

1 **TITLE PAGE**

2 **Title:**

3 Bargaining in chimpanzees (*Pan troglodytes*): the effect of cost, amount of gift, reciprocity and
4 communication

5 **Running title:**

6 Dictator and Ultimatum games in chimpanzees

7 **Authors:**

8 Nereida Bueno-Guerra^{1,2,3}, Christoph J. Völter^{3,4,5}, África de las Heras^{3,4}, Montserrat Colell², Josep
9 Call^{3,4}

10 1 Universidad Pontificia Comillas, Madrid, Spain

11 2 Institut de Neurociències. University of Barcelona, Barcelona, Spain

12 3 Max Planck Institute for Evolutionary Anthropology, Department of Developmental and
13 Comparative Psychology, Leipzig, Germany

14 4 University of St Andrews, School of Psychology and Neuroscience, St Andrews, UK

15 5 Messerli Research Institute, University of Veterinary Medicine Vienna, Medical University of
16 Vienna, University of Vienna, Vienna, Austria

17 **AUTHOR FOOTNOTES:**

18 **Acknowledgments**

19 We thank the two funding institutions which supported the present study: FPU12/00409 grant
20 provided by the Spanish Ministry of Education and held by NBG and La Caixa grant held by AD. We
21 also thank Raik Pieszek for constructing the experimental apparatuses; Hanna Petschauer for schedule
22 arrangements; Cristina Zickert for preparing Figure 4, and the zookeepers at the Leipzig Zoo for their
23 help with the chimpanzees. We also thank Keith Jensen for his helpful comments on an earlier version
24 of this manuscript.

25 **Contributions**

26 Conceived and designed the experiments: NBG, JC, AD, MC. Performed the experiments: NBG, AD.
27 Analyzed the data: CV, JC, NBG. Interpretation of data and writing of the paper: JC, NBG, CV.

28 **Corresponding author:**

29 Nereida Bueno-Guerra (ORCID ID: 0000-0003-1442-7905)
30 Universidad Pontificia Comillas (Facultad de Psicología)
31 Calle Universidad de Comillas, 3-5 (28049, Madrid, Spain)
32 Telephone number: +34 625247086
33 E-Mail: nereidabuenoguerra@gmail.com

34 **ABSTRACT:**

35 Humans routinely incur costs when allocating resources and reject distributions judged to be
36 below/over an expected threshold. The Dictator/Ultimatum Games (DG/UG) are two-player games
37 that quantify prosociality and inequity aversion by measuring allocated distributions and rejection
38 thresholds. Although the UG has been administered to chimpanzees and bonobos, no study has used
39 both games to pinpoint their motivational substrate. We administered a DG/UG using pre-assigned
40 distributions to four chimpanzee dyads controlling for factors that could explain why proposers'
41 behavior varied substantially across previous studies: game order, cost for proposers and amount for
42 recipients. Moreover, players exchanged their roles (proposer/recipient) to test reciprocity. Our results
43 show that proposers offered more in the DG than in the non-social baseline, particularly when they
44 incurred no cost. In UG, recipients accepted all above-zero offers, suggesting absence of inequity
45 aversion. Proposers preferentially chose options that gave larger amounts to the partner. However,
46 they also decreased their offers across sessions, probably being inclined to punish their partner's
47 rejections. Therefore, chimpanzees were not strategically motivated towards offering more generously
48 to achieve ulterior acceptance from their partner. We found no evidence of reciprocity. We conclude
49 that chimpanzees are generous rational maximizers that may not engage in strategic behavior.

50 Words: 200

51 **Keywords:**

52 ultimatum game, dictator game, fairness, inequity aversion, reciprocity, chimpanzees

53 **Word Count:** 35.700 characters (including spaces, text, tables, excluding references) plus 8.314
54 characters (references) = 44.014 characters

55

56

57

58

59

60 INTRODUCTION

61 The last decade has produced abundant comparative research with non-human primates on the
62 evolutionary origins of human prosociality and the sense of fairness. Even though great apes such as
63 chimpanzees engage in cooperative hunting and food sharing in the wild, laboratory studies have
64 consistently found that chimpanzees do not usually provide windfall resources to partners at no cost
65 (Silk et al., 2005) and do not understand justice as humans do (eg. Riedl, Jensen, Call, & Tomasello,
66 2012). Generally, testing procedures involve two conspecifics facing a food distribution task that may
67 potentially trigger phenomena such as inequity aversion (eg. Brosnan & de Waal, 2003; but see
68 Engelmann, Clift, Herrmann, & Tomasello, 2017), no cost prosociality (eg. Horner, Carter, Suchak, &
69 de Waal, 2011), food sharing (Silk, Brosnan, Henrich, Lambeth, & Shapiro, 2013) or reciprocity (eg.
70 Amici et al., 2014). Bargaining games, such as the dictator (DG) and the ultimatum (UG) games
71 (Güth, Schmittberger, & Schwarze, 1982) are particularly appealing because they combine each of
72 these phenomena simultaneously.

73 In both games, a proposer splits a windfall in any way she desires with her partner. Whereas
74 the DG recipient is passive and has to accept the proposer's offer, the UG recipient can either accept
75 or reject the offer. If the offer is accepted, each partner receives the corresponding split but if the offer
76 is rejected nobody receives anything. Since the DG recipient cannot affect the final outcome of the
77 distribution, any non-zero offer by the proposer indicates the latter's prosocial tendency. In contrast,
78 the proposer's offer in the UG is composed of her prosocial tendency plus her strategic estimation of
79 what the recipients are likely to accept. When confronted with resource distribution games, humans
80 take into account their own and their partners' prosocial tendencies and social aversions to avoid
81 conflict. Although there are substantial cross-cultural differences (Camerer, 2003; Engel, 2011; Güth
82 & Kocher, 2014; Henrich et al., 2005; Henrich, Heine, & Norenzayan, 2010), human proposers make
83 offers above zero in both games, usually higher in the UG than the DG, and human recipients often
84 reject options smaller than 20% and sometimes even bigger than 50%. Taken together, these results
85 contradict the rational maximizer's perspective since some humans are willing to give and reject at
86 their own cost (Güth & Kocher, 2014). Importantly, we use the term "rational maximizer" to indicate
87 that when there is something to be gained, subjects take it regardless of what someone else got as a
88 result, even if that someone was responsible for creating that choice in the first place.

89 Current interest in the evolutionary roots of fairness and its psychological underpinnings have
90 led researchers to confront pairs of individuals with various social dilemmas including several
91 versions of the UG (Jensen, Call, & Tomasello, 2007; Kaiser et al., 2012; Proctor, Williamson, de
92 Waal, & Brosnan, 2013). Following the mini-ultimatum procedure developed by Falk and colleagues
93 (2003), Jensen et al. (2007) presented dyads of chimpanzees with preselected pairs of quantities (e.g.,
94 5/5 vs. 8/2, with the first of each pair representing the proposer's allocation). The proposer could

95 select one of the pairs by pulling a rod that brought the offer halfway. Then, the recipient accepted by
96 pulling another rod that delivered the offer to both subjects or rejected by not pulling during 60s, thus
97 ending the trial without any food within reach. Kaiser and colleagues (2012) tested chimpanzees and
98 bonobos in a procedure where they allowed the proposers to “steal” some of the food originally
99 allocated to the recipient before making an offer, to see whether this enhanced rejections. In both
100 studies, proposers did not incur cost to make equal offers whereas recipients showed no inequity
101 aversion since they never rejected non-zero outcomes. Consequently, unlike humans, chimpanzees
102 and bonobos behaved as rational maximizers. With regard to recipients, one argument against this
103 conclusion was that 0-options were accepted approximately half of the time (Jensen et al., 2007).
104 According to some authors, chimpanzees might not have behaved as rational maximizers (Brosnan,
105 2013). According to others (Henrich & Silk, 2013), rejecting 0-option half of the time implies
106 responding at chance, which is compatible with rational maximizing as both accepting and rejecting
107 leads to zero outcome. Smith and Silberberg (2010) offered an alternative explanation. They found
108 that apes’ data were reproducible in humans by increasing the delay to reject from 1 to 5 minutes.
109 Namely, when humans were forced to wait 5 minutes (instead of 1) to reject an offer, they tended to
110 accept anything to initiate the next trial and thus increased their likelihood of obtaining something.
111 This means that 60s may have been too long to wait for chimpanzees (Jensen et al., 2007) who may
112 have accepted 0-offers to initiate a new trial with better prospects.

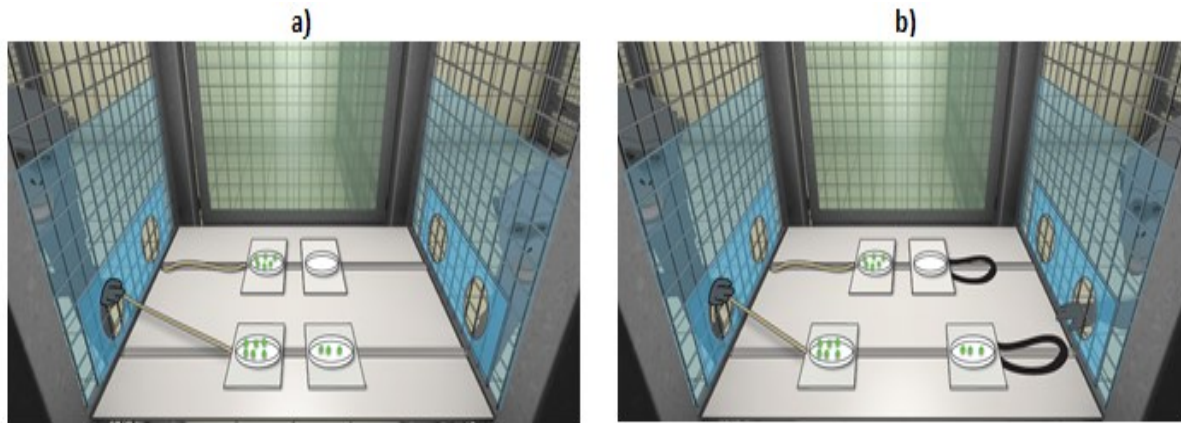
113 Another relevant aspect for bargaining methodologies is the way proposers make offers and
114 recipients respond to them. One solution is using token exchange procedures to substitute the direct
115 presence of food for an object (the token equals some distribution of food) and to emulate a physical
116 interchange. Proctor and colleagues (2013) compared chimpanzees’ responses in an UG and in a
117 preference test using tokens, each of them allocating a different amount of food to the proposer and
118 the recipient (5/1 vs. 3/3). Proposers selected one token, gave it to the recipient who could then either
119 give it to a begging experimenter (accept) or keep it during the next 30s (reject). In their preference
120 test, proposers gave tokens directly to the experimenter while a naïve passive recipient sat in the
121 adjacent cage. Although the authors treated this preference test as a DG, this is unwarranted because
122 the proposer did not give anything directly to the recipient, turning it into a non-social game (Henrich
123 & Silk, 2013). The authors found that proposers selected the 3/3 token more often in the UG than in
124 the preference test. However, the interpretation of this result is controversial. Henrich and Silk (2013)
125 pointed out that the change towards 3/3 was not different from chance in two out of the three dyads.
126 In response, Brosnan and de Waal (2014) claimed that this change of behavior between conditions
127 reflected second-order inequity aversion as chimpanzees might have anticipated a conflict. However,
128 since rejections never occurred and no experimental evidence for that potential anticipation was
129 provided, this remains a mere conjecture. Pairing a prototypical DG with an UG would have been
130 highly desirable because it would have allowed researchers to distinguish intrinsic (i.e., give) from

131 strategic (i.e., give to receive) prosociality. Furthermore, the absence of 0-options or the inclusion of a
132 begging human experimenter may have substantially hindered the appearance of rejections.

133 In sum, the evolutionary picture of fairness based on the UG remains rather ambiguous.
134 Whereas two studies characterize ape proposers as selfish (Jensen et al., 2007; Kaiser et al., 2012)
135 another study characterizes them as prosocial (Proctor et al., 2013) but in any case, whether this is
136 based on intrinsic or strategic motivation remains unclear. Moreover, although all studies have shown
137 that recipients accept any offers above zero, there are different interpretations about the absence of
138 rejections in recipients (Jensen, Call, & Tomasello, 2013; Proctor, Williamson, de Waal, & Brosnan,
139 2013). The goal of this study is to shed light on these issues by comparing chimpanzees' responses in
140 an iterated DG/UG that manipulated the cost to the proposers and the size of the gift to recipients.
141 Players faced each other across a table and the proposer selected one of two food windfalls by pulling
142 a rope that distributed it among the two players. Moreover, in the UG the recipient could accept the
143 proposer's choice by pulling another rope or reject it by not pulling for 15s (see Figure 1b). We are
144 aware that a go/no go paradigm for rejections in UG diminishes exact comparison with UG human
145 procedures, but the reduction of rejection time to 15s decreases the likelihood of unmotivated refusals
146 (Smith & Silberberg, 2010). Two key features of our study deserve special mention. First, our
147 ABACA design alternated between non-social (A) and social games (B and C represented DG or
148 UG), a feature that allowed us to obtain a reliable estimate of the baseline tendency to select each
149 option in the absence of a partner as well as their understanding of the game and the stability of their
150 response.

151 Second, we manipulated the cost for proposers and the size of the gift for the recipient. The
152 latter allowed us to know whether proposers considered their partner's payoff in their offers and
153 whether recipients rejected based on advantageous (rejection of high gift) or disadvantageous
154 (rejection of low gift) inequity aversion. The inclusion of a 6/0 option measured the likelihood of
155 rejecting when receiving nothing and served as an anchor point against which all other options were
156 pitted (6/3, 5/3, 5/9, 6/9, see Table 1 for further information). Importantly, we are aware that using
157 small quantities may produce different recipients' responses than larger rewards. However, it is not
158 only the design feasibility that justifies their use, but also the idea that only when differential rates
159 between the rewards are small, moral emotions are activated, thus allowing us to explore whether they
160 are present in non-human animals. Finally, chimpanzees played reciprocal trials (i.e. every dyad
161 played the same condition switching roles) to see whether second-order inequity aversion or
162 reciprocity occurred. We also scored any communicative acts (see SI).

163 **Figure 1 around here**



164

165 Figure 1. Illustration of the apparatus for the DG (a) and UG (b) in the condition 6/0 (background) 6/3
 166 (foreground). The proposer is depicted on the left and the recipient on the right. In the DG, the
 167 recipient cannot reject the offer. In the UG, the recipient can respond to the offer by pulling the U-
 168 shaped rope (accept) or not (reject) once the proposer has chosen one option.

169 **METHODS**

170 The Committee of Bioethics at the University of Barcelona (IRB00003099) and the ethics committee
 171 of the Wolfgang Köhler Primate Research Center (WKPRC) approved the study.

172 **Participants.** Six chimpanzees (4 males; mean age= 15 years) housed at the WKPRC in Leipzig Zoo
 173 (Germany) participated in the study. We tested four dyads. Even though dyads consisted of forced
 174 partner combinations, we carefully chose kin or nonkin social tolerant partners because previous
 175 studies had shown those partners to be successful in cooperation (eg. Melis, 2006; Suchak, Eppley,
 176 Campbell, & de Waal, 2014). Two subjects (Lobo, Kofi) played twice to informally explore whether
 177 they changed their behavior depending on the partner they were playing with (see Table S1 for
 178 detailed information upon age, sex, rearing history and previous participation in Jensen et al.'s study
 179 (Jensen et al., 2007)).

180 **Materials.** We used two similar apparatuses for the UG and DG (see Figure 1). The DG apparatus
 181 consisted of a PVC table with two parallel guide rails running from the proposer's side to the
 182 recipient's side. A pair of trays located on top of each rail holding various food distributions
 183 constituted one of the options that the proposer could select by pulling a rope so that the trays on the
 184 corresponding rail moved in opposite directions: the closest tray moved toward the proposer and the
 185 farthest tray toward the partner. The UG apparatus was similar except that when the proposer pulled,
 186 the trays in that rail moved in opposite directions but stopped halfway to the recipient making a piece
 187 of Velcro accessible to him so that he could decide whether to pull to complete the movement of the
 188 trays (accept) or not (after 15s reject, see Video for illustrative examples of acceptance and rejection
 189 and SI for further detailed information about the apparatus).

190

Table 1 around here

191

192 Table 1. Conditions and maximizing choices. Quantities used in non-social (Door Open/Door Closed)
193 and social games. Depicted are the outcomes in each non-social condition based on a maximizing
194 outcome. We also provide the labels of each pair of options used in social games to illustrate the
195 factors assessed (cost for the proposer; gift for the recipient)

196

Non-social Door Open	Choice if maximization	Non-social Door Closed	Choice if maximization	Social games UG/DG	Labels in Social games	
					Proposer	Recipient
6/0 and 6/3	6/3	6/0 and 6/3	chance	6/0 and 6/3	No Cost	Small gift
6/0 and 5/3	5/3	6/0 and 5/3	6/0	6/0 and 5/3	Cost	Small gift
6/0 and 5/9	5/9	6/0 and 6/9	chance	6/0 and 6/9	No Cost	Large gift
0/0 and 0/3	0/3	6/0 and 5/0	6/0	6/0 and 5/9	Cost	Large gift

197

198

199 **Food and conditions.** We used small pieces of grapes/pellets, depending on dyads' food preferences.
200 We configured the conditions following Hanus and Call (2007) to have higher differences and lower
201 ratios between final outcomes. Thus, we had four conditions with a default 6/0 option pitted against
202 another option controlling for cost to be generous (in no cost conditions, the proposers could be
203 generous with their partners for free by always earning 6 pieces of food whereas in cost conditions
204 that would imply losing 1 piece of food by deciding between 6/0 and 5/x) and size of gift (in small
205 gift conditions, the proposers could raise their partner's outcome to 3 pieces of food, less than their
206 own profit (i.e. 6/0 and 6/3), whereas in large gift conditions, the partner's outcome would surpass
207 their own (i.e., 6/0 and 6/9). We varied some pairs of quantities between non-social and social games
208 (see Table 1) to test for the chimpanzees' understanding of the task. The condition 0/0 and 0/3
209 increased the salience of the recipient's side allowing us to analyze whether subjects payed attention
210 to the consequences of their choices with respect to the pay-offs on their side. The condition 6/0 and
211 5/0 allowed us to ensure that subjects discriminated quantities (6 vs 5) and the cost was significant to
212 them.

213 **Procedure and design.** We used an ABACA design (A: training non-social, B/C: social games). The
214 training consisted of 6 conditions that were played across 8 sessions of 12 trials each. We conducted
215 the training before the social games and post-training after each social game, therefore each subject
216 played 24 non-social sessions. The state of the door was relevant during the training. The closed door
217 did not allow the subject to gain access to the adjacent cage. Therefore, maximizing the pay-off only
218 required paying attention to the options on the subject's side (the food allocated to the other side could
219 not be obtained). Thus, we could control whether subjects would preferentially choose maximizing
220 quantities (eg. 6/0, obtaining 6, rather than 5/3, obtaining 5, see Door close conditions in Table 1).
221 The open door allowed subjects access to the adjacent cage. Therefore, maximizing the pay-off
222 required the subject to pay attention to trays on **its** side as well as on the other side, understand how
223 trays moved and avoid natural impulses to pick always the closest and highest quantities in order to
224 choose the maximizing option (eg. 5/3, obtaining 8, rather than 6/0, obtaining 6, see open door
225 conditions in Table 1). Table 1 shows how subjects should vary their choices depending on the state
226 of the door to prove their understanding of the game. In each session, one given condition was played
227 during three non-consecutive trials. Chimpanzees played alone and passed the training when they
228 chose the maximizing option at least in 80% of the trials per condition. We counterbalanced the order
229 of the conditions, the sides of each option and the room where the actor played.

230 Each dyad played both UG and DG. Each game consisted of 8 sessions, 12 trials per session. The
231 proposer and recipient roles alternated from trial to trial (e.g., in trial 1 the condition 6/0 and 6/3 is
232 played; Alex plays as proposer and Jahaga as recipient; in trial 2, the condition is maintained but Alex
233 is the recipient and Jahaga the proposer). Therefore, to analyze reciprocity we measured whether
234 dyads matched their choices in each pair of reciprocal trials and whether this remained constant across
235 sessions. The order of the games was counterbalanced across dyads (i.e., ABACA or ACABA). Every
236 trial started with the experimenter placing the food out of sight from the participants. When the
237 proposer chimpanzee chose one option, in DG, both players got access to the food immediately (see
238 Figure 1a) whereas in UG, the experimenter waited for 15 seconds for the recipient to pull from the
239 Velcro (see Figure 1b). If the recipient did not pull, the food was removed. Regardless of rejection or
240 acceptance, the inter-trial interval remained constant.

241 **ANALYSIS**

242 We used Generalized Linear Mixed Models (GLMM; (Baayen, 2008)) with binomial error structure
243 and logit link function to analyze subjects' choices (see Table 2 for an overview of the fitted models).
244 When subjects delivered food to the opposite side we scored 1, otherwise we scored 0. We also
245 examined when recipients in the UG rejected offers and whether the offer in the previous trial (or the
246 average offer in the previous session) affected the offer of the prior recipient in the current trial (short-
247 term reciprocity). We examined the effect of communicative attempts between proposers and

248 recipients. We coded two behaviors: “pointing”, if the subjects placed their index finger or their hand
 249 through the decision window for more than 3s and “interaction”, when the subjects touched or passed
 250 objects to each other through the mesh. We analyzed the two different responses separately. To
 251 examine whether they performed any of these responses at different rates in each social game we used
 252 the frequency of these responses as dependent variables. Moreover, as pointing and interaction could
 253 enhance the probability of the proposer to deliver more food (i.e. choosing 6/3 instead of 6/0) or to
 254 incur a cost (i.e. choosing 5/3 instead of 6/0), we analyzed whether these communication attempts
 255 were related to the proposer’s choice. For further information on the model specification, random
 256 effect structure, model stability and assumptions, see SI.

257 **Table 2 around here**

258 Table 2. Summary of the main GLMMs performed. See more information in SI.

GLMM	Data analyzed	Dependent variables	Predictor variables
Game understanding (GLMM01)	non-social door open and door closed, common conditions	Food for recipient’s side	cost, gift, state of door, session, trial number, training phase, cost x door
Difference UG/DG (GLMM02)	UG, DG, all conditions	Food for recipient	game, cost, gift, (all 2-way interactions), session, trial number
Change of behavior between social and non-social games (GLMM03)	non-social (door closed), UG, DG, common conditions	Food for recipient’s side	game, cost, game x cost
Rejection (GLMM04)	UG, all conditions	Rejection of offer	cost, gift, session, trial number, cost x gift
Reciprocity (GLMM05 / GLMM06)	UG, DG, all conditions	Food for recipient’s side	game, cost, gift, previous prosocial offer, trial number, session, and all 2-way interactions between previous prosocial offer and game, cost, and gift
Pointing (GLMM07)	UG, DG, all conditions	Pointing	game, session, trial number
Effect of pointing on prosocial choices (GLMM08)	UG, DG, all conditions	Food for recipient	recipient pointing, game, cost, session, trial number, type x game, type x cost

259

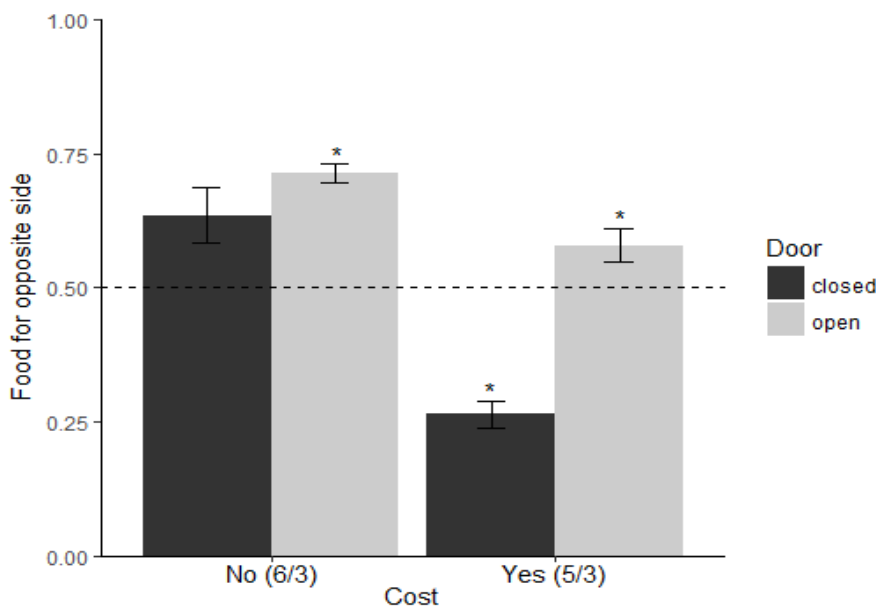
260 **RESULTS**

261 **Non-social games (training)**

262 Figure 2 presents the proportion of trials in which chimpanzees playing alone selected the
 263 option that delivered food to the opposite side instead of the default 6/0 as a function of cost at the

264 subject's side and door state. GLMM01 was significant compared to the null model (likelihood ratio
 265 test: $\chi^2=105.58$, $df=6$, $p<0.001$). We only found a significant interaction between door and cost
 266 (estimate \pm SE: -1.00 ± 0.29 , $\chi^2=11.77$, $df=1$, $p<0.001$; see Table S4). Post-hoc tests revealed that
 267 chimpanzees maximized their payoffs in cost condition when the door was open and they could gain
 268 access to 5+3 pieces of food than when it was closed and they would only get 5 pieces (1.35 ± 0.21 ,
 269 $\chi^2=44.69$, $df=1$, $p<0.001$). In the no cost condition, subjects' choices were not significantly affected
 270 by the door state (0.35 ± 0.21 , $\chi^2=2.87$, $df=1$, $p=0.090$). Moreover, subjects preferentially selected 6/0
 271 over 5/0 (80.1%, $T^+=21$, $N=6$, $p=0.031$) when the door was closed and 0/3 over 0/0 (97.2 %, $T^+=21$,
 272 $N=6$, $p=0.031$) when it was open (see SI for additional analyses). Taken together these results provide
 273 evidence that subjects paid attention to the quantities on their side and on their partner's side.
 274 Furthermore, they adjusted their choices to the state of the door to maximize their outcome.

275 **Figure 2 around here**



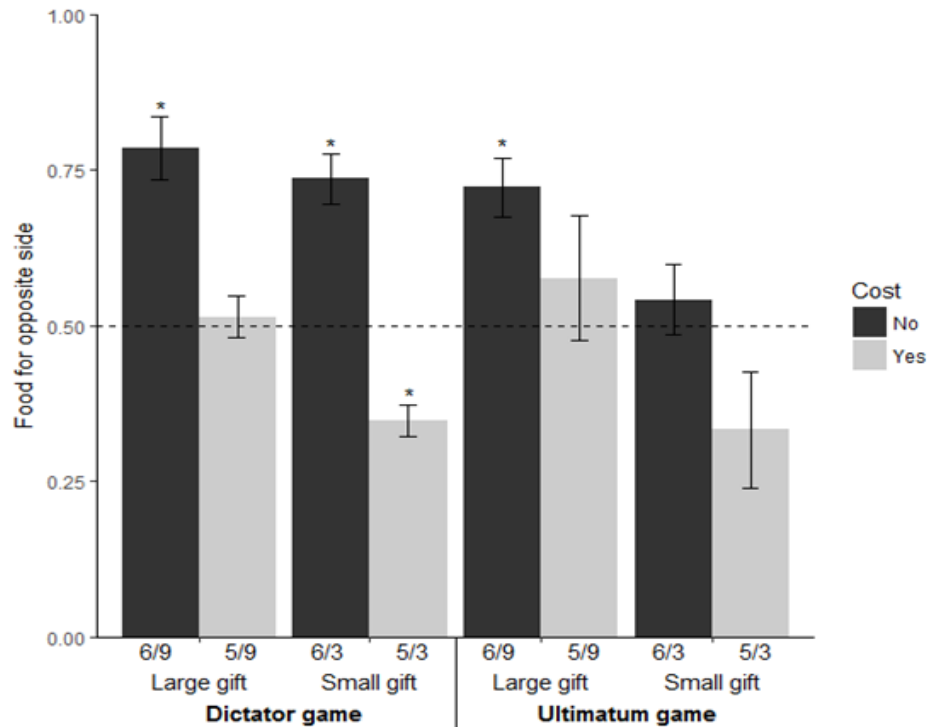
276
 277 Figure 2. Proportion of trials (mean \pm SE) of the common conditions in the Door open/closed non-
 278 social tests in which chimpanzees preferred the option that delivered food to the opposite side (over
 279 the default 6/0 option) as a function of cost and door state. * denotes significant deviations from the
 280 hypothetical chance level (dashed line), $p<0.05$, Wilcoxon signed-rank tests.

281
 282 **Social games**

283 Figure 3 presents the proportion of trials in which chimpanzees selected the options that
 284 delivered food to their partner's side (compared to the default 6/0 option) as a function of game, cost

285 and gift. GLMM02 (see SI) was significant compared to the null model ($\chi^2=82.01$, $df=8$, $p<0.001$),
 286 however we found no significant interactions (all $p>0.1$).

287 **Figure 3 around here**



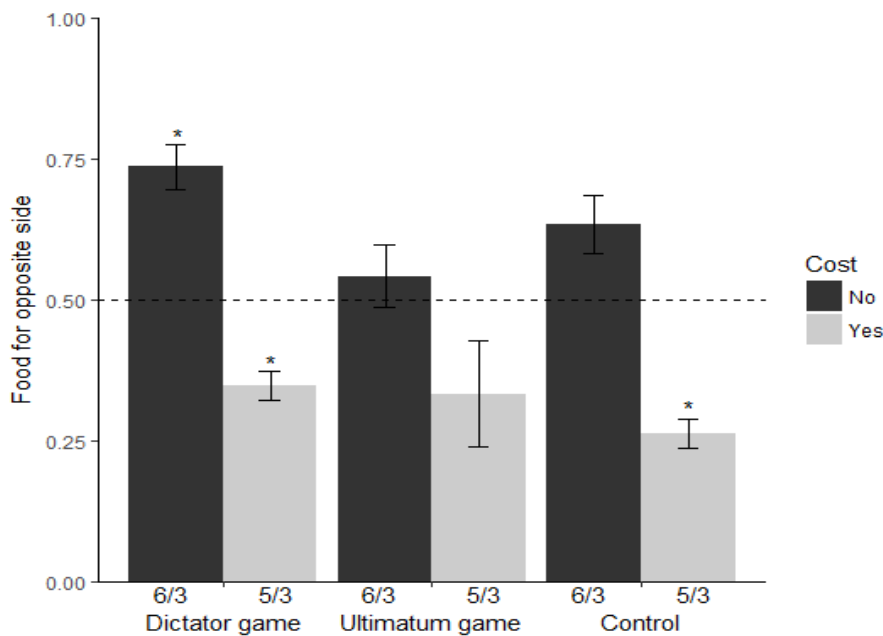
288
 289 Figure 3. Proportion of trials (mean ± SE) in which chimpanzees preferred the option that delivered
 290 food to their partner's side over the default 6/0 option as a function of game (DG, UG), size of the gift
 291 for the partner (x/9 vs. x/3), and cost at the subject's side (cost: 5/x; no cost: 6/x). * denotes
 292 significant deviations from the hypothetical chance level (dashed line), $p<0.05$, Wilcoxon signed-rank
 293 tests.

294 A reduced model without the 2-way interactions was significant compared to the null model
 295 ($\chi^2=76.93$, $df=5$, $p<0.001$; see Table S5). Subjects were more willing to deliver food to the partner
 296 when there was no cost (-1.11 ± 0.16 , $\chi^2=52.96$, $df=1$, $p<0.001$) and when the gift for the partner was
 297 large (-0.63 ± 0.16 , $\chi^2=16.91$, $df=1$, $p<0.001$). Moreover, the likelihood to deliver food to the partner
 298 decreased over sessions (-0.18 ± 0.08 , $\chi^2=5.66$, $df=1$, $p=0.017$). There was no significant difference
 299 between the games (-0.24 ± 0.15 , $\chi^2=2.37$, $df=1$, $p=0.124$) or a significant main effect of trial number
 300 (-0.007 ± 0.08 , $\chi^2=0.008$, $df=1$, $p=0.930$). Taken together these results show that chimpanzees played
 301 DG and UG in a similar way. They delivered food to their partners predominantly when this did not
 302 entail a cost for them but they were also more generous with larger amounts of food for the partner.

303 Figure 4 presents the proportion of trials in which chimpanzees selected the option that
 304 delivered food to their partner's side as a function of game and proposer's cost. We compared the

305 social games and the non-social training (door-closed condition; data pooled across the training
 306 phases because our analyses had shown that performance remained unchanged throughout training
 307 phases, see SI). GLMM03 was significant compared to the null model ($\chi^2= 98.56$, $df=3$, $p<0.001$; see
 308 Table S6). Proposers were more willing to deliver food to the other side when there was no cost for
 309 them (-1.40 ± 0.15 , $\chi^2= 92.63$, $df=1$, $p<0.001$). We found a significant effect of game ($\chi^2= 6.72$, $df=2$,
 310 $p=0.035$), specifically, subjects delivered more food to the other side in DG compared to the non-
 311 social training (0.43 ± 0.19 , $z= 2.33$, $p=0.020$) but not between the UG and training (-0.06 ± 0.19 , $z= -$
 312 0.34 , $p=0.736$). Consequently, chimpanzees only chose the prosocial options significantly more often
 313 when there was no cost associated with it in the DG compared to when they played alone.

314 **Figure 4 around here**



315
 316 Figure 4. Proportion of trials (mean ± SE) in which proposers selected the option that delivered food
 317 to their partner's side as a function of game (non-social control, DG, UG) and cost for the proposer.
 318 *denotes significant deviations from the hypothetical chance level (dashed line), $p<0.05$, Wilcoxon
 319 signed-rank tests.

320
 321 We also analyzed the two games separately. In both the UG and DG, proposers were
 322 significantly more willing to deliver food to the partner when they incurred no cost (UG: -0.91 ± 0.22 ,
 323 $\chi^2=17.69$, $df=1$, $p<0.001$; DG: -1.33 ± 0.28 , $\chi^2=8.27$, $df=1$, $p=0.004$). In the UG, this happened also
 324 when the gift for the partner was large (0.88 ± 0.22 , $\chi^2=16.52$, $df=1$, $p<0.001$). In contrast, no
 325 significant effect of gift was found in DG (0.39 ± 0.22 , $\chi^2=3.16$, $df=1$, $p=0.076$). Moreover, in UG

326 proposers became less inclined to deliver food across sessions (-0.26 ± 0.11 , $\chi^2=5.82$, $df=1$, $p=0.016$).
327 Thus, in both games chimpanzee proposers paid attention to the cost. They seemed to pay attention to
328 the gift for the partner particularly in UG, although they decreased the food delivery over sessions.

329 **Ultimatum game: acceptance rates**

330 Recipients accepted all offers above zero whereas zero offers were accepted in $58.3 \pm 7.1\%$ of
331 trials. GLMM04 was not significant compared to the null-model ($\chi^2=8.09$, $df=5$, $p=0.151$), neither was
332 a reduced without the interaction ($\chi^2=6.89$, $df=4$, $p=0.142$).

333 **Reciprocity**

334 Except for a male-male dyad in which one subject reciprocated prosocial offers (see Tables S9, S10
335 and Figure S2), we found no evidence for short-term reciprocity: neither the offers in the previous
336 trial (GLMM05) nor the average offers in the previous session (GLMM06) had a significant effect on
337 performance.

338 **Communication**

339 All recipients except one sometimes pointed to a preferred option in the social games ($13.4 \pm 5.2\%$ of
340 all trials, range: 0 – 42.7%). Recipients pointed usually before the proposers had chosen ($98.0 \pm 1.7\%$
341 of pointing trials). We found no evidence for a significant difference in pointing frequencies between
342 the UG (mean \pm SE: $22.0 \pm 7.8\%$) and DG ($8.6 \pm 4.4\%$; see Table S13 and GLMM07 in the SI). We
343 found no evidence that pointing changed the likelihood of the proposers providing food for the
344 recipients (GLMM08, see Table S14). Direct interactions between participants occurred only 34 times
345 (5.9% of all trials). Twenty-nine of these interactions occurred in the UG and five in DG. Due to the
346 small number of instances, we could not analyze whether there was a significant effect of these
347 interactions on the proposer's performance.

348 **DISCUSSION**

349 We tested chimpanzees using an iterated UG/DG protocol. Unlike humans, chimpanzee
350 responders behaved as rational maximizers, invariably accepting offers larger than zero, something
351 that is inconsistent with advantageous or disadvantageous inequity aversion, at least in the context of
352 bargaining games and bearing in mind that our study does not cover all the aspects typically addressed
353 in studies with adult humans. This is a very strong finding that has now been replicated in three other
354 studies (Jensen et al., 2007; Kaiser et al., 2012; Proctor et al., 2013). Similarly to Jensen and
355 colleagues' study (2007), chimpanzees accepted more than half of the zero offers. It has been argued
356 that such high acceptance rates might indicate poor understanding of the task (Brosnan, 2013).
357 However, we have provided robust and stable evidence of subjects' understanding of the

358 contingencies of the game, which required paying attention to 1) the quantities on their side, 2) the
359 opposite side, and 3) the consequences of choosing between the two options available. Another
360 explanation for the lack of rational maximization is that long delays to reject may increase “false”
361 acceptances to make a new trial start (Smith & Silberberg, 2010). However, this explanation is
362 unlikely since we reduced the rejection period to 15 seconds (lower than 60s in Jensen et al., 2007 and
363 30s in Proctor et al., 2013) and kept the time between trials constant. Thus, as Henrich and Silk
364 argued (2013), in a game where both accepting and rejecting a zero option invariably leads to a zero
365 outcome, rejections may occur at chance (in accordance with our results) and still be compatible with
366 rational maximization.

367 Proposers provided more food to conspecifics in the DG than when they played alone. In fact,
368 such prosocial offers resemble those made by humans in the same game and are also in line with the
369 change of preferences to offer more in social rather than non-social conditions of Proctor and
370 colleagues's study (2013). However, proposers offered the same in the UG regardless of the presence
371 of the partner, which differs from Proctor et al.'s (2013), where proposers offered more than expected
372 in an UG. Such finding is puzzling from the point of view of classical economics. Brosnan & de
373 Waal (2014) suggested that prosociality or anticipatory avoidance of conflict could explain this result.
374 However, some methodological concerns made these explanations contentious. The absence of
375 rejections might be due to the presence of a begging experimenter as well as to the fact that “neither
376 species was explicitly trained that refusal was an option” (Proctor et al., 2013).

377 We found some evidence of a calculated prosociality that regulates gifts provided the
378 proposers prefer not incurring costs. Probably the proposer first and foremost focused on her own
379 payoffs, and secondarily, on her partner's. Interestingly, proposers did not offer more in the UG than
380 the DG, as would have been expected for the sake of avoiding rejections. Perhaps the recipients'
381 behavior can explain this outcome. While human proposers face high risk of rejection, chimpanzee
382 proposers do not, given the high acceptance rate of their conspecifics. Responders accepting half of
383 the time do not force proposers to be generous, since any selfish offer is likely to be accepted at least
384 half of the time. This would justify the significant decrement of prosocial offers in UG, but it would
385 not explain doing so also at no cost. One explanation might be that proposers facing a rejection of a
386 selfish option would not be willing to reward the partner with food in a future trial and persist in
387 offering less and less food. This would be similar to continue punishing the recipient for rejecting
388 instead of rewarding the recipient to make him more willing to accept. If that was the case, there
389 would be no signs of second-order inequity aversion in chimpanzee proposers after the recipients'
390 refusals, contrary to previous interpretations (Brosnan & de Waal, 2014), but a lack of strategic
391 behavior characteristic of human proposers' performance.

392 Despite large methodological differences, the four studies conducted so far (Jensen et al.,
393 2007; Kaiser et al., 2012; Proctor et al., 2013 and the present one) have consistently shown that
394 chimpanzees seem to differ when they play UG and DG, suggesting a divergent evolutionary pathway
395 in the consideration of fairness. It is especially remarkable that no ape had rejected any offer different
396 from zero so far. Kaiser and colleagues (Kaiser et al., 2012) argued that chimpanzee recipients in
397 these games may not interpret a low offer as unfair. Although chimpanzees share food routinely, they
398 did not usually offer food to each other (Gilby, 2006), so perhaps any offer is surprising and thus no
399 unfairness is perceived. In contrast to humans, where the majority of cultures impose some kind of
400 justice that is likely to be claimed and to cause rejections if not accomplished, non-human primates do
401 not seem to possess an agreement on how to split windfall resources. Hence, rejections are probably
402 only present in societies which define themselves as a community with some agreement on abstract
403 entitlements among its members (which may explain why humans are more likely to reject a low offer
404 from another human but not from a computer (Blount, 1995)). One could argue that we would have
405 obtained different results if we had used much more valuable or much larger rewards. However, due
406 to their natural occurrence, we would argue that smaller rather than very large windfalls are likely to
407 be more common on a daily basis, and consequently, more relevant.

408 The virtual absence of rejections in the UG has also to be squared off with the seemingly
409 contradictory results from other studies with non-human primates. For instance, a task that required
410 the same effort from pairs of individuals but rewarded them differentially fostered rejection in
411 capuchin monkeys (Brosnan & de Waal, 2003 but see also Bräuer, Call, & Tomasello, 2009;
412 Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009). Why did capuchin monkeys
413 reject food in that study and chimpanzees did not when playing the UG? Windfall resources are not
414 common in nature but effortful activities (e.g. hunting, foraging) are. Thus, non-human primates may
415 consider merit rather than equality as a measuring rod for fairness, making deservingness comparable
416 to something factual rather than to something abstract. Therefore, in order to obtain a deeper
417 understanding of non-human primates' concept of fairness and force proposers to face the risk of a
418 potential rejection, novel tasks with factual comparisons, such as different labour investments, are
419 required.

420 Communication and establishing turn taking is one way by which human children manage to
421 split windfalls equally in coordination games (Grüneisen, 2015; Sánchez-Amaro, Duguid, Call, &
422 Tomasello, 2016). We found no evidence that communication or reciprocity fostered a more equitable
423 distribution of payoffs, in accordance to previous findings (Vonk et al., 2008). However, it is
424 interesting to note that in our study only recipients (except for one single occasion) emitted pointing
425 gestures to their proposer partners because pointing is usually reported between human experimenters
426 and captive non-human primates (up to 71% of captive chimpanzees pointed to unreachable food in
427 Leaven's studies (Leavens, Hopkins, & Bard, 2005)) rather than between conspecifics (Itakura, 1996).

428 In our case, pointing did not significantly alter the proposers' subsequent actions, but it seems clear
429 that chimpanzee responders were trying to use some way of local enhancement that was inefficiently
430 understood by proposers, as was previously reported in a similar proposer/recipient design (Silk et al.,
431 2005). It is unlikely that chimpanzee responders in our study were trying to reach the food, because
432 they did not point when the proposer was absent. Therefore, it seems that even when chimpanzees
433 individually use pointing as a referential gesture to humans, they find difficulties to transfer the same
434 meaning within their species, as if response to pointing was very limited between species. It might
435 happen that proposers do not perceive themselves as the addressee of such communication (however,
436 see orangutans' performance on referential pointing plus a discussion about the inferences required to
437 comprehend pointing, Moore, Call, & Tomasello, 2015).

438 **CONCLUSIONS**

439 In conclusion, our results are compatible with the existence of intrinsic (although non-costly)
440 prosociality and rational maximization behavior, but provide no evidence of inequity aversion. There
441 were no signs of reciprocity and proposers did not change their behavior even if it led to rejection
442 (contrary to the strategic behavior characteristic of human proposers' performance). These findings
443 suggest that prosociality, inequity aversion and strategic behavior might have followed different
444 evolutionary pathways in the two species.

445

446

447

448

449

450

451

452

453

454

455

456

457

458

459

460

461
462
463
464
465
466
467
468
469
470
471
472
473
474
475
476
477
478
479
480
481
482
483
484
485
486
487
488

AUTHOR CONTRIBUTIONS

Conceived and designed the experiments: NBG, JC, AD, MC. Performed the experiments: NBG, AD.
Analyzed the data: CV, JC, NBG. Interpretation of data and writing of the paper: JC, NBG, CV.

ACKNOWLEDGMENTS

We thank the two funding institutions which supported the present study: FPU12/00409 grant provided by the Spanish Ministry of Education and held by NBG and La Caixa grant held by AD. We also thank Raik Pieszek for constructing the experimental apparatuses; Hanna Petschauer for schedule arrangements; Cristina Zickert for preparing Figure 4, and the zookeepers at the Leipzig Zoo for their help with the chimpanzees. We are grateful to Keith Jensen and three anonymous reviewers for their helpful comments on an earlier version of this manuscript.

489
490
491
492
493
494
495
496
497
498
499
500
501
502
503
504
505
506
507
508
509
510
511
512
513
514
515
516
517

REFERENCES

- Amici, F., Aureli, F., Mundry, R., Amaro, A. S., Barroso, A. M., Ferretti, J., & Call, J. (2014). Calculated reciprocity? A comparative test with six primate species. *Primates*, *55*(3), 447–457. <https://doi.org/10.1007/s10329-014-0424-4>
- Baayen, R. H. (2008). Analyzing linguistic data: A practical introduction to statistics using R. *Processing*, *2*(3), 353. <https://doi.org/10.1558/sols.v2i3.471>
- Blount, S. (1995). When Social Outcomes Aren't Fair: The Effect of Causal Attributions on Preferences. *Organizational Behavior and Human Decision Processes*, *63*(2), 131–144. <https://doi.org/10.1006/obhd.1995.1068>
- Bräuer, J., Call, J., & Tomasello, M. (2009). Are apes inequity averse? New data on the token-exchange paradigm. *American Journal of Primatology*, *71*(2), 175–181. <https://doi.org/10.1002/ajp.20639>
- Brosnan, S. F. (2013). Justice- and fairness-related behaviors in nonhuman primates. *Proceedings of the National Academy of Sciences of the United States of America*, *110* Suppl, 10416–10423. Retrieved from <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3690609&tool=pmcentrez&rendertype=abstract>
- Brosnan, S. F., & de Waal, F. B. (2014). Evolution of responses to (un)fairness. *Science*, *346*(6207), 1251776. <https://doi.org/10.1126/science.1251776>
- Brosnan, S. F., & de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature*, *425*(6955), 297–299. <https://doi.org/10.1038/nature01963>
- Camerer, C. F. (2003). *Behavioral Game Theory: Experiments in Strategic Interaction: Experiments in Strategic Interaction*. Princeton University Press. Retrieved from

- 518 https://books.google.com/books?id=cr_Xg7cRvdcC&pgis=1
- 519 Engel, C. (2011). Dictator games: a meta study. *Experimental Economics*, 14(4), 583–610.
520 <https://doi.org/10.1007/s10683-011-9283-7>
- 521 Engelmann, J. M., Clift, J. B., Herrmann, E., & Tomasello, M. (2017). Social disappointment explains
522 chimpanzees' behaviour in the inequity aversion task. *Proceedings of the Royal Society B:
523 Biological Sciences*, 284(1861), 20171502. <https://doi.org/10.1098/rspb.2017.1502>
- 524 Falk, A., Fehr, E., & Fischbacher, U. (2003). On the Nature of Fair Behavior. *Economic Inquiry*,
525 41(1), 20–26. <https://doi.org/10.1093/ei/41.1.20>
- 526 Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: harassment and reciprocal
527 exchange. *Animal Behaviour*, 71(4), 953–963. <https://doi.org/10.1016/j.anbehav.2005.09.009>
- 528 Grüneisen, S. (2015). *The development of strategic coordination: An investigation into children's
529 abilities to solve coordination problems*. Max Planck Institute for Evolutionary Anthropology.
530 Retrieved from <http://hdl.handle.net/11858/00-001M-0000-002B-57DA-5>
- 531 Güth, W., & Kocher, M. G. (2014). More than thirty years of ultimatum bargaining experiments:
532 Motives, variations, and a survey of the recent literature. *Journal of Economic Behavior &
533 Organization*, 108, 396–409. <https://doi.org/10.1016/j.jebo.2014.06.006>
- 534 Güth, W., Schmittberger, R., & Schwarze, B. (1982). An experimental analysis of ultimatum
535 bargaining. *Journal of Economic Behavior & Organization*, 3(4), 367–388.
536 [https://doi.org/10.1016/0167-2681\(82\)90011-7](https://doi.org/10.1016/0167-2681(82)90011-7)
- 537 Hanus, D., & Call, J. (2007). Discrete quantity judgments in the great apes (Pan paniscus, Pan
538 troglodytes, Gorilla gorilla, Pongo pygmaeus): The effect of presenting whole sets versus item-
539 by-item. *Journal of Comparative Psychology*, 121(3), 241–249. [https://doi.org/10.1037/0735-
540 7036.121.3.241](https://doi.org/10.1037/0735-7036.121.3.241)
- 541 Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., ... Tracer, D. (2005). "Economic
542 man" in cross-cultural perspective: behavioral experiments in 15 small-scale societies. *The
543 Behavioral and Brain Sciences*, 28(6), 795-815; discussion 815-55.
544 <https://doi.org/10.1017/S0140525X05000142>
- 545 Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and
546 Brain Sciences*, 33(2–3), 61–83. <https://doi.org/10.1017/S0140525X0999152X>
- 547 Henrich, J., & Silk, J. B. (2013). Interpretative problems with chimpanzee ultimatum game.
548 *Proceedings of the National Academy of Sciences of the United States of America*, 110(33),

549 E3049. <https://doi.org/10.1073/pnas.1307007110>

550 Henrich, J., & Silk, J. B. (2013). Supplemental to: Interpretative Problems with Chimpanzee
551 Ultimatum Games. *SSRN Electronic Journal*. <https://doi.org/10.2139/ssrn.2250049>

552 Horner, V., Carter, J. D., Suchak, M., & de Waal, F. B. M. (2011). Spontaneous prosocial choice by
553 chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*,
554 *108*(33), 13847–13851. <https://doi.org/10.1073/pnas.1111088108>

555 Itakura, S. (1996). An exploratory study of gaze-monitoring in nonhuman primates. *Japanese*
556 *Psychological Research*, *38*(3), 174–180. <https://doi.org/10.1111/j.1468-5884.1996.tb00022.x>

557 Jensen, K., Call, J., & Tomasello, M. (2007). Chimpanzees are rational maximizers in an ultimatum
558 game. *Science (New York, N.Y.)*, *318*(5847), 107–109. <https://doi.org/10.1126/science.1145850>

559 Jensen, K., Call, J., & Tomasello, M. (2013). Chimpanzee responders still behave like rational
560 maximizers. *Proceedings of the National Academy of Sciences of the United States of America*,
561 *110*(20), E1837. <https://doi.org/10.1073/pnas.1303627110>

562 Kaiser, I., Jensen, K., Call, J., Tomasello, M., Fehr, E., Fischbacher, U., ... Yamagishi, T. (2012).
563 Theft in an ultimatum game: chimpanzees and bonobos are insensitive to unfairness. *Biology*
564 *Letters*, *8*(6), 942–945. <https://doi.org/10.1098/rsbl.2012.0519>

565 Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005). Understanding the Point of Chimpanzee
566 Pointing. *Current Directions in Psychological Science*, *14*(4), 185–189.
567 <https://doi.org/10.1111/j.0963-7214.2005.00361.x>

568 Melis, A. P. (2006). Chimpanzees Recruit the Best Collaborators. *Science*, *311*(5765), 1297–1300.
569 <https://doi.org/10.1126/science.1123007>

570 Moore, R., Call, J., & Tomasello, M. (2015). Production and Comprehension of Gestures between
571 Orang-Utans (*Pongo pygmaeus*) in a Referential Communication Game. *PLOS ONE*, *10*(6),
572 e0129726. <https://doi.org/10.1371/journal.pone.0129726>

573 Proctor, D., Williamson, R. A., de Waal, F. B. M., & Brosnan, S. F. (2013). Chimpanzees play the
574 ultimatum game. *Proceedings of the National Academy of Sciences*, *110*(6), 2070–2075.
575 <https://doi.org/10.1073/pnas.1220806110>

576 Proctor, D., Williamson, R. A., de Waal, F. B. M., & Brosnan, S. F. (2013). Reply to Jensen et al.:
577 Equitable offers are not rationally maximizing. *Proceedings of the National Academy of*
578 *Sciences of the United States of America*, *110*(20), E1838. Retrieved from
579 <http://www.ncbi.nlm.nih.gov/pubmed/23814870>

580 Riedl, K., Jensen, K., Call, J., & Tomasello, M. (2012). No third-party punishment in chimpanzees.
581 *Proceedings of the National Academy of Sciences of the United States of America*, 109(37),
582 14824–14829. <https://doi.org/10.1073/pnas.1203179109>

583 Sánchez-Amaro, A., Duguid, S., Call, J., & Tomasello, M. (2016). Chimpanzees coordinate in a
584 snowdrift game. <https://doi.org/10.1016/j.anbehav.2016.03.030>

585 Silberberg, A., Crescimbene, L., Addessi, E., Anderson, J. R., & Visalberghi, E. (2009). Does
586 inequity aversion depend on a frustration effect? A test with capuchin monkeys (*Cebus apella*).
587 *Animal Cognition*, 12(3), 505–509. <https://doi.org/10.1007/s10071-009-0211-6>

588 Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P., & Shapiro, S. J. (2013). Chimpanzees share
589 food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food
590 transfers. *Animal Behaviour*, 85(5), 941–947. <https://doi.org/10.1016/j.anbehav.2013.02.014>

591 Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., ... Schapiro, S. J.
592 (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*,
593 437(7063), 1357–1359. <https://doi.org/10.1038/nature04243>

594 Smith, P., & Silberberg, A. (2010). Rational maximizing by humans (*Homo sapiens*) in an ultimatum
595 game. *Animal Cognition*, 13(4), 671–677. <https://doi.org/10.1007/s10071-010-0310-4>

596 Suchak, M., Eppley, T. M., Campbell, M. W., & de Waal, F. B. M. (2014). Ape duos and trios:
597 spontaneous cooperation with free partner choice in chimpanzees. *PeerJ*, 2, e417.
598 <https://doi.org/10.7717/peerj.417>

599 Vonk, J., Brosnan, S. F., Silk, J. B., Henrich, J., Richardson, A. S., Lambeth, S. P., ... Povinelli, D. J.
600 (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to
601 unrelated group members. *Animal Behaviour*, 75(5), 1757–1770.
602 <https://doi.org/10.1016/j.anbehav.2007.09.036>

603

604

605

606

607

608

609
610
611
612
613
614
615
616
617
618
619
620
621
622
623
624
625
626
627
628
629
630
631
632
633
634
635
636
637
638

FIGURE LEGENDS

Figure 1. Illustration of the apparatus for the DG (a) and UG (b) in the condition 6/0 (background) 6/3 (foreground). The proposer is depicted on the left and the recipient on the right. In the DG, the recipient cannot reject the offer. In the UG, the recipient can respond to the offer by pulling the U-shaped rope (accept) or not (reject) once the proposer has chosen one option.

Table 1. Conditions and maximizing choices. Quantities used in non-social (Door Open/Door Closed) and social games. Depicted are the outcomes in each non-social condition based on a maximizing outcome. We also provide the labels of each pair of options used in social games to better illustrate the factors assessed (cost for the proposer; gift for the recipient)

Table 2. Summary of the main GLMMs performed. See more information in SI.

Figure 2. Proportion of trials (mean \pm SE) of the common conditions in the Door open/closed non-social tests in which chimpanzees preferred the option that delivered food to the opposite side (over the default 6/0 option) as a function of cost and door state. * denotes significant deviations from the hypothetical chance level (dashed line), $p < 0.05$, Wilcoxon signed-rank tests.

Figure 3. Proportion of trials (mean \pm SE) in which chimpanzees preferred the option that delivered food to their partner's side over the default 6/0 option as a function of game (DG, UG), size of the gift for the partner ($x/9$ vs. $x/3$), and cost at the subject's side (cost: $5/x$; no cost: $6/x$). * denotes significant deviations from the hypothetical chance level (dashed line), $p < 0.05$, Wilcoxon signed-rank tests.

Figure 4. Proportion of trials (mean \pm SE) in which proposers selected the option that delivered food to their partner's side as a function of game (non-social control, DG, UG) and cost for the proposer. *denotes significant deviations from the hypothetical chance level (dashed line), $p < 0.05$, Wilcoxon signed-rank tests.