF00141682.

523 Nishida T, Hosaka, K. 1996. Coalition strategies among adult male chimpanzees of the
 524 Mahale Mountains, Tanzania. In: McGrew W, Marchant L, Nishida T, eds. *Great*
 525 *Ape Societies*. Cambridge: Cambridge University Press, 114-134.

526 Plomin R, DeFries JC, Loehlin JC. 1977. Genotype-environment interaction and
 527 correlation in the analysis of human behavior. *Psychological Bulletin* 84:309-322.

528 Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli D J, Richardson AS, Lambeth SP,
529 Mascaro J, Shapiro SJ. 2005. Chimpanzees are indifferent to the welfare of
530 unrelated group members. *Nature* 437:1357-1359. doi: 10.1038/nature04243.

531 Skerry AE, Sheskin M, Santos LR. 2011. Capuchin monkeys are not prosocial in an
532 instrumental helping task. *Animal Cognition* 14:647-654. doi: 10.1007/s10071-
533 011-0399-0.

534 Skoyles JR. 2011. Chimpanzees make mean-spirited, not prosocial, choices. *Proceedings*
535 *of the National Academy of Sciences* 108:E835-E835.

536 Suchak M, Epplé, TM, Campbell MW, de Waal FBM. 2014. Ape duos and trios:
537 spontaneous cooperation with free partner choice in chimpanzees. *PeerJ* 2:e417

538 Suchak M, de Waal FBM. 2012. Monkeys benefit from reciprocity without the cognitive
539 burden. *Proceedings of the National Academy of Sciences* 109:15191-15196. doi:
540 10.1073/pnas.1213173109.

541 Takimoto A, Fujita K. 2011. I acknowledge your help: capuchin monkeys' sensitivity to
542 others' labor. *Animal Cognition* 14:715-725. doi: 10.1007/s10071-011-0406-5.

543 Tennie C, Jensen K, Call J. 2016. The nature of prosociality in chimpanzees. *Nature*
544 *Communications* 7:13915.

545 Vonk J, Brosnan SF, Silk JB, Henrich J, Richardson AS, Lambeth SP, Schapiro SJ,
546 Povinelli DJ. 2008. Chimpanzees do not take advantage of very low cost
547 opportunities to deliver food to unrelated group members. *Animal Behaviour*
548 75:1757-1770. doi: 10.1016/j.anbehav.2007.09.036.

549 Warneken F, Tomasello M. 2006. Altruistic Helping in Human Infants and Young
550 Chimpanzees. *Science* 311:1301-1303. doi: 10.1126/science.1121448.

551 Warneken F, Hare B, Melis AP, Hanus D, Tomasello M. 2007. Spontaneous altruism by
552 chimpanzees and young children. *PLoS Biology* 5:e184.

553 Warneken F, Tomasello M. 2009. The roots of human altruism. *British Journal of*
554 *Psychology* 100:455-471. doi: 10.1348/000712608X379061.

555 Watts DP. 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale
556 National Park, Uganda. *Behavioral Ecology and Sociobiology* 44:43-55.

557 Yamamoto S, Humle T, Tanaka M. 2012. Chimpanzees' flexible targeted helping based
558 on an understanding of conspecifics' goals. *Proceedings of the National Academy*
559 *of Sciences* 109:3588-3592. doi: 10.1073/pnas.1108517109.

560

561

562