Chimpanzees, bonobos and children successfully coordinate in conflict situations

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Social animals need to coordinate with others to reap the benefits of group-living even when individuals' interests are misaligned. We compare how chimpanzees, bonobos and children coordinate their actions with a conspecific in a Snowdrift game, which provides a model for understanding how organisms coordinate and make decisions under conflict. In study 1, we presented pairs of chimpanzees, bonobos and children with an unequal reward distribution. In the critical condition the preferred reward could only be obtained by waiting for the partner to act, with the risk that if no one acted, both would lose the rewards. Apes and children successfully coordinated to obtain the rewards. Children used a "both-partner-pull" strategy and communicated during the task while some apes relied on an "only-one-partner-pulls" strategy to solve the task although there were also signs of strategic behavior as they waited for their partner to pull when that strategy led to the preferred reward. In study 2, we presented pairs of chimpanzees and bonobos with the same setup as in study 1 with the addition of a non-social option that provided them with a secure reward. In this situation, apes had to actively decide between the unequal distribution or the alternative. In this setup, apes maximized their rewards by taking their partners' potential actions into account. In conclusion, children and apes showed clear instances of strategic decision-making to maximize their own rewards while maintaining successful coordination.

Keywords: coordination, conflict, snowdrift, chimpanzees, bonobos, children

Introduction

Many animal species regularly face situations in which individuals need to coordinate to overcome conflicts of interest. Most research has focused on how groups decide on the direction of travel when individuals have differing preferences [1-2] but, as with humans, there are many other contexts involving a conflict of interest. For instance, lions [3] during inter-group encounters or chimpanzees [4] that lag behind in cooperative hunting events waiting for others to start the chase may avoid fighting, injuries and energy expenditure [5]. But if everyone waits, no hunt will ensue. Recent evidence suggests that some chimpanzees solve the coordination problem by starting the hunt and thus paying the initiation costs (acting as "impact-hunters") [6]. However, it remains unclear whether the benefits that "impact-hunters" obtain from the hunt outweigh the initiation costs. In other words, it is unclear whether these subjects strategically take into account the potential costs and benefits of the hunt when they initiate it.

Situations of the type described above can be understood as collective-action problems [7, 8], or at the dyadic level, as Snowdrift dilemmas (SD) [9-12]. The SD occurs when an individual (A) would prefer another individual (B) to carry out a costly action that benefits both A and B. However, if B does not act, it is better for A to act alone rather than not act at all. Therefore the preference for A would be 1st) to wait for B to act, 2nd) divide the cost by acting together and 3rd) pay all the cost of the action. One crucial difference between the SD and other classical games such as the Prisoners Dilemma (PD) [13] is that the worst case scenario in the SD occurs when both partners defect while in the PD occurs when the individual cooperates but the partner defects. Consistent with the idea that cooperation is less risky in a SD than in PD, both agent-based simulations [14] and human behavioural experiments [15, 16] have found higher and more stable levels of cooperation in SD than PD.

In general, models in which mutual defection is the worst-case scenario offer a better explanatory model of the emergence of cooperation and helping in natural conditions [17]. Although models like the Stag Hunt game [18] –a situation in which each individual can decide between an individual option that provides a secure but less preferred reward or a social option in which participants need to collaborate to obtain a highly preferred reward– show crucial differences between the way chimpanzees and humans manage the challenge of coordinating actions and maintaining high levels of cooperation [19, 20], SD models seem a better fit for situations in which chimpanzees need to coordinate actions towards common goals [21-24], especially as soon as there is conflict of interest. Recently, two studies have investigated how chimpanzees [25] and five-year-old children [26] coordinate their actions in SD dilemmas. Chimpanzee dyads were presented with a task in which they could access food by pulling a weighted tray. Individuals could pull together and split the costs or they could pull alone and do all the work. However, if after a certain period of time neither individual had pulled, the experimenters removed the rewards. Chimpanzees solved the dilemma, cooperating on an average of 70% of trials. However, in situations where the tray was very heavy (and thus more difficult to pull) chimpanzees waited longer before pulling. Additionally, the difference between the weight pulled by the individual pulling first and pulling second increased across sessions. The authors concluded that the chimpanzees may have tried to avoid being the first one pulling to reduce the risk of pulling alone, while still maintaining successful coordination. In another study, Grueneisen and Tomasello [26] presented pairs of five-year-old children with a different version of a SD: two toy trains with rewards in the cargo. Each child controlled one train which had to arrive at its own station positioned behind the partners train to retrieve the rewards. However, if both trains continued along the track they were on, they would crash into each other before arriving to their stations and all rewards would be lost. Thus, one child needed to swerve onto a side track at the cost of some cargo. Therefore, it was in each child's interest to wait for the partner to swerve. Children rarely crashed the trains by taking turns swerving.

Although these two studies demonstrated that both species can solve SD dilemmas, they are not directly comparable because chimpanzee dyads had the option to cooperate and share costs within trials [25], whereas children did not [26]. Consequently, the current study presented children and two nonhuman great ape (henceforth ape) species, chimpanzees and bonobos, with the same SD dilemma paying special attention to any indication of strategic decision-making (i.e., waiting to pull). Although bonobos have not been studied in SD dilemmas, previous studies on cooperation indicate that they performed better than chimpanzees under some conditions that required higher tolerance towards conspecifics [27]. Study 1 investigated subjects' decisions in a SD and a competitive condition (COM). The best strategy in the SD condition was to wait for a partner to pull and thus obtain the higher of two rewards. However, as in the classical SD situation, it was better to pull if no-one pulled. We compared SD to COM, which required subjects to pull faster than the partner to obtain the higher reward. If subjects behaved strategically, we expected a higher latency to pull in the SD than COM and a higher frequency of both individuals pulling in COM than SD. Finally, based on a recent study [20], we expected communication to play a role in children's coordination but not in chimpanzees or bonobos. We conducted a follow-up study with apes (Study 2) because some individuals in Study 1 had shown indications of strategic decision making by waiting to pull in the SD condition. We used the same apparatus (and conditions) as in Study 1a except that we added an alternative option for each individual. We hypothesized that this would allow subjects to better manage the risk by choosing the alternative option depending on the options available in the apparatus and their partner's preferences.

Study 1a: Chimpanzees and Bonobos Snowdrift

Subjects

We tested 10 captive chimpanzees (5 females; M_{age}= 20.5 years) and 6 captive bonobos (5 females; M_{age}=13.7 years) housed at the Wolfgang Kohler Primate Research Center in Leipzig zoo (see Table 1 in the electronic supplementary materials, henceforth ESM, for more information about the apes in study 1a and 2). During the first phase of the study, the chimpanzees made up 5 unique pairs and the bonobos made up 3 unique pairs. In the second phase pairs were reshuffled to create 5 new chimpanzee pairs and 3 new bonobo pairs.

Materials

We presented ape dyads with a rotating blade (10x91 cm) (Figure 1a) attached to a platform (88.5x96.5 cm) placed between two rooms. Each end of the rotating blade was baited by different amounts of fruit (banana slices for chimpanzees and half grapes for bonobos). Subjects faced each other across the platform, each with access to one side of the apparatus. Two identical ropes (76 cm) were attached to the interior end of the blade with Velcro (see Figure 1a) and fed into each subjects' room. Subjects could access the apparatus via a small window on either side of the platform; the experimenter opened these windows at the start of a trial but the windows remained closed between trials. Apes could only access the interior or the exterior end of the blade by pulling the rope towards them or by waiting for the partner to pull from the other side, respectively. Thus, when a subject pulled its rope, the roped end of the blade rotated towards her while the free end rotated towards her partner.

Figure 1. Experimental set-up of study 1a (Figure 1a), study 1b (Figure 1b) and study 2 (Figure 1c).

Design and procedure

We used a within-subjects design with two conditions (SD & COM). In the SD condition, one piece of fruit was placed on the roped end of the blade and four pieces on the free end, thus creating a SD dilemma because the subject's best choice was to wait for the partner to pull and bring the free end within her reach. In the COM condition, the four pieces of fruit were placed on the roped end while the free end was baited with one piece. In this condition subjects should pull earlier than their partner to obtain the higher reward.

At the start of a trial, two experimenters allowed subjects access to their respective ropes by opening the windows. The subjects then had 30 seconds to pull the rope and get the rewards placed on the rotating blade or wait for the partner to pull. If no ape pulled after the 30 seconds, the experimenter removed all rewards and ended the trial. In case both individuals pulled simultaneously, one or both ropes disconnected from the blade resulting in a random movement and a possible loss of all rewards.

Training phases

Prior to the test phase all subjects completed two training phases (see ESM for more details of the training phases).

Phase 1. Individual training

This training phase served to expose the subjects to the task's main contingencies including how to access the rewards. Subjects were required to pull the blade to retrieve food. After pulling the rope subjects could access both rooms and retrieve the food from both sides of the apparatus.

Phase 2. Dyadic training

This training served to demonstrate that, depending on the condition, subjects could get either high or low rewards by either pulling themselves or by waiting for a partner to pull.

Test sessions

After completing the training phases each dyad received eight 8-trial test sessions (4 SD and 4 COM trials in a randomised order). Subjects only received one session per day and switched sides between sessions. Test sessions were identical to the dyadic training sessions except that both subjects had access to their own rope. After completing eight sessions with their first partner (phase 1) each subject was paired with another one for another eight sessions (phase 2).

Coding

Our measure of coordination success was the percentage of trials in which dyads succeeded, defined as trials in which at least one member obtained a reward. We scored three further dependent variables: subjects' latencies to pull, their pulling rate (derived in three different measures) and communication (see ESM for details of interobserver reliability measures for all studies). We defined the latency to pull as the elapsed time between the opening of the doors and the first pulling action). We defined a pulling action as either the first instance of blade movement towards a subject or the first instance of tension between the ropes of both subjects, which occurred when both subjects pulled simultaneously. Communication was defined as any vocal or gestural communicative acts directed towards the partner or the partner´s actions, such as attention-getters (see ESM for details). It is possible, though, that we may have missed more subtle cues of communication.

We calculated three measures derived from the subject's pulling rate. First, we considered whether apes behaved strategically by comparing the number of strategic choices (i.e., proportion of pulls in the COM condition plus the proportion of non-pull decisions in the SD condition) to the levels expected by chance. With this information we also classified subjects as pullers (pulling ≥ 75% of trials in both conditions), non-pullers *(*pulls ≤ 25% of trials in both conditions) and strategisers (COM pulling > SD pulling resulting in a food intake significantly above chance in both conditions). Second, we scored conflict trials defined as both subjects pulling simultaneously and investigated whether their likelihood of occurrence increased by the occurrence of a conflict in the previous trial. Finally, we investigated subjects' flexibility defined as the change in pulling behaviour shown between subjects (see the ESM for details).

Statistical analysis

All analyses were conducted using linear mixed models (LMM) or generalized linear mixed models (GLMM). In all models significance was set at $P < 0.05$ (see ESM for full details of the statistical analysis).

Results and discussion

Overall, dyads obtained the rewards in 98% of trials. Subjects waited longer to pull during SD than COM trials (Model 1, LMM: $\chi^2_1 = 9.181$, N = 1019, P = 0.002, CI [0.057, 0.483]). From their pulling rates, we classified four subjects as "pullers", three as "non-pullers" and two as "strategisers". The remaining seven subjects were unclassified. The two "strategisers" (one male chimpanzee and one female bonobo) pulled in COM trials and not in SD trials (binomial test, $p < 0.005$), a behavior that resulted in a maximization of their payoffs (see Table 1 in ESM). However, when we considered strategies at the dyadic level a different picture emerged. In nine of 16 dyads one subject pulled in most of trials (>75%) while the other almost never pulled (<25%). Thus, a high proportion of dyads displayed a strategy based on only one subject pulling in both conditions. Pulling rates also indicated that apes were more likely to pull simultaneously in

COM than SD trials (Model 2, GLMM: χ^2_1 = 6.607, N = 895, P = 0.01). Previous conflict trials had no effect on their subsequent response (Model 2, GLMM: χ^2_1 = 5.286, N = 895, P = 0.071) (see ESM for detailed information of Model 1 and 2). We found that subjects' behavior changed between partners: 31% of subjects modified their behavior (varying their pulling rates by more than 50% between partners; see Figure 2 in ESM). Finally, we found that apes almost never communicated with their partner to solve the task (individuals protested on 0.01 % trials).

In sum, chimpanzees and bonobos came up with an efficient, simple solution to coordinate in this task, the "only-one-partner-pulls" strategy. Although this strategy prevented subjects from maximizing their own payoffs, the randomized presentation of the rewards led to an almost equal division of rewards between partners. Moreover, two subjects behaved strategically although it was unclear why so few did so (2 out of 16 individuals) and what strategic level their decisions entailed. Next we presented 5-year-old children with the same basic task to compare their strategies to those of apes (study 1a) and subsequently probed ape strategic behavior further by varying potential payoffs for the subject and the partner in study 2.

Study 1b: Children Snowdrift

Subjects

We tested 20 pairs of- 5- to 5.5-year-old children (10 pairs of girls and 10 pairs of boys) in kindergartens in the Leipzig area. All participants were recruited from a database of children whose parents had provided written consent to take part in child development and comparative studies. The children in each pair were from the same kindergarten.

Materials

In general, dyads were presented with the same task as chimpanzees and bonobos (Figure 1b). The apparatus was a wooden box with a lid that prevented children from directly accessing the rewards. We made a few minor changes to accommodate the apparatus for children (see ESM for differences between study 1a and study 1b).

Design and Procedure

The procedure the same as the one used in study 1a except for three differences. First, children were only tested with one partner. Second, we used tokens (wooden blocks during training and more valuable plastic marbles ("jewels") during test sessions) as rewards, which children had to collect during the study. Third, children received three sessions (24 trials in total) compared to 16 sessions (128 trials) for the apes (see ESM for other minor differences between study 1a and study 1b design and procedure).

Test sessions

After the training, each dyad performed three test sessions on two consecutive days. The first session was conducted after the training and the second and third sessions were conducted on a second day. Each session consisted of eight trials and children swapped sides after completing trial four. Children received two COM and two SD trials in a randomised order from each side of the apparatus. At the beginning of each trial, Experimenter 1 showed the reward locations to the children before allowing them to access to the ropes. In the test sessions, children collected their rewards and kept them in their own plastic tubes previously provided by the experimenters (see ESM for details of the test sessions).

Coding

We analysed the same dependent measures as in study 1a, excluding flexibility because children only played with one partner. Additionally, we adjusted our coding to include verbal communication (see ESM for communication coding details). We only analysed verbal communication related to the task by focussing on the five following types: *imperative*: deontic verbs used to direct their partners' actions (e.g. "You should pull"), *protests:* statements of disapproval and objection about a partner action's or intention (e.g. "No, I also wanted"), *informative:* acts aimed at informing partners about a child's current or impending actions or intentions (e.g. "I am going to pull now"), *turn-taking:* stating previous or future actions aimed at influence others' decisions. This type of communication could be coupled with either *imperative, protests or informative* (e.g. "I pull because you pulled before"; "Next time you pull") and *deception:* acts aimed at explicitly cheating their partners.

Results and discussion

Overall, dyads obtained the rewards in almost all trials (99%). Children increased their latency to pull across sessions in SD trials and decreased it in COM trials (Model 3, LMM: χ^2_1 = 4.913, N = 478, P = 0.027, CI [-0.023, 0.223]; Figure 2) indicating that like apes, they distinguished the conditions. Based on their pulling rates, we classified most children as "pullers" (24 of 40) and one child was classified as a "non-puller". Three children made strategic decisions significantly above chance (binomial test, $p < 0.005$) by pulling in COM trials and not pulling in SD trials (see ESM for a detailed comparison between children' and apes' strategies). At the dyadic level, only one dyad followed the "only-one-partner-pulls" strategy described for apes. Instead, most child dyads followed a "both-partners-pull" strategy regardless of the condition. In contrast to apes, children both pulled equally often in COM (53 % of times together) compared to SD trials (43 % of times together) (Model 4, GLMM: χ^2_4 = 5.305, N = 420, P = 0.257). Finally, we found that children communicated more often in SD than COM trials (Model 5, GLMM: χ^2_1 = 4.72, N = 480 P = 0.03, CI [-0.219, 2.464]). Communication occurred in 33% of the trials (in 96 SD and 56 COM trials out of 240 trials per condition). Although we could not analyze statistically the distribution of children communicative types, we found that imperative utterances (e.g. "you should pull") were mostly used in situations in which they needed a partner to act against the partners' self-interest (58% of 96 communicative acts in SD trials). In contrast, no communicative type predominated in competitive situations (see ESM for detailed information of Models 3, 4, 5 and Figure 4 in ESM).

Figure 2. Latency of the 1st puller to pull the rope in SD and COM trials across the three test sessions. The dotted line represents the fitted model and the shadowed areas represent the CI at 95%. Latencies in seconds are presented in a logarithmic scale. Data from children in study 1b.

In summary, children were as successful as apes and made a similar proportion of strategic choices compared to apes (53% of strategic choices in children, 51% in chimpanzees and 54% in bonobos). However, they did so with much less experience with the task -24 compared to 128 trials suggesting that, in contrast to apes, they learned faster the contingencies of the task. Unlike apes, we found that most children followed a "both-partners-pull" strategy regardless of the condition, which may not be that different in terms of complexity to the apes' "only-one-partner-pulls" strategy. However, children showed more signs of strategic decision-making than apes: they used communication to influence their partner decisions and learned to distinguish both conditions after only three sessions (Figure 2).

Study 2: Chimpanzees and bonobos Snowdrift with alternative option

In the previous study, although a majority of ape dyads engaged in the "only-one-partner-pulls" strategy, some apes showed indications of strategic decision making. To further investigate individuals´ decision-making strategies in conflict situations, we used the same apparatus of Study 1a with the addition of an alternative option for each individual.

Subjects

We tested 8 captive chimpanzees (3 females; M_{age}= 13.5 years) and 4 captive bonobos (3 females; M_{age}= 13.5 years) housed at the Wolfgang Kohler Primate Research Center in Leipzig zoo. Seven chimpanzees and all bonobos had taken part in study 1a. Each individual was tested with three partners. During the first phase of the study, the chimpanzees made up four unique pairs and the bonobos made up two unique pairs. In the second and third phase, pairs were shuffled to create another four new chimpanzee pairs and two new bonobos' pairs per phase.

Materials

We presented pairs of individuals with the same apparatus used in study 1a with two main additions. In this new setup, subjects needed to move a sliding door either to the left or the right side to access the apparatus. If they moved the sliding door to the right side they could access the ropes as in the original apparatus. However, if they slid the door towards the left they could directly access an alternative option (Figure 1c). The alternative option consisted of a fixed platform (10X10 cm) attached to the Plexiglas frame located approximately 5 cm above the apparatus to not interfere with the rotation of the blade. When the sliding door was opened to one side, another locking mechanism prevented it from being moved back to its original position. Therefore, subjects could only make one choice per trial (see ESM for details of the materials).

Design and procedure

Subjects were tested in a within-subjects design in the same two conditions as study 1a (SD and COM). In this set-up the rotating blade was baited with one and five food pieces. The alternative platforms could be baited with either zero, one, three or five food pieces depending on the condition presented (non-social condition levels). Both alternative platforms were baited with the same food quantity on a given trial. Chimpanzees and bonobos received the same kind of food as in study 1a.

At the beginning of a trial, two experimenters simultaneously removed the pin that had prevented choosing between options and apes had 10 seconds to make their choices. When a subject opened the window to the alternative platform, they could immediately access the reward. When a subject opened the door to the blade they could either wait for the partner to pull the rope or pull themselves (as in study 1a). We defined an apes' choice for the rotating blade as the "social option" and the alternative platform as the "non-social option".

Test sessions

After completing the training phases (see ESM for details of the training phases), every dyad performed eight test sessions. Each session contained four SD and four COM trials presented in a randomized order. In the alternative platform, the levels of the non-social condition (0, 1, 3 or 5) were randomly presented between sessions, each level was presented in two sessions. In the test sessions, both subjects had access to either the rope attached to the rotating tray or the alternative option. Subjects switched sides between sessions. After the eight sessions with their first partner (phase 1) each subject was paired with two further partners for another two blocks of eight sessions (phase 2 and 3).

Coding

We measured the percentage of successful trials (defined as in study 1). Additionally, to study how chimpanzees and bonobos solved this new version of the game, we focused on two main dependent variables: choices and latencies (further divided in two latency measures). Choices were defined as the proportion of trials in which each subject chose the social or the non-social option. The first latency measure consisted of the elapsed time between the pins' removal and the sliding of the door halfway to one side (at which point they could not change direction). The second latency measure was the elapsed time between accessing the social option and pulling the rope (defined as in study 1a). These latencies allowed us to assess whether the 2nd actors made strategic decisions contingent on the previous action of the 1st actors during the same trial.

To determine who acted in 1st and 2nd position (by acting we mean the initial decisions to slide the door to access either the social or non-social option), we only considered those trials in which both individuals acted at different times (at least $\frac{1}{25}$ of a second). The average time between 1st and 2nd actors was less than 2 seconds. Then, for each combination of social and non-social conditions (8 combinations) we categorized the strategic choices of the 2nd actors. Moreover, we took into account those instances where the 2nd actors could maximize their rewards by taking into account the previous action of 1st actors (see the two combinations of non-social option 3 in Table 1). In other words, in these two combinations 2nd actors strategic choices differed depending on 1^{st} actors actions. Finally, we calculated the proportion of strategic choices for each of the 8 combinations and we compared them to chance levels.

Table 1. Rational choices dependent on the combination of social and non-social options.

Social option	Non-social option	Strategic choice
SD and COM	0	Social option
SD and COM	1	Social option
SD	3	Same action of 1^{st} actor
COM	3	Opposite action to 1^{st} actor
SD and COM	5	Non-social option

Results and discussion

Overall, ape dyads obtained the rewards in 92% of trials. Both ape species behaved rationally by choosing the social option when there were no rewards available in the non-social alternative (93% of trials). As expected, the proportion of choices towards the non-social option relative to the social option also increased as the rewards in the alternative platform increased. This change was not driven solely by the number of rewards in the alternative option but also by the social condition: the switch in preference from the social to the non-social option was steeper in SD trials compared to COM trials (Model 6, GLMM: χ^2_1 = 9.572, P = 0.002, N = 2218, CI [0.284, 2.258], Figure 3).

Figure 3. Percentage of chimpanzees and bonobos' decisions towards the social choice as a function of the number of food pieces in the non-social and the social option (SD and COM trials) in study 2.

Our first latency measure was the time taken to open the door to either platform. When there was no reward in the non-social platform apes waited longer to open the doors in SD trials compared to COM trials, replicating the findings from study 1a. However, as the rewards in the non-social platform increased, apes tended to decrease their latency to decide, and the differences between SD and COM conditions decreased. This decrease in latency occurred in conjunction with a change in their decisions, from the social to the non-social option (see Figure 3) (Model 7, LMM: χ^2_1 = 6.62, N = 2216, P = 0.01, CI [-0.007, 0.295], see Figures 6 and 7 in the ESM). Overall, chimpanzees were faster than bonobos in both conditions (Model 7, LMM: χ^2_1 = 8.06, N = 2216, P = 0.004, CI [-1.061, -0.099]) but there were no significant interactions between species and conditions.

Our second latency measure focused on whether subjects waited further for their partner to pull in the SD condition, or whether the decision to open the door always led to immediate pulling of the rope. We found that both chimpanzees and bonobos did indeed wait longer to pull in SD trials compared to COM trials. Additionally, as the rewards in the non-social option increased apes tended to wait longer to pull (Model 8, LMM: χ^2_1 = 3.888, N = 773, P = 0.048, CI [-0.044, 0.37], see Figures 8 and 9 in the ESM), with a more pronounced effect in bonobos. This was unexpected as at that point the content of the non-social option was already inaccessible and thus should not play a role in their decision to wait. However, these results should be interpreted cautiously as they are based on a small subset of trials (see Figure 3).

Overall, we found that the individuals acting second made strategic decisions on 85% of the trials. Moreover, when they could respond to the decision that the first actor had made in that trial –in non-social option 3, they made strategic choices on 75% of trials. However, they only chose significantly above chance when there were 0 or 5 food rewards baited in the alternative platform ($P < 0.02$; see Model 9 for detailed results of the pair-wise comparisons derived from the model and Figure 10 in ESM). Finally, we also found that 2nd actors differed in their choices depending on the previous choices of the 1st actors and the combination of social and non-social conditions presented (combinations Non-social option 1-SD, Non-social option 3-COM and Non-social option 5-COM) (Model 10, GLMM: $\chi^2_2 = 12.53$, $N = 396$, $P = 0.002$). Moreover, a further inspection of the model revealed that the probability of 2nd actors to choose the social option increased when 1st actors chose the social option in Non-social option 1-SD ($P = 0.02$) but the choice was not significantly affected in the other two combinations (Non-social option 3-COM: $P = 0.22$; Non-social option 5-COM: $P = 0.4$). See ESM for detailed information of Model 6-10.

In sum, results of study 2 substantially clarified those from study 1a by showing that when apes had access to an alternative option, their decisions were clearly strategic. They understood the payoffs of the game and acted rationally according to all the rewards involved by maximizing their benefits, as shown in previous social dilemmas [28]. This may have simply been due to increased experience, as all individuals completed study 1a before study 2. However, if this were the case, we would have expected changes across sessions in study 1a. We suggest that one important factor is that the inhibitory demands of study 1a were higher. Subjects faced the decision to either act on the apparatus (pull) or not at all, but in study 2 apes could decide between the two actions (sliding the door left or right). Thus, one possible way to interpret our results is that when apes had to actively decide between different alternatives, it may have been easier for them to inhibit and compare their potential options and act appropriately according to the payoffs of the game in order to maximize their rewards.

General Discussion

Using the Snowdrift dilemma to investigate how pairs of children, chimpanzees and bonobos coordinate their actions to overcome conflicts of interest, we found that all three species coordinated their actions effectively and succeeded in over 90% of the trials. All species showed clear indications of strategic decision making, trying to maximize their own rewards while maintaining high levels of coordination. In study 1, children's communicative acts revealed clear signs of strategic behavior but no such indication was observed among apes. In study 2, in which apes had access to an alternative (non-social) option, their decisions were clearly strategic even though communication between partners was still virtually nonexistent.

Children are skilled at coordinating for mutual gain from a young age [20, 26, 29-31]. Even in situations where the risk of coordination failure is increased, children are able to use communication and theory of mind reasoning to avoid this risk [20, 26, 29 and 32]. However, the goals of partners in those studies were aligned (i.e. there was no conflict of interest between partners). The current study showed that even when facing with a potential conflict of interest, children's rate of coordination failure was very low. Crucially, their success in the task cannot be attributed to a failure to appreciate the conflict of interest because their communicative exchanges indicated that they encouraged their partners to pay the higher cost to maximize their own rewards.

Our results are consistent with Grueneisen and Tomasello. [26] who also observed high levels of coordination in five-year-old children playing a version of the SD game. Coordination in that study was maintained by turn-taking, which also has been shown to enable resource sharing in a collaborative task [33]. Note however, that children in those studies always depended on their partner to obtain either the preferred reward [26] or all the rewards [33]. In contrast, our procedure eliminated a strict partner dependency because SD trials were randomly intermixed with COM trials in which children competed to obtain the preferred reward by pulling first, without the need of their partner's action. Besides preventing partner dependency, mixing SD and COM trials may have made a turn-taking strategy much more cognitively demanding than previous studies (and therefore useless) because it would have required children to keep track of all their previous actions and outcomes to maximize efficiency. However, a consequence of this strategy is that the coordination was maintained despite a skewed reward distribution between partners (also observed in Grueneisen et al. [26]), perhaps because receiving some reward was more important than the social comparison, but further research is needed to determine the effects of resource inequality on coordination.

Apes also solved the SD dilemma successfully (coordination in 98% of the trials) but their behavior differed from children's in two important ways: there was little communication between partners and only one partner pulled in most dyads. This strategy produced an equal distribution of rewards between partners, which may seem surprising given that apes behaved as rational maximizers in other studies [28, 34]. However, the observed equal distribution may have been a by-product of the one-partner-pulling strategy combined with the counterbalancing of payoffs across multiple trials. Even when one of the partners was a passive participant (always waiting) it does not necessarily mean that they were indifferent to the outcomes. Apes experienced pulling in both conditions during the training and experimental sessions, and there is evidence suggesting that subordinate chimpanzees wait to pull a rope to "negotiate" a better reward distribution with a dominant individual [35]. Thus, it is conceivable that some apes preferred to obtain lower rewards instead of competing for higher rewards to avoid conflict [21]. However, in our case it is difficult to ascertain whether not pulling was a strategic decision, or some individuals were content with the food received for not pulling at all.

Study 2 directly addressed this ambiguity by offering an alternative option to inaction. Based on their change in preference from social to non-social choices (and their associated timing), apes generally behaved more strategically in study 2 compared to study 1. However, apes not always maximized their rewards in all conditions. For instance, when apes were confronted with the COM condition (five pieces of food in the roped end) and the alternative option was baited with three pieces of food, they sometimes preferred the lower but secure reward even when they pulled first (20% of times they chose the non-social option). Perhaps an aversion to either risk or even competition with their partners led them to select lower value (but secure) rewards in those cases. In the absence of risk, chimpanzees prefer to act alone rather than to collaborate provided both actions yield the same rewards [34] but they switch to collaborative options that result in better outcomes than acting alone [34, 36]). However, if social risks increase, as in the current study or other tasks [20], they may prefer lower but more secure rewards, thus managing a trade-off between competition and reward maximization.

Based on previous findings [37, 38], we expected bonobos to be more risk averse (preferring the secure option) than chimpanzees but we found no clear inter-specific differences. A possible explanation for this result is that most studies have focused on non-social risk effects. Interestingly, in a study in which bonobos could choose between feeding alone or co-feeding with strangers, they preferred the social option [39] despite the potential social risks involved. Thus, we need further studies comparing chimpanzees and bonobos across different social and non-social risk tasks to fully understand possible differences between these two species.

Finally, we investigated whether apes took advantage of situations in which they already had information about their partner's decisions (i.e. when their partner acted before them) and whether they varied their choices depending on their partner´s previous choices. Overall, individuals acting second chose strategically. However, in those conditions where the strategic choice of second actors differed depending on what their partner had chosen in that trial, they did not perform significantly above chance. Moreover, in some combinations of social and non-social conditions, the decisions of individuals acting second were affected by their partners' previous choice, suggesting that they were taking into account their partners previous actions. Our results are consistent with previous studies in competitive contexts showing that chimpanzees can adjust their strategies in anticipation of likely decisions of partners [40, 41] but we did not see clear strategic responses to a partner's specific decision. The short time that apes had to respond to their partner and the random presentation of conditions within sessions may have contributed to this outcome. We found that apes anticipated their partner's likely behaviour when they faced a symmetrical conflict of interest in which both participants started with the same probabilities to maximize their pay-offs. However, to explore in more detail whether apes act strategically in response to their partners' decisions, future research could focus on how apes solve conflicts of interest when only one individual has bargaining leverage (i.e. only one member of the pair has access to an alternative option).

In conclusion, using a Snowdrift game to model situations such as group hunting or agonistic intergroup encounters in which individuals need to overcome a conflict of interest to coordinate with others, we found that pairs of children, chimpanzees and bonobos successfully solved this social dilemma. However, they did so in different ways. Whereas both partners pulled and communicated in children, one of the partners did most of the pulling in apes with virtually no communication. Nevertheless, an additional study that included an additional secure option revealed that apes behaved strategically by choosing options that maximized their own payoffs, which in some cases included delaying (or accelerating) their choices to net the largest reward available.

Ethical Statement

The study was ethically approved by an internal committee at the Max Planck Institute for Evolutionary Anthropology. Animal husbandry and research comply 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.

Data accessibility

Data available from the Dryad digital depository: http://datadryad.org/review?doi=doi:10.5061/dryad.8638h

Authors' contributions

A.S, S.D, J.C and M.T conceived the study. A.S conducted the research, A.S coded and analysed the data, A.S, S.D, J.C and M.T wrote and revised the paper.

Competing interests

Authors declare no competing interests.

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