

ACCEPTED MANUSCRIPT

Chimpanzees and children avoid mutual defection in a social dilemma

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1 Abstract

2

3 Cooperation often comes with the temptation to defect and benefit at the cost of others. This
4 tension between cooperation and defection is best captured in social dilemmas like the
5 Prisoner's Dilemma. Adult humans have specific strategies to maintain cooperation during
6 Prisoner's Dilemma interactions. Yet, little is known about the ontogenetic and phylogenetic
7 origins of human decision-making strategies in conflict scenarios. To shed light on this question,
8 we compared the strategies used by chimpanzees and 5-year old children to overcome a social
9 dilemma. In our task, waiting for the partner to act first produced the best results for the subject.
10 Alternatively, they could mutually cooperate and divide the rewards. Our findings indicate that
11 the two species differed substantially in their strategies to solve the task. Chimpanzees became
12 more strategic across the study period by waiting longer to act in the social dilemma. Children
13 developed a more efficient strategy of taking turns to reciprocate their rewards. Moreover,
14 children used specific types of communication to coordinate with their partners. These results
15 suggest that while both species behaved strategically to overcome a conflict situation, only
16 children engaged in active cooperation to solve a social dilemma.

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29 Keywords: Social dilemma, Prisoner's Dilemma, cooperation, coordination, chimpanzees,
30 children.

31 1. Introduction

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33 Cooperation is a widespread phenomenon in nature: from unicellular organisms to human
34 societies, evolutionary complexity can only be explained through cooperative processes in which
35 biological entities work together to achieve common benefits (Smith and Szathmary, 1995).
36 Sometimes cooperation is the best strategy for all agents (Boucher, 1988; Clutton-Brock, 2009)
37 but on other occasions cooperation comes together with the possibility to defect and reap the
38 benefits from the cooperative acts of others. This tension between cooperation and defection
39 is best captured by social dilemmas (Dawes, 1980). A well-known example is the Prisoner's
40 Dilemma model (Rapoport and Chammah, 1965; Tucker, 1950). This model describes a scenario
41 in which two players can either cooperate or defect. Mutual cooperation is always better than
42 mutual defection. However, for the individual player it is always better to defect regardless of
43 the other player's decision, leading to mutual defection if both play rationally. To solve this
44 conundrum, theoretical analyses have proposed different strategies such as "tit for tat", an
45 effective strategy in which each player will first cooperate and then subsequently replicate the
46 partners' previous action (Axelrod and Hamilton, 1981; Nowak and Sigmund, 1993).

47 However, these theoretical findings contrast with experimental research showing that people
48 tend to cooperate more than expected in a wide range of Prisoner's Dilemmas, including one-
49 shot interactions (Cooper et al., 1996; Kiyonari et al., 2000) and iterated versions of the dilemma
50 (Cooper et al., 1996; Dal Bo and Frechette, 2011; Wedekind and Milinski, 1996). This is consistent
51 with results from other games such as the Dictator and the Ultimatum Game in which people
52 tend to behave altruistically towards others (Camerer, 2003; Heinrich et al., 2001, although see
53 Smith and Silberberg, 2010).

54 Humans possess uniquely cooperative motivations to help and share with others from a young
55 age (Brownell et al., 2013; Liskowski et al., 2006; Warneken and Tomasello, 2006). We already
56 deviate from the rational assumptions of the Ultimatum (Bueno-Guerra et al., 2016; Wittig et
57 al., 2013) and the Dictator Games (Benenson et al., 2007) as children. To our knowledge, only
58 two studies have investigated how children solve a Prisoner's Dilemma. Matsumoto et al. (1986)
59 presented four-year-old children with a simplified version of the dilemma. In that task, pairs of
60 children had to choose between competition or cooperation cards and the rewards they would
61 obtain were determined according to the Prisoner's Dilemma payoff matrix. During the task
62 children were encouraged to discuss their strategies. Overall, the authors found that children
63 increased their likelihood to mutually cooperate across sessions and that the degree of

64 friendship was positively related with mutual cooperation. A more recent study with
65 considerably older children (Blake et al., 2015) presented 10- and 11-year-old children with an
66 anonymous computer-based Prisoner's Dilemma game. They found that children cooperated
67 more often in iterated versions of the dilemma in comparison to one-shot interactions. These
68 results suggest that the adult patterns of decision making in social dilemmas are already present
69 at a young age.

70 Such cooperative behaviour towards non-kin in social dilemmas is an important feature of
71 human evolution but very little experimental work has been done on how closely related species
72 respond to these dilemmas. The Prisoner's Dilemma model has been used to investigate the
73 nature of animal cooperation —whether different social interactions could be understood as
74 instances of the Prisoner Dilemma (Dugatkin, 1988; Raihani and Bshary, 2011; Wilkinson, 1984).
75 But, other than few studies with distantly related species (Stephens et al., 2002; Wood et al.,
76 2016), little emphasis has been placed in using the Prisoner's Dilemma as a framework to explore
77 in detail the proximate decision-making strategies that social animals such as great apes require
78 to resolve situations of conflict.

79 Like humans, great apes such as chimpanzees often face conflict situations in their daily lives;
80 situations that can be interpreted as social dilemmas like the Prisoner's Dilemma. For instance,
81 chimpanzees may want other group members to take action during cooperative hunts or during
82 intergroup aggression. Thus, from a comparative perspective it is of special interest to compare
83 the decision-making strategies of our closest living relatives, the chimpanzees (*Pan troglodytes*),
84 with those of children in social dilemmas. Comparing these two populations in non-trivial
85 scenarios, as it might be for human adults, can tell us more about cooperative problem solving
86 and its evolution. Furthermore, the study of children in these types of tasks can shed light on
87 the ontogeny of human cooperative strategies. Taken together, this approach contributes to our
88 understanding of the evolutionary roots of human cooperation and decision-making.

89 There has been a considerable amount of experimental studies on cooperation in apes, in
90 particular chimpanzees. This work shows overall, that chimpanzees cooperate with each other
91 when this strategy leads to the best outcomes for themselves (Bullinger et al., 2011; Duguid et
92 al., 2014; Hirata and Fuwa, 2007; Melis et al., 2006). When it comes to situations in which
93 chimpanzees can distribute resources between themselves and a partner, such as the Dictator
94 game, they tend to benefit themselves whenever possible. So much so that Jensen and
95 colleagues describe chimpanzees as “rational maximizers” (i.e. employing strategies to maximize
96 their rewards regardless of others; e.g. Jensen et al., 2007; Jensen, 2016; Silk et al., 2005; but

97 see e.g. Proctor et al., 2013 and Schmelz et al., 2017 for evidence of chimpanzees making
98 prosocial choices at a cost to themselves).

99 As well as showing some ability to coordinate actions for mutual benefit (such as in a Stag Hunt
100 game; Bullinger et al., 2011a; Duguid et al., 2014), chimpanzees can also coordinate when
101 conflicts of interest arise. For example, chimpanzees and bonobos can negotiate unequal reward
102 distributions in the Snowdrift game (Sudgen, 1986) and avoid the complete breakdown of
103 cooperation and thus avoid complete loss of rewards (Melis et al., 2009; Sánchez-Amaro et al.,
104 2016, 2017). Notably, in contrast to the Prisoner's Dilemma, in the Snowdrift game if the partner
105 defects, cooperation leads to a better outcome than defection. Thus, the question arises: would
106 chimpanzees and children still be able to coordinate their actions in a social dilemma when
107 unilateral cooperation is not beneficial for co-operators, as in the Prisoner's Dilemma? In other
108 words, can chimpanzees and children avoid mutual defection when cooperation comes with the
109 risk of losing all rewards to another?

110 To answer our question, we investigated the strategies chimpanzees and five-year old children
111 use to solve a social dilemma inspired by the Prisoner's Dilemma. We created the dilemma using
112 an apparatus consisting of a rectangular tray positioned between the two subjects, baited with
113 one reward at either end. The tray could be moved up and down via ropes attached at either
114 end (one accessible to each subject). In the *social dilemma* condition (Figure 1a), the tray started
115 at the bottom. When only one subject pulled their rope (i.e. that individual cooperates), their
116 side of the tray moved upwards and all rewards rolled down to the partner—the worst possible
117 outcome. An individual's best strategy was to wait for their partner to pull from the rope and
118 then obtain all the rewards (i.e. defection). Alternatively, they could pull together and share the
119 rewards once the tray reached the top position (i.e. mutual cooperation). Finally, if neither
120 individual pulled the rope within 15 seconds (i.e. mutual defection) they both lost access to the
121 rewards after.

122 Our *social dilemma* shares with the Prisoner's Dilemma two main features. Namely, that
123 defection on a cooperative partner leads to better outcomes than mutual cooperation and that
124 mutual cooperation is better than mutual defection. However, both dilemmas differed in two
125 important aspects. First, in our *social dilemma* mutual cooperation resulted in the same number
126 of rewards as a turn-taking strategy (individuals alternating between cooperation and defection)
127 rather than more as in the iterated Prisoner's Dilemma. Second, for an individual mutual
128 defection and unilateral cooperation both resulted in no rewards.

129 We compared behaviour in this dilemma to a *competitive* situation, using the same apparatus.
130 In this condition (Figure 1b), the tray started at the top position and the subject could obtain all
131 the rewards by pulling faster than his partner. In *competitive* trials pairs of chimpanzees and
132 children could also pull together and divide the rewards once the tray reached the bottom
133 position (Figure 1c and Table 1 for a representation of the payoff matrix of both games).
134 Subjects were able to see each other and communicate freely throughout the task. This method
135 deviates from traditional game-theoretical studies (Blake et al., 2011; Bohnet and Frey, 1999;
136 Bouas and Komorita, 1996) in which individuals play with strangers and are not allowed to
137 communicate. Instead it mirrors more recent studies using game-theoretical paradigms to
138 investigate the scope of human and non-human animals' abilities to cooperate in more
139 naturalistic situations (Brosnan et al., 2011; Duguid et al., 2014; Sánchez-Amaro et al., 2017;
140 McClung et al., 2017). Importantly, the dynamic nature of the task meant that even if individuals
141 initially pulled together during a *social dilemma* trial, any individual could turn it into a
142 *competitive* trial by ceasing to pull –causing the rewards to roll down to the side of the defector
143 just as in *competitive* trials. This, feature deviates from other cooperative games in which
144 unilateral acts are never rewarded (Duguid et al., 2014; Melis et al., 2009).

145 In line with previous studies (Melis et al., 2009; Sánchez-Amaro et al., 2016, 2017), we expect
146 chimpanzees to behave strategically (e.g. waiting longer for their partners to pull) to maximize
147 their rewards. Therefore, we expect high levels of mutual defection and loss of rewards in
148 chimpanzees as a result of their longer latencies to retrieve the rewards (after 15 seconds the
149 rewards were removed from the tray). In contrast, based on previous findings (Grueneisen and
150 Tomasello, 2016; Melis et al., 2016), we expect five-year old children to engage in cooperative
151 strategies to divide the rewards while maintaining high levels of cooperation.

152

153 **2. Methods**

154

155 *2.1 Subjects*

156 We tested 14 captive chimpanzees (7 males; $M_{age} = 21.1$ years; see table 1 in ESM) housed at the
157 Wolfgang Köhler Primate Research Center in Leipzig zoo and 20 pairs of 5- to 5.5-year old
158 children (10 pairs of boys and 10 pairs of girls) in kindergartens in the Leipzig area. Pairs of
159 children were always from the same kindergarten and thus, familiar to each other.

160 During the first test phase of the study, the chimpanzees made up 7 unique pairs. After phase
161 one, ten chimpanzees completed four cooperative training sessions with a human experimenter
162 before they were tested again with the same partner for the second test phase. The remaining
163 four subjects could not participate further as two individuals (from different pairs) moved to
164 another zoo.

165

166 2.2 Ethics statement

167 The study was ethically approved by an internal committee at the Max Planck Institute for
168 Evolutionary Anthropology. The study complies with the 'EAZA Minimum Standards for the
169 Accommodation and Care of Animals in Zoos and Aquaria', the 'WAZA Ethical Guidelines for the
170 Conduct of Research on Animals by Zoos and Aquariums' and the ASAB/ABS 'Guidelines for the
171 Treatment of Animals in Behavioural Research and Teaching'. Children studies were carried out
172 with the written informed consent of the participants, and in accordance with all applicable laws
173 and rules governing psychological research in Germany.

174

175 2.3 Materials

176 The ape apparatus consisted of a rectangular tray (91x10cm) positioned between the two
177 subjects (Figure 1). The apparatus was completely visible from both subjects' perspective. The
178 tray could move vertically in the space between the two subjects. A rope was connected at either
179 end of the tray so that each subject could pull from one end of the rope. The tray was baited
180 with a grape at each end. The tray could either start at the bottom of the vertical space (*social*
181 *dilemma* condition) or at the top (*competitive* condition). If one ape pulled the rope in the *social*
182 *dilemma* condition, the tray would lift from the pulled end and tilt so that both grapes would
183 roll down to the other side, where a partner could retrieve them (Figure 1a). In contrast, if one
184 ape pulled in the *competitive* condition, that end of the tray would drop from the top position
185 and the tray would tilt so that the grapes would roll down to the puller's side (Figure 1b).
186 Therefore, pulling during *social dilemma* trials was defined as *cooperation* while pulling in
187 *competitive* trials was defined as *competition*. Not pulling in *social dilemma* trials was defined as
188 *defection*. Alternatively, in both conditions chimpanzees could coordinate their actions to pull
189 from their ropes simultaneously, moving the tray up (in the *social dilemma* condition) or down
190 (in the *competitive* condition) while maintaining the horizontal position of the tray (i.e. mutual
191 cooperation). Upon reaching the top or bottom each individual could access one grape (Figure
192 1c). Subjects could adjust their pulling actions until the rewards rolled down (above an angle of

193 approx. 20 degrees) or they could retrieve the rewards from the upper or lower windows. See
194 also Figure 1 in the Electronic Supplementary Material (ESM) for an example of the children’s
195 apparatus.

196 The mechanism that allowed the tray to be raised and lowered consisted of a Plexiglas tower
197 (65cm high) at either end of the tray. The end of the tray rested on two brackets that could slide
198 up and down the towers. The position of the brackets (and thus the tray) was maintained, when
199 there was no force on the rope, by counterweights —metal cylinders of 0.5kg— attached to the
200 brackets.

201 Each Plexiglas tower was attached to a Plexiglas frame. The Plexiglas frames had two windows,
202 one at the top and another at the bottom position that could be opened or closed by the
203 experimenters, depending on the condition and whether the chimpanzees were allowed to
204 access the ends of the tray. Under the apparatus there were two ramps, down which the grapes
205 rolled to within reach of the chimpanzees in their respective cages.

206 The ropes were connected to its corresponding bracket through a system of pulleys that allowed
207 the vertical movement of the elevators along the towers when the subjects pulled. The baited
208 rewards could be accessed from three different locations: directly from the tray through the
209 windows at the top or at the bottom position, or from the ramps under the apparatus.

210 In general, pairs of children were presented with the same task as chimpanzees. The apparatus
211 was built inside a box made of wood and Plexiglas that prevented children from directly
212 accessing the rewards (60x42x50 cm; vertical towers were 36.5 cm high). The front side of the
213 box was open to allow Experimenter 1 (henceforth E1 and E2 for the second experimenter)
214 access to the apparatus. The box was placed on the ground between both children. Children
215 collected glass marbles as rewards instead of food. They collected their rewards in opaque
216 plastic containers. Therefore, it was difficult for children to keep track of their rewards once
217 inside the box containers to make it more similar to the apes, which ate the rewards
218 immediately.

219

220 *2.4 Procedure and Design*

221 Chimpanzees and children were tested in a within-subjects design in the *social dilemma* and the
222 *competitive* conditions. Subjects could either pull (i.e. unilateral cooperation) or do nothing (i.e.
223 to defect) in *social dilemma* trials, and pull (i.e. to compete) or do nothing and lose the rewards
224 during *competitive* trials. If only one individual acted, the rewards would fall onto the ramps and

225 could be collected from under the tray. If both individuals coordinated during *social dilemma*
226 trials (tray at the lower position), they would lift the tray from the bottom position and obtain
227 the rewards through the top windows. In contrast, in *competitive* trials (tray at the top position)
228 subjects would pull down the tray from the top position to obtain the rewards through the lower
229 windows. At the start of a test session, one experimenter opened either the top windows for
230 *social dilemma* trials or the lower windows for *competitive* trials. At the start of a trial, one
231 reward was baited at each end of the tray. The subjects then had 15 seconds to act. After this
232 time, an experimenter would remove any rewards left on the tray.

233 Each pair of chimpanzees completed 16 test sessions separated into two test phases of eight
234 sessions. Each phase contained four sessions per condition. Each condition was presented in a
235 block of four sessions per phase (e.g. four *competitive* sessions followed by four *social dilemma*
236 sessions). In the case of children, each pair performed one test session per condition (see details
237 of the test' instructions in the ESM). The order of conditions was counterbalanced between
238 pairs. Chimpanzees switched sides of the apparatus between sessions while children swapped
239 sides half-way through each session (fourth trial). In the case of chimpanzees, after the
240 cooperation training, each pair was tested for another eight test sessions (test phase 2). These
241 pairs started the second test phase with the condition they finished the first test phase.

242

243 2.5 Training

244 Before the test sessions, both species completed several training phases to understand the task
245 contingencies. Chimpanzees conducted an individual training phase that demonstrated the
246 payoff contingencies of the task and how to access the rewards. Children took part in a short
247 pre-training phase in which they could see how the apparatus functioned. Subsequently, both
248 species engaged in a social training phase. In this training phase we demonstrated that,
249 depending on the condition, individuals could gain or lose rewards by either pulling themselves
250 or by waiting for a partner to pull –in the case of chimpanzees the partner was a human stooge
251 while children performed this training phase with their peers. In addition, chimpanzees took
252 part in coordination training between the two test phases. The purpose of this training was to
253 show chimpanzees that they could potentially coordinate their actions with their partner and
254 divide the rewards —by pulling together with a human experimenter and subsequently
255 accessing the rewards through the windows. Children only participated in one test session.
256 Therefore, we did not present them with the coordination training. The inclusion of this training

257 before the test would have prevented comparisons between species. See more details of the
258 different training phases for each specie in the ESM.

259

260 2.6 Coding

261 We scored four dependent measures: efficiency, latency to pull, pulling rates (including
262 individual strategies derived from individual pulling rates) and whether subjects coordinated
263 their actions within trials. Efficiency was defined as the proportion of trials in which at least one
264 member of a pair was successful at retrieving at least one reward. Latency was the elapsed time
265 between the experimenters baiting the rewards on the tray until the first pulling action
266 occurred. A pulling action was the first movement (upwards or downwards, depending on
267 condition) of either end of the tray. Coordination was defined as trials in which both individuals
268 pulled together and split their rewards (i.e. mutual cooperation).

269 From the pulling rates —regardless of the reward distribution— we calculated the proportion of
270 strategic decisions: competing in *competitive* trials and defection in *social dilemma* trials. This
271 was used as a basis for classifying subjects in three qualitative categories: *strategisers* as subjects
272 that obtained rewards at rates significantly above chance in both conditions (chance level set at
273 50%) by competing in *competitive* and defecting in *social dilemma* conditions, *pullers* pulling in
274 at least 75% of trials in both conditions and *non-pullers* pulling in 25% or less of the trials in both
275 conditions. The subjects not placed in any of these three categories were counted as
276 *unclassified*.

277 In addition to the previous measures, we examined whether children verbally communicated
278 during the task. We focused on three types of communication. *Imperatives*: deontic verbs used
279 to direct their partner's actions; *informatives*: communication aimed at informing partners
280 about a child's current or intended actions; and *protests*: statements of disapproval and
281 objection about a partner action's or intention. Moreover, we coded *pointing gestures* towards
282 partners. For every trial, we coded whether children pairs communicated (by either one or both
283 children) and whether each of the four categories of communication (*imperative*, *protests*,
284 *informative* and *pointing gestures*) occurred within a trial (by either one or both children).
285 Communication was scored from the moment E1 showed the rewards to the children until the
286 children inserted their rewards into their boxes. In the case of chimpanzees, throughout coding
287 and testing no communication was noted by the experimenter (as was the case in previous
288 studies; Sanchez-Amaro et al., 2017). However, the visibility from the camera angles was not
289 clear enough to confirm this with an acceptable level of certainty. Thus, the authors

290 acknowledge that we cannot make strong conclusions about the role of communication for
291 chimpanzees in this task.

292

293 *2.7 Statistical details*

294 The main analyses included in this study were conducted using Linear Mixed models (LMM) and
295 Generalized Linear Mixed Models (GLMM) (Baayen et al., 2008) and were run using R statistics
296 (version 3.1.1). We ran all LMM with Gaussian error structure and identity link function and all
297 GLMM with binomial structure and logit link function. All continuous variables were z-
298 transformed when required.

299 All full models were compared to a null model excluding all the test variables. Only when the
300 comparison between the full and the null model was significant we further investigated the
301 significance of the test variables. The drop1 function of the lme4 package (Bates, 2010) was used
302 to test each variable's significance (including possible interactions between test predictors).
303 Non-significant interactions were removed to produce a new reduced model. A likelihood ratio
304 test with significance set at $p < 0.05$ was used to compare models and to test the significance of
305 the individual fixed effects (Barr et al., 2013). The 95% confidence intervals (CI) of the reduced
306 models were calculated when appropriate.

307 To rule out collinearity, Variance Inflation Factors (VIF) were checked (Field, 2005). All VIF values
308 were close to 1. For every model, model stability was assessed by comparing the estimates
309 derived by a model based on all data with those obtained from models with the levels of the
310 random effects excluded one at a time. All models were stable. In linear mixed models it is not
311 possible to obtain effect sizes for each predictor. It is only possible to report size effects for the
312 effect sizes as a whole (or fixed and random effects together) (Nakagawa & Schielzeth, 2013;
313 Nakagawa et al., 2017). These general effect sizes were not considered informative for the
314 purpose of these studies and were not reported.

315 Besides the main analysis (LMM and GLMM), we performed additional analysis when necessary
316 (binomial tests and correlation analysis) using R statistics (version 3.1.1).

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321 3. Results

322

323 Overall, at least one individual of the pair obtained rewards in a majority of trials (89%
324 chimpanzees; 95% children). While all unsuccessful trials (mutual defection) by chimpanzees
325 occurred in the *social dilemma* condition (22% trials), children's failures were divided between
326 conditions (6% of *competitive* trials and 2% of *social dilemma* trials). We found that both species
327 waited longer to act in the *social dilemma* condition compared to the *competitive* condition.
328 Chimpanzees were more likely to wait before pulling in *social dilemma* trials compared to
329 *competitive* trials ($\chi^2_1 = 7.33$, $N = 720$, $p = 0.007$). In trials in which they did wait, they waited
330 longer to pull in the *social dilemma* condition and decreased their latencies to pull in the
331 *competitive* condition across sessions ($\chi^2_1 = 12.51$, $N = 720$, $p < 0.001$; Figure 2) and trials ($\chi^2_1 =$
332 12.58, $N = 720$, $p < 0.001$; Figure 2). The average latency to first pull during *social dilemma* trials
333 was 2.95 seconds (SE = 0.17 seconds), in comparison, to 0.63 seconds (SE = 0.06 seconds) during
334 *competitive* trials. Children, in contrast, became faster across sessions in both conditions ($\chi^2_1 =$
335 7.94, $N = 303$, $p = 0.005$) but did wait longer overall to pull during *social dilemma* trials ($\chi^2_1 = 6.15$,
336 $N = 303$, $p = 0.013$). The average latency to first pull by child dyads during *social dilemma* trials
337 (2.93 seconds, SE = 0.19 seconds) was slightly longer than in *competitive* trials (2.34 seconds, SE
338 = 0.18 seconds).

339 Pulling rates indicated that 29% of chimpanzees behaved strategically according to our
340 classifications, i.e., pulling mainly in competitive but not in *social dilemma* trials (binomial tests,
341 $N = 56-128$ trials, $p < 0.005$; see Figure 3). In contrast, only 4% of children were classified as
342 strategic (binomial tests, $N = 16$ trials, $p < 0.005$; see Figure 3). Instead, children took turns to
343 reciprocate their rewards. We found that children were much more likely to take turns than
344 predicted by chance (children took turns in 73% of trials; Intercept: estimate = 1.01, SE = 0.45, p
345 < 0.001), irrespective of the condition presented and their experience with the task ($\chi^2_4 = 2.363$,
346 $N = 211$, $p = 0.669$).

347 There was a strong correlation between the proportion of strategic choices that chimpanzees
348 made and the number of rewards they obtained: the most strategic individuals tended to
349 maximize their gains ($r = 0.83$). This correlation was moderate in children ($r = 0.5$), perhaps as a
350 result of their general tendency to reciprocate the rewards in both conditions.

351 Both children and chimpanzees mutually cooperated (i.e. pulled simultaneously and divide the
352 rewards) in a small number of trials (10.6% chimpanzees; 6% children). Chimpanzees divided the

353 rewards mainly in *competitive* trials (95% of cases simultaneous pulling occurred in the
354 competitive condition), perhaps as a by-product of both individuals competing to obtain all the
355 rewards. However, when they pulled simultaneously, they did so more often after the 2nd phase
356 of the study, after they had participated in a coordination training with a human partner ($\chi^2_1 =$
357 5.61, $N = 759$, $p = 0.018$)—65% of trials in which chimpanzees coordinated for mutual
358 cooperation occurred in the 2nd phase of the study. Children did not participate in coordination
359 trials. They were equally likely to mutually cooperate in both conditions to divide their rewards.

360 Finally, children verbally communicated about their current or impending actions in 32% of
361 trials. They tended to communicate more often during *social dilemma* trials ($\chi^2_4 = 8.75$, $N = 320$,
362 $p = 0.068$), using mainly *imperative* (e.g. “you must pull”) and *informative* (e.g. “I pull this time”)
363 forms of verbal communication in both conditions (see methods section). See ESM for
364 information on models and binomial tests.

365 **4. Discussion**

366

367 The results of the current study demonstrate that chimpanzees and children are able to solve
368 (i.e. avoid mutual defection) a social dilemma in which unilateral cooperation leads to the loss
369 of rewards, but they differ in their strategies to do so.

370 Similarly to previous studies exploring children’s behaviour in the other Prisoner’s Dilemmas and
371 other conflicts of interest (Blake et al., 2011; Grueneisen and Tomasello, 2016; Matsumoto et
372 al., 1986; Melis et al., 2016), children in our study engaged in turn-taking to overcome repeatedly
373 presented conflicts of interest. Although children in our study, unlike previous studies, had the
374 possibility to coordinate their actions by acting together and dividing the rewards in each trial—
375 a strategy that would have resulted in the same rewards as perfect turn-taking—they rarely did
376 so. There are several reasons that may explain their preference for turn-taking over mutual
377 cooperation.

378 First, during training children only experienced pulling alone, not pulling with a partner. This
379 could have hindered exploration of further strategies (i.e., mutual cooperation). However, 20%
380 of pairs divided the rewards at least once in either the *social dilemma* or the *competitive*
381 condition although no pair mutually cooperated in more than half of their trials. Second, in our
382 task mutual cooperation might have been more demanding than turn-taking in terms of
383 coordinated sensorimotor and planning abilities (Vesper et al., 2016). In particular, children
384 needed to carefully time their actions to achieve and maintain the horizontal position of the tray

385 to access the rewards. Moreover, due to the dynamic nature of the task, children may have tried
386 to avoid the potential risk of cheating during mutual collaboration—when both individuals pull
387 together in a *social dilemma* trial one can always stop pulling and obtain all the rewards. By
388 taking turns, children simultaneously reduced sensorimotor demands derived from coordination
389 and avoided potential cheating within trials but still demonstrated a sense of trust in their
390 collaborative partner by reciprocating. Evidence from other studies has shown that 5-year-old
391 children are capable of forming joint goals based on a mutual sense of “strategic trust” (Hamann
392 et al., 2012; Tomasello, 2016) in which both individuals understand what they must do to
393 achieve joint success. Thus, in this task children did not need to mutually coordinate their actions
394 with their partners to solve the task if they mutually trusted each other. The ability to
395 communicate may have contributed to enhanced trust between children, as suggested by recent
396 findings in adults (Cohen et al., 2010). However, we should emphasize that although we are not
397 aware of studies comparing the strategies of children from different cultures in these types of
398 games, previous work has highlighted the use of different strategies to distribute collaborative
399 outcomes among children of different cultures (Schaffer et al., 2015; Zeidler et al., 2016). Thus,
400 it is possible that children from other populations may use different cooperative strategies to
401 distribute rewards (i.e. division of rewards by the end of the game).

402 Although children used a turn-taking strategy to cooperate in both types of conditions, they did
403 distinguish between them. Children waited longer to pull in *social dilemma* trials compared to
404 *competitive* trials. Yet, overall, children tended to decrease their latencies to pull across sessions.
405 This might have been the product of the turn-taking strategy—once a turn-taking strategy was
406 established, there was little need to wait for the partner to pull in either condition. With
407 increasing experience, it is likely that children better understood the contingencies of the game
408 and thus were faster to operate the apparatus.

409 Finally, we found that children communicated slightly more often during *social dilemma*
410 compared to *competitive* trials, but this difference was not significant. This might be partially
411 explained by the fact that children solved both situations similarly: they took turns equally across
412 conditions and became faster across the study period. This might also explain why, in general,
413 children used similar types of communication across conditions. This finding contrasts with
414 other studies showing that children flexibly adjust their communication between conditions of
415 a game (when either the risk of coordination failure or competing interests vary between
416 conditions) to achieve successful coordination (Duguid et al., 2014; Sánchez-Amaro et al., 2017).
417 One possibility is that, given the competitive nature of the *social dilemma*, communication did
418 not have a big effect in their partners’ decisions and so, they adjusted their communication to a

419 lesser degree compared to situations without a conflict of interest in which communication plays
420 an important role in coordinating decisions (e.g. Duguid et al., 2014). This interpretation would
421 be consistent with findings with adults showing that communication has a stronger effect on
422 their partners' decisions in mutually cooperative context, such as the Stag Hunt, compared to
423 more competitive situations, such as the Prisoner's Dilemma (Duffy and Feltovich, 2002).

424 Chimpanzees were also able to distinguish the social dilemma from the competitive situation.
425 They behaved more strategically with experience, waiting longer for their partners to pull by the
426 end of the study in the *social dilemma* condition. They also became faster across sessions in the
427 *competitive* condition, further implying that they learned the contingencies of the study and
428 adapted their behaviour to maximize their own rewards over time.

429 Chimpanzees did not collaborate to solve the task and divide the benefits. Instead, they waited
430 for their partner to pull; the only strategy that could lead them to maximize their rewards. The
431 lack of collaboration cannot be explained by a general inability to cooperate for mutual benefits:
432 across several cooperative experimental set-ups, chimpanzees have proven to be skilful
433 collaborators (Duguid et al., 2014; Melis et al., 2006). Even when conflicts of interest arise or
434 unilateral cooperation lead to rewards for both members of a pair (Melis et al., 2009; Sánchez-
435 Amaro et al., 2016). Our results are perhaps better understood in the context of chimpanzees
436 acting as rational maximizers to increase their own benefits as suggested by Jensen and
437 colleagues (2007). According to this idea, chimpanzees only cooperate if this strategy leads to
438 the highest possible rewards for themselves. It is also not surprising, therefore, that in our task
439 most of the coordination occurred during *competitive* trials. This outcome likely resulted from
440 both chimpanzees pulling at the same time in an attempt to maximize their own rewards. In
441 fact, chimpanzees almost never collaborate in *social dilemma* trials even after the cooperative
442 training. In *social dilemma* trials, unlike in *competitive* trials, chimpanzees could always defect
443 (i.e., stop pulling at any time while their partner pulls). This risk of losing all the rewards might
444 have prevented chimpanzees from collaborating during *social dilemma* trials. Additionally, it is
445 possible that the level of motor coordination required might have reduced the likelihood of
446 mutual cooperation. Chimpanzees could have maximized their rewards by taking turns to pull
447 across trials —as the children did. However, consistent with previous findings (Melis et al., 2016),
448 they did not develop any clear turn-taking strategy, adding to the evidence that chimpanzees,
449 in experimental tasks, do not engage in direct reciprocity to maximize their rewards (Amici et
450 al., 2014; Brosnan et al., 2009; Melis et al., 2008).

451 As expected, chimpanzees failed to obtain the rewards (i.e. mutual defection) in a substantial
452 amount of *social dilemma* trials (in 22% of trials). Interestingly enough, chimpanzee dyads still
453 managed to maintain cooperation even when this resulted in unbalanced payoffs between
454 individuals: chimpanzees who benefited the most within a pair obtained 81% of the rewards
455 during *social dilemma* trials while the most successful children obtained 58.5% of the total
456 rewards in that condition (see tables 5 and 6 in ESM). This leads to the question of why an
457 individual would continue to pull for no reward. One possible interpretation of these results is
458 that chimpanzees pulled because there was a possibility of reward: in 30% of successful *social*
459 *dilemma* trials both individuals pulled to some extent and first pullers obtained rewards in 53%
460 of these trials. This interpretation only makes sense if we take into account the dynamic nature
461 of the task: once both individuals were pulling, subjects could turn a *social dilemma* trial into a
462 *competitive* one by ceasing to pull or held the rope steady while the partner continued to pull –
463 their side of the tray would fall and all the rewards would roll down to them. So, initiating action
464 but not pulling enough for the rewards to roll to their partner can lead to success. Therefore,
465 chimpanzees preferred to take those risks in an attempt to increase their own benefits, in
466 contrast to children who might have avoided collaboration due to the extra risks of losing
467 rewards. This strategy is more viable in our social dilemma because the punishment for being a
468 sucker (pulling for another) is the same as mutual defection unlike in a classic Prisoner’s Dilemma
469 where being a sucker is worse than mutual defection.

470 An alternative possibility is that chimpanzees acted prosocially towards their partners. This
471 interpretation would be consistent with results showing that chimpanzees help others to obtain
472 benefits (Horner et al., 2011; Melis et al., 2011; Schmelz et al., 2017; Yamamoto et al., 2009;
473 2012; but see Amici et al., 2014 and Tennie et al., 2016). However, this interpretation needs to
474 be made with caution; in previous studies chimpanzees helped partners mainly when there was
475 no possibility to obtain food for themselves. In our study the two chimpanzees that obtained
476 fewer rewards for themselves were paired with the two most dominant and strategic
477 individuals; these subjects may have refrained from engaging in competitive interactions with
478 dominant group members, only pulling when the dominant partner did not pull. In addition, if
479 chimpanzees were acting prosocially we would not expect them to wait longer to pull in *social*
480 *dilemma* trials compared to *competitive* trials.

481 It is also possible that some chimpanzees, despite understanding the contingencies of the task,
482 could not inhibit pulling in a situation in which they had no alternative. However, this seems
483 unlikely to explain all cases of unilateral cooperation. Many previous studies have shown that
484 chimpanzees from different labs can inhibit acting for longer periods of time (i.e., 3 minutes) to

485 obtain a preferred reward in non-social contexts (Amici et al., 2008; Beran and Evans, 2006;
486 Rosati et al., 2007) and in social contexts (Bullinger et al., 2011b; Duguid et al., 2014; Melis et
487 al., 2009). Trials in our study lasted a maximum of 15 seconds, below that of most of the studies
488 cited.

489 By using a social dilemma inspired by the Prisoner's Dilemma to further investigate the strategies
490 chimpanzees and children use to overcome conflict situations, we found significant differences
491 between species. Children seemed to be sensitive to the specific nature of the social dilemma.
492 They adjusted their decisions in a similar way to adults in these scenarios—cooperating across
493 iterated presentations of the social dilemma and using verbal communication to coordinate
494 their decisions. Overall, the increased latency to act in *social dilemma* trials is consistent with
495 chimpanzees trying to maximise their rewards. Some chimpanzees clearly acted strategically to
496 maximize their rewards by pulling mainly in *competitive* but not in *social dilemma* trials. Others
497 appeared to behave prosocially by unilaterally pulling in the *social dilemma* condition. However,
498 this behaviour was a relatively low risk way to gain potential rewards, thus is not necessarily
499 prosocially motivated. This is in line with previous literature suggesting that chimpanzees use
500 strategies to maximize their benefits—even if such strategies lead to unbalanced pay-offs
501 between participants—rather than developing sustainable cooperative solutions to social
502 dilemmas.

503 The Prisoner's Dilemma is a key model for the study of the evolution of cooperation (Axelrod
504 and Hamilton, 1981; Nowak and Sigmund, 1993). In this study we created a social dilemma with
505 two important features in common with the Prisoner's Dilemma; we could then compare the
506 strategies that children and chimpanzees use to solve this conflict of interest. The results of this
507 comparison shed light onto the ontogenetic and phylogenetic evolution of human cooperation.
508 We find more evidence that humans from childhood develop the means to find collaborative,
509 equitable solutions to social dilemmas. In contrast, although chimpanzees do not elaborate
510 these cooperative strategies and are more likely to fail, they do avoid complete loss of rewards
511 resulting in a more imbalanced solution. In all, the results are consistent with the hypothesis
512 that, at some point in our evolutionary history, humans began to depend heavily (in comparison
513 to other social primates) on their collaborative partners to survive (Tomasello et al., 2012;
514 Sterelny, 2016), giving rise to the selection of skills for collaboration in contemporary humans.

515

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531 **Figures and Tables captions**

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533 Figure 1. Experimental set-up of the study with chimpanzees' social dilemma condition (1a),
534 competitive condition (1b) and collaboration example (1c). See Figure 1 in ESM for a
535 representation of the children set-up.

536 Figure 2. Chimpanzee latency of the 1st puller to pull the rope in social dilemma (SD) and
537 competitive trials (COM) across sessions (left) and across trials (right). Latencies in seconds are
538 presented on a logarithmic scale.

539 Figure 3. Proportion of strategic choices in both social dilemma and competitive trials for all
540 subjects of the two species. The most strategic individuals in both conditions are in the top-right
541 corner of the plot. The size of the dots represents frequencies of subjects for different scores.

542 Table 1. Payoff matrix of the *social dilemma* and the *competitive* conditions.

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