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# Chimpanzees and children avoid mutual defection in a social dilemma

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## Abstract

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

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

## 1. Introduction

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

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

Humans possess uniquely cooperative motivations to help and share with others from a young age (Brownell et al., 2013; Liszkowski et al., 2006; Warneken and Tomasello, 2006). We already deviate from the rational assumptions of the Ultimatum (Bueno-Guerra et al., 2016; Wittig et al., 2013) and the Dictator Games (Benenson et al., 2007) as children. To our knowledge, only two studies have investigated how children solve a Prisoner's Dilemma. Matsumoto et al. (1986) presented four-year-old children with a simplified version of the dilemma. In that task, pairs of children had to choose between competition or cooperation cards and the rewards they would obtain were determined according to the Prisoner's Dilemma payoff matrix. During the task children were encouraged to discuss their strategies. Overall, the authors found that children increased their likelihood to mutually cooperate across sessions and that the degree of friendship was positively related with mutual cooperation. A more recent study with considerably older children (Blake et al., 2015) presented 10- and 11-year-old children with an anonymous computer-based Prisoner's Dilemma game. They found that children cooperated more often in iterated versions of the dilemma in comparison to one-shot interactions. These results suggest that the adult patterns of decision making in social dilemmas are already present at a young age.

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

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

There has been a considerable amount of experimental studies on cooperation in apes, in particular chimpanzees.  This work shows overall, that chimpanzees cooperate with each other when this strategy leads to the best outcomes for themselves (Bullinger et al., 2011; Duguid et al., 2014; Hirata and Fuwa, 2007; Melis et al., 2006). When it comes to situations in which chimpanzees can distribute resources between themselves and a partner, such as the Dictator game, they tend to benefit themselves whenever possible. So much so that Jensen and colleagues describe chimpanzees as "rational maximizers" (i.e. employing strategies to maximize their rewards regardless of others; e.g. Jensen et al., 2007; Jensen, 2016; Silk et al., 2005; but see e.g. Proctor et al., 2013 and Schmelz et al., 2017 for evidence of chimpanzees making prosocial choices at a cost to themselves).

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

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

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

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

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

## 2. Methods

### *2.1 Subjects*

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

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

### *2.2 Ethics statement*

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

### *2.3 Materials*

The ape apparatus consisted of a rectangular tray (91x10cm) positioned between the two subjects (Figure 1). The apparatus was completely visible from both subjects' perspective. The tray could move vertically in the space between the two subjects. A rope was connected at either end of the tray so that each subject could pull from one end of the rope. The tray was baited with a grape at each end. The tray could either start at the bottom of the vertical space (*social dilemma* condition) or at the top (*competitive* condition). If one ape pulled the rope in the *social dilemma* condition, the tray would lift from the pulled end and tilt so that both grapes would roll down to the other side, where a partner could retrieve them (Figure 1a). In contrast, if one ape pulled in the *competitive* condition, that end of the tray would drop from the top position and the tray would tilt so that the grapes would roll down to the puller's side (Figure 1b). Therefore, pulling during *social dilemma* trials was defined as *cooperation* while pulling in *competitive* trials was defined as *competition*. Not pulling in *social dilemma* trials was defined as *defection*. Alternatively, in both conditions chimpanzees could coordinate their actions to pull from their ropes simultaneously, moving the tray up (in the *social dilemma* condition) or down (in the *competitive* condition) while maintaining the horizontal position of the tray (i.e. mutual cooperation). Upon reaching the top or bottom each individual could access one grape (Figure 1c). Subjects could adjust their pulling actions until the rewards rolled down (above an angle of approx. 20 degrees) or they could retrieve the rewards from the upper or lower windows. See also Figure 1 in the Electronic Supplementary Material (ESM) for an example of the children's apparatus.

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

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

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

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

### *2.4 Procedure and Design*

Chimpanzees and children were tested in a within-subjects design in the *social dilemma* and the *competitive* conditions. Subjects could either pull (i.e. unilateral cooperation) or do nothing (i.e. to defect) in *social dilemma* trials, and pull (i.e. to compete) or do nothing and lose the rewards during *competitive* trials. If only one individual acted, the rewards would fall onto the ramps and could be collected from under the tray. If both individuals coordinated during *social dilemma* trials (tray at the lower position), they would lift the tray from the bottom position and obtain the rewards through the top windows. In contrast, in *competitive* trials (tray at the top position) subjects would pull down the tray from the top position to obtain the rewards through the lower windows. At the start of a test session, one experimenter opened either the top windows for *social dilemma* trials or the lower windows for *competitive* trials. At the start of a trial, one reward was baited at each end of the tray. The subjects then had 15 seconds to act. After this time, an experimenter would remove any rewards left on the tray.

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

### *2.5 Training*

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

### *2.6 Coding*

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

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

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

*2.7 Statistical details*

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

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

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

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

## 3. Results

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

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

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

Both children and chimpanzees mutually cooperated (i.e. pulled simultaneously and divide the rewards) in a small number of trials (10.6% chimpanzees; 6% children). Chimpanzees divided the rewards mainly in *competitive* trials (95% of cases simultaneous pulling occurred in the competitive condition), perhaps as a by-product of both individuals competing to obtain all the rewards. However, when they pulled simultaneously, they did so more often after the 2nd phase of the study, after they had participated in a coordination training with a human partner ($\chi_1^2$ = 5.61, *N* = 759, *p* = 0.018)—65% of trials in which chimpanzees coordinated for mutual cooperation occurred in the 2nd phase of the study. Children did not participate in coordination trials. They were equally likely to mutually cooperate in both conditions to divide their rewards.

Finally, children verbally communicated about their current or impending actions in 32% of trials. They tended to communicate more often during *social dilemma* trials ($\chi_4^2$ = 8.75, *N* = 320, *p* = 0.068), using mainly *imperative* (e.g. “you must pull”) and *informative* (e.g. “I pull this time”) forms of verbal communication in both conditions (see methods section). See ESM for information on models and binomial tests.

## 4. Discussion

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

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

First, during training children only experienced pulling alone, not pulling with a partner. This could have hindered exploration of further strategies (i.e., mutual cooperation). However, 20% of pairs divided the rewards at least once in either the *social dilemma* or the *competitive* condition although no pair mutually cooperated in more than half of their trials. Second, in our task mutual cooperation might have been more demanding than turn-taking in terms of coordinated sensorimotor and planning abilities (Vesper et al., 2016). In particular, children needed to carefully time their actions to achieve and maintain the horizontal position of the tray to access the rewards. Moreover, due to the dynamic nature of the task, children may have tried to avoid the potential risk of cheating during mutual collaboration–when both individuals pull together in a *social dilemma* trial one can always stop pulling and obtain all the rewards. By taking turns, children simultaneously reduced sensorimotor demands derived from coordination and avoided potential cheating within trials but still demonstrated a sense of trust in their collaborative partner by reciprocating. Evidence from other studies has shown that 5-year-old children are capable of forming joint goals based on a mutual sense of "strategic trust" (Hamann et al., 2012; Tomasello, 2016) in which both individuals understand what they must do to achieve joint success. Thus, in this task children did not need to mutually coordinate their actions with their partners to solve the task if they mutually trusted each other. The ability to communicate may have contributed to enhanced trust between children, as suggested by recent findings in adults (Cohen et al., 2010). However, we should emphasize that although we are not aware of studies comparing the strategies of children from different cultures in these types of games, previous work has highlighted the use of different strategies to distribute collaborative outcomes among children of different cultures (Schaffer et al., 2015; Zeidler et al., 2016). Thus, it is possible that children from other populations may use different cooperative strategies to distribute rewards (i.e. division of rewards by the end of the game).

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

Finally, we found that children communicated slightly more often during *social dilemma* compared to *competitive* trials, but this difference was not significant. This might be partially explained by the fact that children solved both situations similarly: they took turns equally across conditions and became faster across the study period. This might also explain why, in general, children used similar types of communication across conditions. This finding contrasts with other studies showing that children flexibly adjust their communication between conditions of a game (when either the risk of coordination failure or competing interests vary between conditions) to achieve successful coordination (Duguid et al., 2014; Sánchez-Amaro et al., 2017). One possibility is that, given the competitive nature of the *social dilemma*, communication did not have a big effect in their partners' decisions and so, they adjusted their communication to a lesser degree compared to situations without a conflict of interest in which communication plays an important role in coordinating decisions (e.g. Duguid et al., 2014). This interpretation would be consistent with findings with adults showing that communication has a stronger effect on their partners' decisions in mutually cooperative context, such as the Stag Hunt, compared to more competitive situations, such as the Prisoner's Dilemma (Duffy and Feltovich, 2002).

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

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

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

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

It is also possible that some chimpanzees, despite understanding the contingencies of the task, could not inhibit pulling in a situation in which they had no alternative. However, this seems unlikely to explain all cases of unilateral cooperation. Many previous studies have shown that chimpanzees from different labs can inhibit acting for longer periods of time (i.e., 3 minutes) to obtain a preferred reward in non-social contexts (Amici et al., 2008; Beran and Evans, 2006; Rosati et al., 2007) and in social contexts (Bullinger et al., 2011b; Duguid et al., 2014; Melis et al., 2009). Trials in our study lasted a maximum of 15 seconds, below that of most of the studies cited.

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

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

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**Figures and Tables captions**

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

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

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

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

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