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One for You, One for Me: Humans' Unique Turn-Taking Skills

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Abstract

Long-term collaborative relationships require that any jointly produced resources be shared in mutually satisfactory ways. Prototypically, this sharing involves partners dividing up simultaneously available resources, but sometimes the collaboration makes a resource available to only one individual, and any sharing of resources must take place across repeated instances over time. Here, we show that beginning at 5 years of age, human children stabilize cooperation in such cases by taking turns across instances of obtaining a resource. In contrast, chimpanzees do not take turns in this way, and so their collaboration tends to disintegrate over time. Alternating turns in obtaining a collaboratively produced resource does not necessarily require a prosocial concern for the other, but rather requires only a strategic judgment that partners need incentives to continue collaborating. These results suggest that human beings are adapted for thinking strategically in ways that sustain long-term cooperative relationships and that are absent in their nearest primate relatives.

Keywords

collaboration, problem solving, turn taking, chimpanzees, *Pan troglodytes*, children, reciprocity, sharing

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Many of the activities that are typical of any human society are collaborative enterprises in which multiple individuals work together for their mutual benefit (Rawls, 1971). To maintain these collaborative enterprises over time, individuals not only must remain motivated themselves, but also must make sure that their partners remain motivated as well. This means, among other things, that collaborating individuals must share the spoils of their collaboration in ways that all partners find satisfactory (Brosnan & de Waal, 2014; Tomasello, 2009).

Often, a collaborative activity generates resources that can be easily monopolized, which can lead to conflicts between partners and so to a breakdown of collaboration over time. In humans, one common solution to this problem is to compromise by taking turns (Neill, 2003; Nowak & Sigmund, 1994). Alternating turns in obtaining a collaboratively produced resource does not require a prosocial concern for the other, but requires only strategic thinking that partners need incentives to continue collaborating. Such turn taking can be seen as a special case of reciprocal helping, in which individuals work collaboratively but alternate who profits from the acquired resources. By taking turns, individuals can compromise and maintain cooperation in conflict-of-interest situations.

Humans' nearest primate relatives engage in various collaborative activities as well (Boesch & Boesch-Achermann, 2000; Muller & Mitani, 2005) and understand the role of the partner in the collaborative enterprise (Melis, Hare, & Tomasello, 2006a; Melis & Tomasello, 2013). But when a collaborative activity generates resources that one individual can easily monopolize, typically the dominant individual takes most of it, which leads to the subordinate losing interest (Hare, Melis, Woods, Hastings,

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& Wrangham, 2007; Melis, Hare, & Tomasello, 2006b). Humans, in contrast, are from a young age better adapted to collaborate in acquiring resources. By age 3, human children employ social and communicative strategies to coordinate actions with a partner and share jointly acquired resources equally even when they could easily be monopolized (Hamann, Warneken, Greenberg, & Tomasello, 2011; Warneken, Grafenhain, & Tomasello, 2012).

Traditionally, the study of reciprocal behavior has focused on individuals' unilateral decisions regarding the provision of altruistic favors. Several observational studies suggest that chimpanzees can keep track of previous interactions with others, and exchange reciprocally grooming, food, and coalitionary support (e.g., de Waal, 1997; Mitani, 2006). However, the exact psychological mechanisms underlying these reciprocal interactions are unclear. The rich interpretation is that interactants understand the interdependency of their actions and the long-term benefits of exchanging favors, so that their behavior is a planned strategy to ultimately profit themselves. However, reciprocity may also be underlain by simpler psychological mechanisms. For example, it may be based on *emotional bookkeeping* (similar to de Waal's, 2000, *attitudinal reciprocity*), in which individuals develop emotional attitudes toward partners based on past interactions with them, but not necessarily memories of these specific interactions (Evers, de Vries, Spruijt, & Sterck, 2015; Schino & Aureli, 2009). A cognitively more complex mechanism, which still does not require anticipation of future benefits, is *calculated reciprocity*, in which individuals remember exactly who did what to whom and when, and base their decisions to help on these past interactions (de Waal, 2008). Neither of these mechanisms (*attitudinal or calculated* reciprocity) necessarily involves understanding the long-term consequences of reciprocation or expecting partners to reciprocate in the future. Such a level of understanding may be important, or even necessary, however, when individuals have to compromise between their own and their partner's desires.

There have been only two experimental paradigms designed to investigate whether chimpanzees are capable of short-term reciprocation in a situation in which they could altruistically help one another (Brosnan et al., 2009; Yamamoto & Tanaka, 2009a, 2009b). The results of both studies were mainly negative, suggesting that chimpanzees do not easily learn about the benefits of alternating favors. Therefore, naturally occurring instances of reciprocation among chimpanzees are probably based on the simpler psychological mechanisms just described (past-driven attitudinal or calculated reciprocity). However, it is also possible that the specific tasks used in these studies were cognitively too demanding for chimpanzees. In particular, it is unclear whether the subjects understood fully the contingencies of the tasks, and whether they had enough cues to infer the recipient's goal, something crucial to elicit altruistic helping in experimental tasks (Melis et al., 2011; Yamamoto, Humle, & Tanaka, 2009). For example, in the study by Brosnan et al. (2009), subjects performed very poorly in the control condition, in which they could benefit themselves, which suggests either a lack of understanding of the task or a lack of motivation to participate in it.

Although these studies suggest that reciprocal helping to solve new problems may not come naturally to chimpanzees, no studies to date have tested nonhuman primates for their ability to share collaboratively produced resources by taking turns obtaining resources across trials. A collaboration task that requires subjects to choose between two possible distributions for which they have conflicting preferences may facilitate their understanding of each other's goals and the need for compromise.

There is evidence that by age 3, children engage in various forms of reciprocal helping, keeping track of past interactions and preferentially interacting with and behaving prosocially toward previously helpful partners (House, Henrich, Sarnecka, & Silk, 2013; Levitt, Weber, Clark, & McDonnell, 1985; Warneken & Tomasello, 2013). However, it is only later in ontogeny, by age 5, that children also anticipate the benefits of reciprocal interactions, sharing resources with a partner who can reciprocate more than with one who cannot (Engelmann, Over, Herrmann, & Tomasello, 2013; Sebastian-Enesco & Warneken, 2015; see also Robbins & Rochat, 2011). But none of these studies tested turn taking over time as a specific solution to sharing collaboratively produced resources.

In the current study, therefore, we gave pairs of 3- and 5-year-old children and chimpanzees a collaboration task in which equal rewards could be obtained only if the members of a pair worked together first to reward one and then to reward the other. Neither species had previously been tested in a paradigm in which partners can distribute collaboratively produced rewards in "fair" ways only by taking turns being the sole beneficiary.

Method

Children's experiment

Subjects. We tested 96 preschoolers (equal numbers of boys and girls) in same-sex dyads. The members of half of the dyads (n = 24) were 3.5-year-olds (M = 3.4 years, range = 3.3–3.67 years), and the members of the other half (n = 24) were 5-year-olds (M = 4.9 years, range = 4.8–5.2 years). Two additional dyads of 5-year-olds and one dyad of 3.5-year-olds were tested but not included in the final sample because of experimenter errors and failure to follow the instructions.

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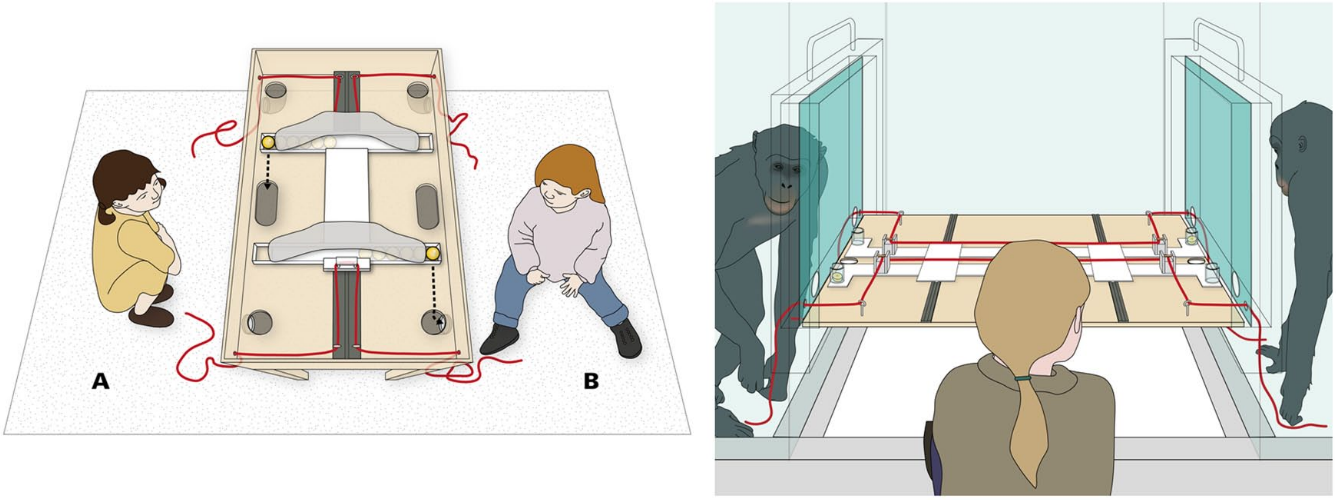

Fig. 1. Schematic representation of the setup and apparatus in the children's and chimpanzees' experiments. In each experiment, the apparatus consisted of two interconnected parallel trays that could be moved to the left or right from the subjects' point of view. The two individuals had to pull simultaneously on the same tray in order to align its reward with an access hole (i.e., one of the four holes at the ends of the table). (In the demonstration phase, not illustrated here, both sides of one tray had rewards.) Once subjects pulled one tray in one direction, the reward on the opposite tray disappeared down a center hole between the two trays (e.g., if the children pulled the left tray from B's perspective, B obtained a reward, whereas the reward that A could have obtained if they had pulled the other tray was lost).

Procedure. The children were tested at local day-care centers, and each child was paired with a familiar partner from the same group at the center. Each dyad was tested on two different days, and both sessions were videotaped. On the first day, we conducted a dominance test and introduced the apparatus to the children, and on the second day, we conducted the actual turn-taking test. We measured the dominance relationship between partners, because we hypothesized that in the absence of an alternation strategy, dominant individuals would monopolize the rewards.

We assessed the dominance relationship between the 2 children in a dyad by observing their behavior in the presence of toys that could be monopolized. After the dominance test, the children were introduced to the rewards and the apparatus for the turn-taking test (see Fig. 1). The rewards were stickers contained inside golden balls (one sticker per ball). In addition, there were transparent balls, which contained no stickers. The apparatus consisted of two interconnected parallel trays, each with a space for a ball at each end. The trays could be moved from side to side atop a table with holes from which the children could access the balls. The children were allowed to choose a sticker book, where they could stick the stickers they obtained. The children were positioned across from each other at the apparatus, and the two experimenters instructed them on how to pull together in order to move the trays so that any balls on one of the trays would drop down into an access hole. At the same time, any balls on the other tray would disappear into a center hole that the children had no access to (i.e., the reward-trap hole). In the demonstration phase, both sides of each tray were always filled equally: One tray had an empty transparent ball at each side, and the other had a sticker-containing golden ball at each side. Thus, the children had no conflicting preferences regarding which tray to pull (see Fig. S1 in the Supplemental Material available online). The goal was to familiarize the children with the cooperation task and the fact that after they pulled in one direction, the rewards of the second tray would become inaccessible.

One day later, the children participated in the turn-taking test. Each dyad performed the cooperation task in a room by themselves, facing each other with the apparatus between them. We placed the rewards in the apparatus in such a way that the children had opposing preferences regarding which tray to pull. That is, each tray contained golden balls at only one side (the other side was empty), and the two trays contained golden balls at opposite sides. Because pulling one tray meant losing the reward of the other tray, only 1 child could access a reward on each trial (Fig. 1). Each dyad participated in one session of 24 trials. After every 6 trials, the children left the room while the experimenter refilled the apparatus. The side of the tray that was baited alternated from block to block.

Chimpanzees' experiment

Subjects. Twelve chimpanzees, 6 males and 6 females ranging from 6 to 35 years of age, participated in this study (see Table S1 in the Supplemental Material). All

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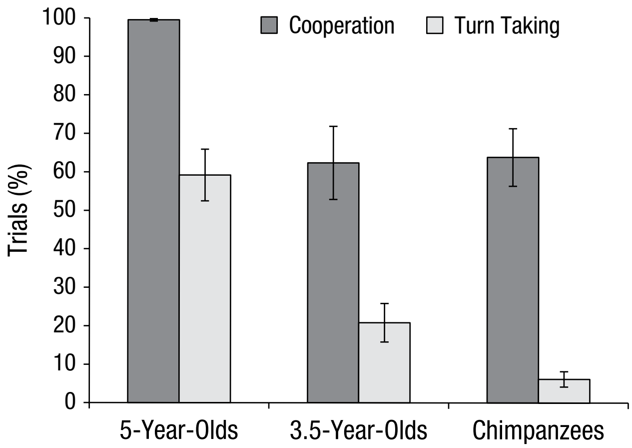

Fig. 2. Mean percentage of trials in which the 5-year-old children (n = 24), 3.5-year-old children (n = 24), and chimpanzees (N = 12) cooperated (pulling any tray together) and in which they took turns. Error bars represent ±1 *SEM*.

were born in captivity and were either mother or nursery reared. The chimpanzees were housed in a 6,159-m^2 living area at the Wolfgang-Koehler-Primate-Research-Center at the Leipzig Zoo, Germany. They were fed their usual daily diet, and water was available ad libitum. They were never food or water deprived for this study.

Procedure. The chimpanzees were introduced to the cooperation apparatus and the contingencies of the task in various steps (see Fig. S2 in the Supplemental Material). First, they were individually familiarized with the apparatus and learned that the two ropes (one on each side of the booth) needed to be pulled simultaneously in order to make the rewards accessible. Afterward, they learned the cooperative aspect of the task. Both trays were baited, so that the chimpanzees learned to coordinate pulling the same tray and also that after they pulled one tray, the rewards of the second tray became inaccessible because they fell into the reward-trap hole in the center of the apparatus. In the first step, one of the trays was baited with bananas and the other one with carrots, and in the second step, both trays were baited with bananas. Once all the chimpanzees demonstrated competence in these pretests, we started the turn-taking test, in which only one side of each tray was baited, as in the children's experiment. The apparatus was refilled after every trial by the experimenter. The main difference from the children's study was that each chimpanzee was tested with 2 different partners, and that the chimpanzees received a total of 96 trials (48 trials with each partner) instead of 24. The subjects changed partners after every two 12-trial sessions (for additional details about the experimental procedure, see the Supplemental Material).

Results

Children's experiment

On average, the 5-year-olds succeeded in delivering the reward to someone in 99.5% of the trials, whereas the 3.5-year-olds succeeded in only 62.3% of the trials (Fig. 2). The lower success rate of the 3.5-year-olds was mainly due to 8 dyads that were unable to find any solution to the conflict of interest (see the Supplemental Material). Furthermore, the 5-year-olds regularly employed a turn-taking strategy (alternating who obtained the reward in consecutive trials; see Video S1 in the Supplemental Material), whereas very few of the 3.5-year-olds did (Fig. 2).

We conducted a generalized linear mixed model (GLMM) with a binomial error structure and logit link function to examine the effects of age, gender, and trial number (and the interaction of age and trial number) on the likelihood of partners taking turns in consecutive trials. We included dyad identity as a random effect to control for repeated measures. Overall, the full model was significantly different from a more parsimonious model that included only gender as a predictor, likelihood ratio test: $\chi^2(3) = 9.99$, $p = .019$. There was no interaction between age and trial number, but both had main effects: The 5-year-olds exhibited more turn taking than the 3.5-year-olds (estimate = 0.768, SE = 0.310, Z = 2.477, p = .013), and turn taking increased as the experiment progressed (estimate = 0.286, SE = 0.134, Z = 2.136, p = .033). There was no effect of gender. A second GLMM showed that, overall, the dominant children did not receive more rewards than the less dominant ones (estimate = −0.054, SE = 0.438, Z = −0.124, p = .902; see the Supplemental Material for details about this GLMM).

We also conducted a GLMM with a negative binomial error structure and log link function to analyze the possible effects of age, gender, trial number, and the interaction between age and trial number on latency of pulling a tray. Again, we included dyad identity as a random effect. Overall, the full model was a better fit than a more parsimonious model that included only gender as a predictor, likelihood ratio test: $\chi^2(3) = 70.5$, $p < .001$. The model showed an interaction between age and trial number (estimate = −0.309, SE = 0.104, Z = −2.983, p = .003); the latencies among the 5-year-olds decreased over time, but the latencies among the 3.5-year-olds did not change so much (Fig. 3; note that for both age groups, latencies were slightly longer in the first trial of each session: Trials 7, 13, and 19).

The difference in behavior between the two age groups was also apparent when we analyzed the children's verbal demands to pull to their own advantage (e.g., pointing to their own side and saying "here" or "my side"). Although the two age groups made verbal

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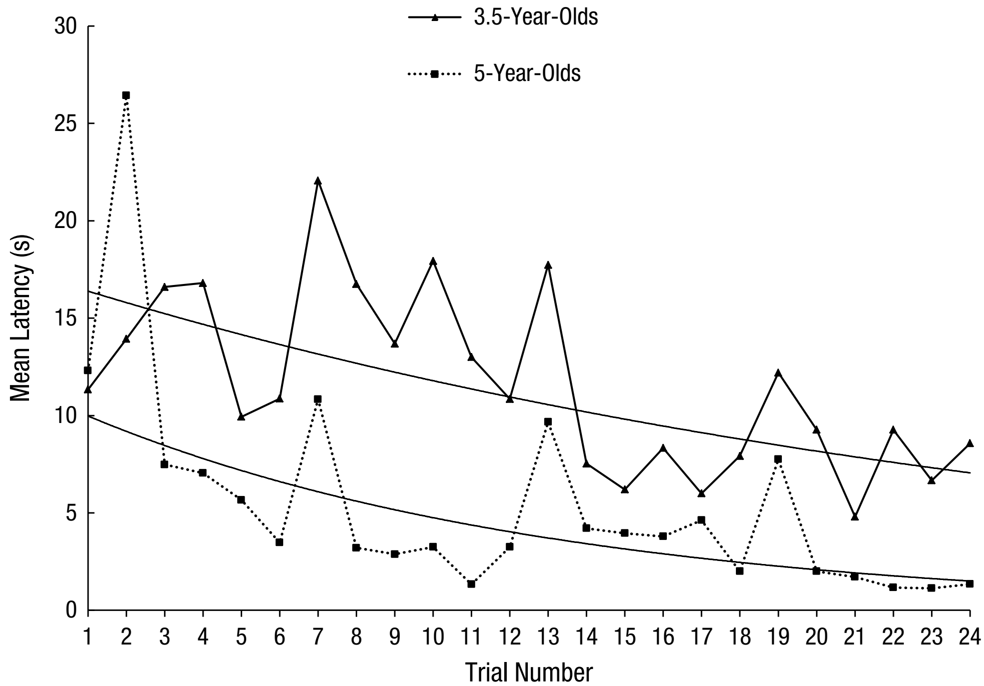

Fig. 3. Trial-by-trial latencies of pulling for the 5-year-olds and 3.5-year-olds (n = 24 per group). The graph shows the observed data along with best-fitting regression lines.

demands at similar rates (3-year-olds: M = 12.1 demands/pair, SE = 1.6; 5-year-olds: M = 12.45 demands/pair, SE = 0.8; Mann-Whitney U = 187, p = .89), there was a qualitative difference in how these demands were made. We predicted that if the children were sensitive to the balance between what the two partners were getting, and were not just trying to monopolize the rewards, they would demand more, and their demands would be more successful, following trials in which their partner obtained the reward than following trials in which they themselves obtained the reward (i.e., the demand was not for more but indicated that "it is my turn now"). Two GLMMs revealed an interaction effect of age and outcome on the previous trial on both the frequency of demands and the success of demands. The younger children made demands independently of whether they had obtained the reward in the previous trial, whereas the 5-year-olds made fewer demands after trials in which they had obtained the reward than after trials in which they had not (estimate = −1.166, SE = 0.398, Z = −2.931, p = .003; Fig. 4a). Similarly, 5-year-olds' demands were more successful when they had not obtained the reward in the previous trial than when they had, whereas this was not the case among the 3.5-year-olds, for whom the outcome of the previous trial did not seem to have any effect (estimate = −1.038, SE = 0.499, Z = −2.080, p = .038; Fig. 4b).

Finally, we categorized all dyads according to whether they took turns on every trial, developed a turn-taking strategy over the course of the experiment, struggled to develop a clear strategy, had one partner who monopolized the rewards, or were completely unsuccessful in finding a solution. Table 1 shows that although some 3.5-year-olds developed a turn-taking strategy, none of the pairs had such a strategy from the beginning, and a number of them were unable to solve the dilemma at all. In contrast, the majority of 5-year-olds either took turns from the beginning or developed this strategy relatively quickly. Nine pairs of 5-year-olds and three pairs of 3.5-year-olds verbally agreed at some point during the test to take turns, saying things such as "now for you but next time for me, OK?" or "let's always take turns" (Table 1).

Chimpanzees' experiment

On average, the chimpanzees succeeded in delivering the reward to someone in 64% of the trials (see Fig. 2). As opposed to the dyads of 3.5-year-olds, all the chimpanzee dyads were able to cooperate for several consecutive trials, but a GLMM that included the effect of session and trial (within session) on the likelihood of success showed an effect of session, indicating that cooperation decreased as the experiment progressed (estimate = −0.62, SE = 0.187, Z = −3.305, p < .001). A closer look at the chimpanzees' behavior in the unsuccessful trials revealed that in 42% of these trials, the subjects were at the apparatus but could not agree on which side to pull, whereas in the remaining trials (58%), 1 or both

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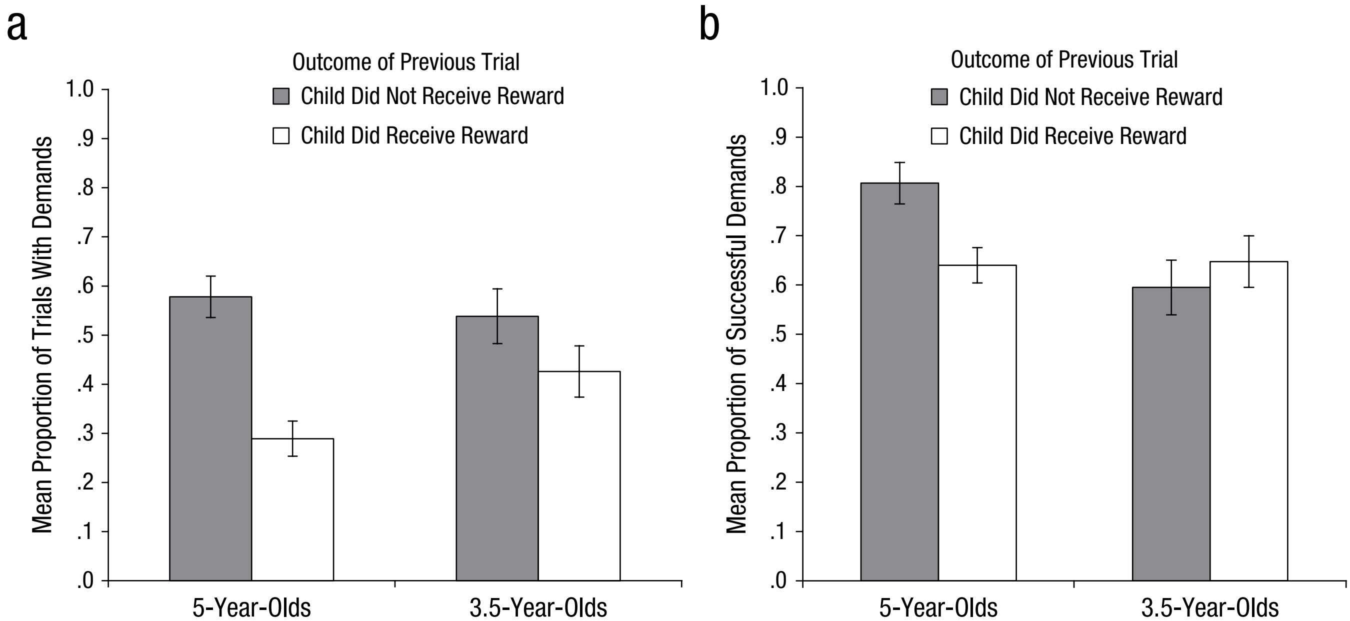

Fig. 4. Children's verbal demands to pull (to their own advantage) as a function of whether the child making the demand had or had not received the reward on the previous trial. The graph in (a) shows the mean proportion of trials on which the children made demands to pull, and the graph in (b) shows the mean proportion of demands that were successful. Results are presented separately for the 5-year-olds and the 3.5-year-olds. Error bars represent ±1 *SEM*.

subjects left the apparatus (31% and 27% of the trials, respectively). No chimpanzee pair developed a consistent turn-taking strategy. On average, the chimpanzees alternated turns on 6.1% of the trials (range = 0–23%; Fig. 2). The dyad that alternated the most alternated 10 times in total (including in 4 consecutive trials, as shown in Fig. 5; see Fig. S3 in the Supplemental Material for trial-by-trial outcomes for other dyads). Note, however, that this turn-taking pattern was observed at the beginning of the experiment and did not stabilize over time; by the end of the study, it was the same individual who obtained the rewards in all but 1 trial. A GLMM of the data from all subjects confirmed that instead of taking turns, a given individual tended to obtain the rewards on several consecutive trials (i.e., there was a significant effect of the side to which the trays were pulled on the previous trial, estimate = 4.505, $SE = 1.15$, $Z = 3.917$, $p < .001$).

Dominants did not get more food than subordinates, and dyads did not cooperate faster or slower as the study progressed (mean latency to pull = 23 s, range = 14–35 s; see Video S2 in the Supplemental Material). Although the chimpanzees used attention getters (e.g., clapping, whimpering, shaking the rope vigorously) before pulling in any direction, we did not find that these attention getters increased their likelihood of obtaining the reward (see the Supplemental Material for details on these additional analyses).

Table 1. Number of Dyads Exhibiting Different Overall Patterns in the Children's Experiment

Age group	Dyads with perfect turn taking	Dyads that developed turn taking	Struggling dyads	Monopolizing dyads	Unsuccessful dyads
5-year-olds	8 (2)	6 (5)	4 (1)	5 (1)	0
3.5-year-olds	0	2 (2)	7 (1)	7	8

Note: The table indicates the number of dyads in each of five categories: those that began taking turns immediately (perfect turn taking), those that developed a turn-taking strategy at some point and never regressed, those in which both children obtained rewards but exhibited continuous competition or discussion (struggling), those in which one child monopolized the rewards (i.e., obtained the reward in at least 75% of the trials), and those that were unable to find any kind of solution to the dilemma (unsuccessful). Note that one dyad of 5-year-olds was not included in any of the categories because of a bias to pull only to one of the sides. Although, overall, more-dominant children did not obtain more rewards than less-dominant ones, in 8 of the 12 monopolizing dyads, it was the dominant individual who obtained the majority of the rewards. The numbers in parentheses indicate the number of dyads in which at least one of the members verbally suggested taking turns at least once during the experiment.

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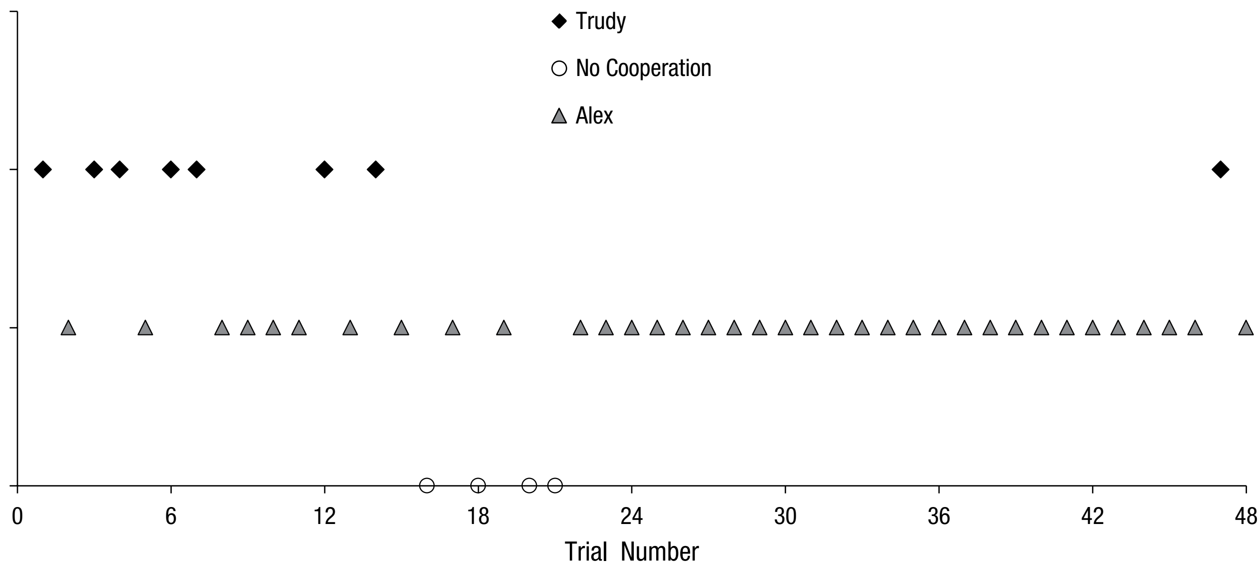

Fig. 5. Trial-by-trial outcomes of the chimpanzee dyad that alternated the most (Trudy-Alex). For each trial, the marker indicates who got the reward (or if there was no cooperation and no one did).

In an attempt to create conditions that would maximize the likelihood that the chimpanzees would take turns, we conducted a follow-up study in which alternation could take place within, rather than between, trials. That is, we blocked the reward-trap hole in the center of the apparatus, so that after one dyad member obtained a reward, the dyad could immediately pull the other tray for the other dyad member to obtain a reward. On average, subjects cooperated (so that at least one member of a dyad obtained a reward) in 59% of the trials (range = 21%–94%). However, as in the main experiment, the chimpanzees did not develop a turn-taking strategy. On average, they pulled the second tray in only 3.1% of the trials (range = 0–21%), and this strategy did not stabilize over time.

Discussion

This study shows that the capacity to establish a turn-taking strategy by accepting a short-term loss to reach a mutually satisfying long-term solution undergoes a major shift in humans between the ages of 3 and 5 years. Like the 3.5-year-olds, the chimpanzees did not develop a turn-taking strategy, even though they participated in more trials and had more opportunities to learn than the children did. Although the chimpanzees initially were successful fairly often, their levels of success decreased as the study progressed. This shows that humans, but not chimpanzees, develop in ontogeny a major mechanism to support cooperative interactions: the capacity to forgo an immediate benefit in order to balance their own desires with their partner's desires—not necessarily out of concern for the other but merely strategically. Although the children in both age groups demanded pulling to their side, only the 5-year-olds seemed to take into consideration the outcome of the previous trial; they demanded less often and complied with their partner's demands more often if they had just obtained a reward themselves (recognizing that, in some sense, it was now the partner's turn). Furthermore, a larger number of the 5-year-olds explicitly proposed to take turns, either referring to immediately upcoming trials (e.g., "next one for me, OK?") or using more general terms (e.g., "let's always take turns").

Although one could argue that the task could be solved by learning a simple rule such as "pull first to one side and then the other to get a reward," the fact that only the 5-year-olds were able to develop such a turn-taking strategy shows that learning such a rule is not simple. It is unlikely that the 3.5-year-olds and chimpanzees did not understand their partner's desires, as the children talked and the chimpanzees pulled toward their preferred side and used attention getters. It is also unlikely that the 3.5-year-olds and chimpanzees found it difficult to change their response from trial to trial, as they did so in the pretests, when there was no conflict of interest between partners. We can also conclude that language is neither sufficient nor necessary to establish a turn-taking strategy, given that the 3.5-year-olds and 5-year-olds made verbal demands at similar levels, and many of the successful pairs did not verbally agree on taking turns. The difference seemed to be in the willingness of the older children to recognize and respect the legitimacy of the partner's demands or desires.

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Although additional studies will be necessary to identify the exact psychological prerequisites for turn taking, we think that the cognitive requirements for this type of turn taking have been underestimated (see Stevens & Hauser, 2004). The task requires both individuals in the dyad to be able to inhibit immediate preferences and be willing to give up their reward on every other trial. Several skills that develop between the ages of 3 and 5 years may be particularly important for the emergence of a turn-taking strategy: for example, the ability to think about temporal sequences (linking a present action to past and future ones), the patience to wait one's turn or delay gratification, and ability to incorporate fairness considerations in the decision process (McCormack & Atance, 2011; Rochat et al., 2009).

Children at 3.5 years of age are capable of behaving more prosocially toward previously prosocial individuals than toward others (Olson & Spelke, 2008; Warneken & Tomasello, 2013). However, it seems that past-driven reciprocity is not sufficient to develop a turn-taking strategy. The developmental difference observed in this study fits well with the findings by Sebastian-Enesco and Warneken (2015). Together, these studies suggest that the capacity to anticipate how one's own behavior might influence a partner's subsequent behavior and the capacity to think about temporal sequences (McCormack & Atance, 2011) are planning and future-oriented skills needed to solve such a cooperation dilemma.

Regarding the chimpanzees' lack of a turn-taking strategy, it is important to emphasize that some individuals were capable of obtaining the rewards repeatedly, so that a certain level of cooperation was observed. However, the lack of a more balanced strategy that incentivized both individuals to continue pulling led to a decrease in cooperation over time. In another bargaining study in which chimpanzees had conflicting preferences over which tray to pull but both partners received a reward regardless of which tray was chosen (one tray had 10 rewards on one side and 1 reward on the other, whereas the other tray had 5 rewards on each side), some dyads were capable of compromising by accepting the lower (5-5) payoff in order to maintain cooperation with a partner (Melis, Hare, & Tomasello, 2009). The current task required forgoing completely a potential immediate benefit and hoping for a future return, something that may be more challenging for chimpanzees than for children because of their more limited skills in inhibitory control and planning in social contexts (Boysen, Berntson, Hannan, & Cacioppo, 1996; Carlson, Davis, & Leach, 2005; Dufour & Sterck, 2008; Stevens & Hauser, 2004).

Despite the decreasing levels of cooperation among the chimpanzees and the fact that some of the 3.5-year-olds were not able to cooperate at all, some dyads in both of these groups maintained cooperation for several trials. It is possible that some individuals of both species remained motivated to pull as long as there was a slight possibility of obtaining the reward every now and then. It is also possible that occasionally both the children and the chimpanzees were willing to do something for the partner regardless of their own reward (e.g., Brownell, Svetlova, & Nichols, 2009; Melis et al., 2011). And finally, and especially in the children's case, it is also possible that the children found the pulling task rewarding in itself. The important outcome, though, is that because neither the chimpanzees nor the younger children developed an equitable turn-taking strategy, overall cooperation levels among these subjects were lower than among the 5-year-olds.

There is naturalistic evidence suggesting that chimpanzees engage in long-term reciprocal interactions, alternating between being the donors and the recipients of prosocial actions (de Waal, 1997; Gomes, Mundry, & Boesch, 2009; Mitani, 2006). However, it is unlikely that they engage in reciprocal interactions motivated by the prospect of payback and future selfish benefits (something that is sometimes implied as an explanation for animals' altruistic behaviors, though it confuses proximate and ultimate levels of explanation; see de Waal, 2008, for a discussion on the topic). Chimpanzees' reciprocal interactions, like those of 3.5-year-olds, could be based on (a) a basic motivation to altruistically help others in certain situations (Melis et al., 2011; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Yamamoto et al., 2009) and (b) skills that allow individuals to keep track of past interactions with others via either an emotional-bookkeeping system or a more cognitively advanced mechanism, such as calculated reciprocity (de Waal, 2008; Schino & Aureli, 2009; see also Melis, Hare, & Tomasello, 2008).

This study shows that, in addition, humans at around 5 years of age come to understand the necessity to forgo an immediate benefit in order to maintain a collaborative interaction with a partner, learning about the mutual benefits of taking turns. This is extremely advantageous not only because it can solve conflict-of-interest situations in a mutually beneficial way, but also because it helps expand the range of situations in which individuals act prosocially (i.e., prosocial behavior need not necessarily be motivated by a concern for the welfare of others but may instead be motivated by anticipation of long-term cooperation). The fact that these skills in humans do not develop until age 5 suggests that turn taking requires sophisticated cognitive skills that may be lacking in chimpanzees. Future studies of human development will need to investigate further the specific cognitive skills that enable turn taking.

Action Editor

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Author Contributions

All the authors contributed to the study's design. Testing and data collection were performed by J. Kalbitz and P. Grocke. A. P. Melis and P. Grocke performed the data analysis. A. P. Melis and M. Tomasello wrote the manuscript. All the authors approved the final version of the manuscript for submission.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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