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 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 from 5 years of age human children stabilize cooperation in such cases by taking turns across instances in obtaining the 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 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 in a way that their nearest primate relatives are not.

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

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 only strategic thinking that partners need incentives to continue collaborating. This 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 a number of different collaborative activities as well (Muller & Mitani, 2005; Boesch & Boesch-Achermann, 2000), 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 (Melis, Hare, & Tomasello, 2006b; Hare, Melis, Woods, Hastings, & Wrangham, 2007). Humans, in contrast, are from a young age better adapted to collaborate acquiring resources. By age 3 human children employ different social and communicative

strategies to coordinate actions with a partner and share jointly acquired resources equally even when they could easily be monopolized (Warneken, Grafenhain, & Tomasello, 2012; Hamann, Warneken, Greenberg, & Tomasello, 2011).

Traditionally, the study of reciprocal behaviour 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. Mitani, 2006; de Waal, 1997). 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 *attitudinal reciprocity* sensu de Waal, 2000) in which individuals develop emotional attitudes towards partners based on past interactions with them, without necessarily remembering these specific interactions (Schino & Aureli, 2009; Evers et al. 2015). A cognitively more complex mechanism, which still does not require anticipation of future benefits, is *calculated reciprocity* in which individuals are capable of remembering exactly who did what to whom and when, and base their decisions to help on these past interactions (de Waal, 2008). None of these mechanisms (*attitudinal or calculated* reciprocity) necessarily involve individuals understanding the long-term consequences of reciprocation or individuals expecting partners to reciprocate in the future. Such a level of understanding may be important, or even necessary, when individuals have to compromise between their own and the 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 subjects could altruistically help one another (Brosnan et al., 2009; Yamamoto & Tanaka, 2009a, b). Both studies found mainly negative results which suggest that chimpanzees do not easily learn about the benefits of alternating favors. Therefore, naturally occurring instances of reciprocation are probably based on the simpler psychological mechanisms described above (past-driven reciprocity as in attitudinal or calculated reciprocity). However, it is also possible that the specific tasks of these studies were cognitively too demanding for chimpanzees. In particular, it is unclear whether the subjects understood fully the contingencies of the task, and whether they had enough cues to infer the recipient's goal, something crucial to elicit altruistic helping in experimental tasks (Yamamoto, Humle & Tanaka, 2009; Melis et al. 2011). For example, in 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 lack of motivation to participate in it.

Although these studies suggest that reciprocal helping to solve new problems may not come natural to chimpanzees, no studies to date have tested nonhuman primates for their ability to share collaboratively produced resources by taking turns across trials. Such a coordination task that requires collaboration despite conflicting preferences may facilitate subjects' understanding of each other's goals and the need for compromise.

In children there is evidence showing that by age 3 they engage in various forms of reciprocal helping, keeping track of past interactions and preferentially interacting and behaving prosocially towards previously helpful partners (Levitt, Weber, Clark, & McDonnell, 1985; House, Henrich, Sarnecka, & Silk, 2013; 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 (Sebastian-Enesco & Warneken, 2014; Engelmann et al., 2013; see also Robbins & Rochat, 2011). But none of these studies looked at 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 two of them worked together first to reward one and then to reward the other. Neither species has previously been tested in such a paradigm in which partners can distribute collaboratively produced rewards in "fair" ways only by taking turns being the sole beneficiary.

Methods

Children's experiment

Participants

We tested 96 preschoolers in same-sex dyads (with equal numbers of boys and girls). Half of the dyads (N=24) were 3.5-year-olds (M= 3.4 years, range= 3.3–3.67 years) and the other half (N=24) 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-year-olds were tested but not included in the final sample due to experimenter errors and one dyad not following the instructions.

Procedure

Children were tested at local day-care centres and paired with a familiar partner from their same group at the day-care centre. Each dyad was tested in two different days. In the first day we conducted a dominance test and the introduction to the apparatus, and in the second day the

actual Turn-Taking test (TT-test hereafter). We measured the dominance relationship between partners, because we hypothesized that in the absence of an alternating strategy, dominant individuals would monopolize the rewards. We assessed the dominance relationship between the two children in a dyad by observing their behaviour in the presence of toys that could be monopolized. After the dominance test, children were introduced to the rewards and the apparatus (see Figure 1). They were shown that the golden balls contained stickers inside (1 sticker per ball) and the transparent balls were empty. Children were also allowed to choose a sticker book, where they could stick the stickers. The experimenters instructed the children how to pull together in order to place the rewards in front of the access holes. In the demonstration phase, both sides of each tray were always filled equally: either with transparent empty balls (0-0) or with sticker-containing golden balls (1-1). Thus, children had no conflicting preferences regarding which tray to pull (see Figure S1 in supplemental material). The goal was to familiarize them with the cooperation task and the fact that they had to pull together and that after pulling in one direction the rewards of the second tray became inaccessible. One day later, children participated in the TT-test (1-0 vs.0-1). Pairs of either 3- or 5-year-old children were in a room by themselves facing each other with the cooperation apparatus between them For the test we placed the rewards in the apparatus in such a way that children had opposing preferences regarding which tray to pull. Each tray contained the golden balls in only one side, whereas the other side remained empty. Pulling one tray meant losing the reward of the other tray. Therefore, on a given trial one child alone could access her reward (Figure 1). Each dyad participated in one session of 24 trials. There was a break every six trials, in which children left the room while the experimenter refilled the apparatus. The side of the tray baited was counterbalanced across blocks of six trials.
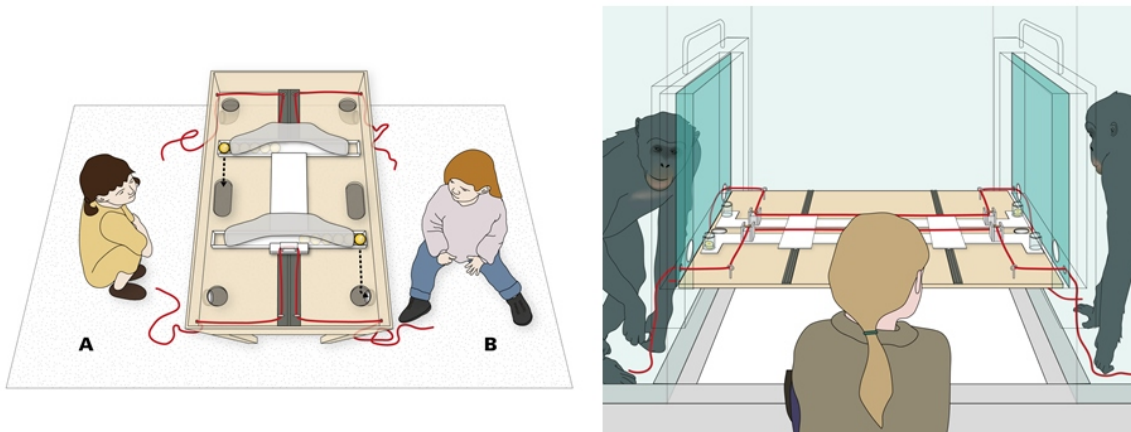
Figure 1. Schematic representation of the set-up and apparatus of the children and chimpanzees. The apparatuses consisted of two interconnected parallel trays that could be moved to the left or right from the subjects' point of view. The two individuals had to pull simultaneously on the same tray in order to align the rewards with the access holes. Once subjects pulled one tray in one direction, the reward placed on the opposite tray disappeared down the hole between the two trays (e.g. if children pulled the left tray from B's perspective, B obtained her reward, whereas A lost hers). Children received four blocks of six trials each (each trial having one obtainable reward). Chimpanzees received a total of 96 trials administered in sessions of 12 trials each.

Chimpanzees' experiment

Subjects

Twelve chimpanzees, six males and six females ranging between six and thirty-five years of age participated in this study (see Table S1 in supplemental material). All individuals were

born in captivity and were either mother or nursery reared. The chimpanzees were housed in a living area of 6159 m² at the Wolfgang-Koehler-Primate-Research-Center (WKPRC) in Leipzig Zoo, Germany. The subjects were fed according to their daily diet and water was available *ad libitum*. They were never food or water deprived for this study.

Procedure

Subjects were introduced to the cooperation apparatus and the contingencies of the task in various steps (see Figure S2 in supplemental material). First, subjects were individually familiarized with the apparatus and learned that the two ropes (one on each side of the booth) needed to be simultaneously pulled in order to make the rewards accessible. Afterwards, subjects learned the cooperative aspect of the task. Both trays were baited, so that subjects had to learn to coordinate pulling from the same tray and the fact that after pulling one tray the rewards of the 2nd tray became inaccessible. In a first step, one of the trays was baited with bananas and the other one with carrots, and in a second step, both trays were baited with bananas. Once all subjects demonstrated competence in these pretests we started the Turn-Taking test (TT-test), in which only one side of each tray was baited (1-0 vs. 0-1). The apparatus was refilled after every trial by the Experimenter. The main difference to the children study was that each chimpanzee was tested with two different partners, and that chimpanzees received a total of 96 trials (48 trials witch each partner) instead of 24 like the children. Subjects changed partners every two sessions of 12 trials each (for details see supplemental material).

Results

On average, 5-year-olds succeeded in delivering the reward to someone in 99.5% of the trials whereas 3.5-year-olds succeeded in only 62.3% of the trials (Figure 2). The lower success rate of the 3.5-year-olds was mainly due to 8 dyads which were unable to find any solution to the conflict of interests (see Supplemental Material). Furthermore, 5-year-olds regularly employed a turn-taking strategy (alternating obtaining the reward in two consecutive trials; see video and supplemental material), whereas very few 3.5-year-olds did (Figure 2).
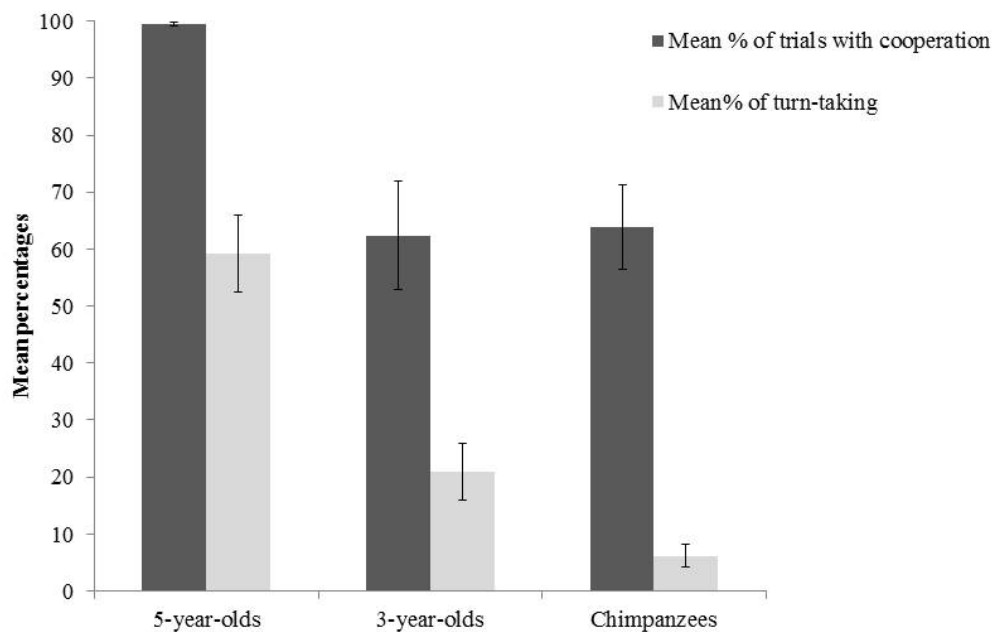
Figure 2. Mean percentage of trials (+/-SEM) cooperating (pulling together any tray) and mean percentage of trials with turn-taking (+/-SEM) among the two age groups of human children (*N*=24 for each age group) and chimpanzees (*N*=12).

We conducted a generalized linear mixed model (GLMM) with binomial error structure and logit link function that looked at the effect of age, gender and trial (and interaction of age and trial) on the likelihood of individuals taking turns in two 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 comprising only gender (likelihood ratio test: χ^2 = 9.99, df= 3, p= 0.019). There was no interaction between age and trial, but both factors were predictive as main effects: 5-year-olds exhibited more turn-taking than 3.5-year-olds (Estimate $\pm$ SE = 0.768$\pm$ 0.310, Z=2.477, p=0.013) and turn-taking increased as the study progressed (Estimate $\pm$ SE = 0.286$\pm$ 0.134, Z=2.136, p=0.033). There was no effect of gender. An analysis of dominance showed that overall dominant children did not monopolize more rewards than the less dominant ones (Estimate $\pm$ SE =-0.054 $\pm$0.438, Z=-0.124, p=0.902, see supplemental materials for details about the GLMM).

We also conducted a GLMM with negative binomial error structure and log link function to analyse the latencies to pull and the effect that age, sex and trial had on them, as well as a possible interaction between age and trial number. We included the same random effect as in the previous model (dyad identity). Overall, the full model was significant (likelihood ratio test: χ^2 = 70.5, df= 3, p< .001) in comparison to a more parsimonious model (comprising only gender). The results showed an interaction between age and trial number (Estimate $\pm$ SE= -0.309 $\pm$ 0.104, Z=-2.983, p=0.003), with the latencies among the 5-year-olds decreasing over time, whereas the latencies among the 3.5-year-olds not changing so much (Figure 3).
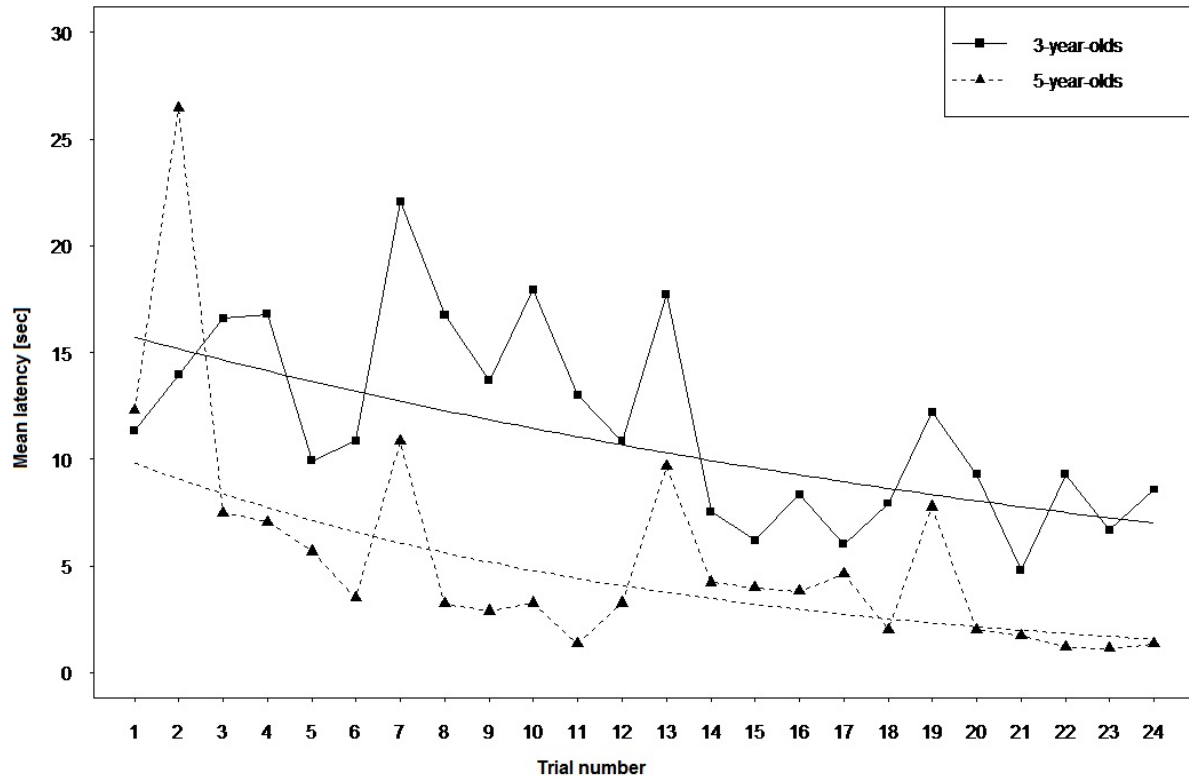
Figure 3. Trial by trial latencies to pull in the two age groups of children. Five-year-olds (*N*=24), but not three-year-olds (*N*=16), were significantly faster coming to an agreement as the study progressed. One can also see the slightly longer latencies in both age groups to come to an agreement on the first trial of each session (Trials 7, 13 and 19).

The difference in behaviour between the two age groups also became apparent after analysing the verbal demands to pull to their own advantage (e.g. "here", while pointing/indicating their side, "my side"). We predicted that if children were sensitive to the balance between what the two partners were getting, and were not just trying to convince the other to pull continuously for them, they should demand more, and demands should be more successful, following trials in which the other obtained the rewards (i.e., the demand was not for

more but that "It is my turn now"). Two GLMMs revealed an interaction between age and previous trial's success. The younger children made demands independently of whether they obtained the reward in the previous trial, whereas 5-year-olds made less demands after a previous successful trial (Estimate ± SE= -1.166 ± 0.398, Z=-2.931, p=0.003; Figure 4a), and the likelihood of a demand being successful when children had not obtained the reward in the previous trial was higher among the 5-year-olds than the 3.5-year-olds (Estimate ± SE= -1.038 ± 0.499, Z=-2.080, p=0.038; Figure 4b).
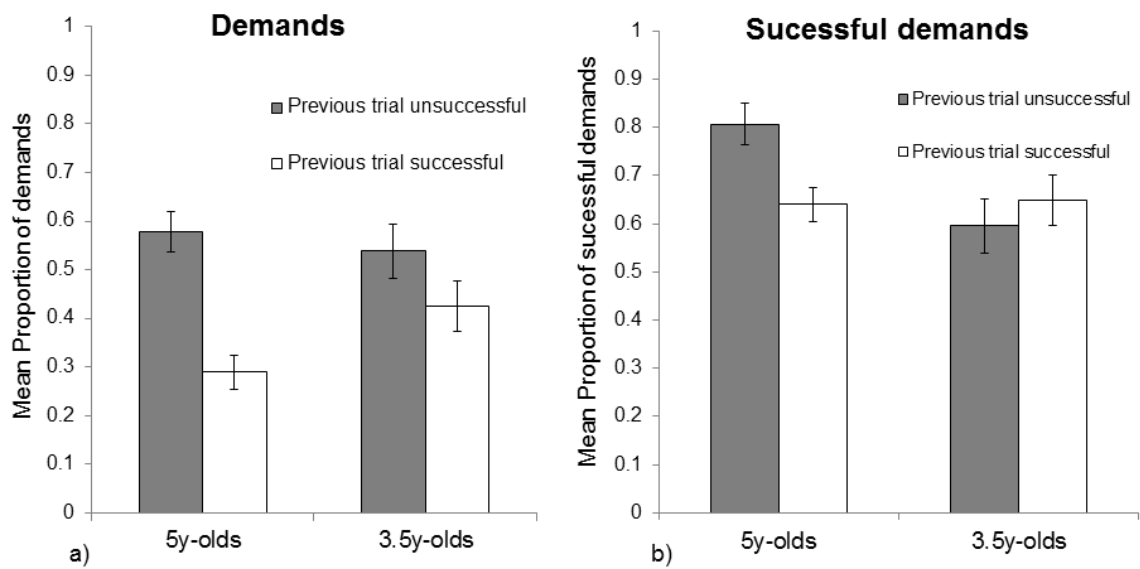
Figure 4. a) Verbal demands to pull to their own advantage and b) successful demands depending on whether in the previous trial the "demanding" child had obtained the reward.

Finally, we categorized all dyads from perfect turn-takers to unsuccessful pairs. Table 1 shows that although some 3.5-year-olds developed a turn-taking strategy, none of the pairs did it 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 the 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. Number of dyads exhibiting different overall patterns between perfect turn-taking and no success (no cooperation on any trial). The numbers in parenthesis indicate the number of dyads verbally suggesting to take turns (at least once during the study). One dyad of 5-year-olds was not included in any of the categories below due to their side bias pulling. The turn-taking-developers started at some point and finished the study taking turns (once they began taking turns they never regressed). The struggling pairs are pairs without a clear strategy, in which both children in the dyad obtained rewards, but there was continuous competition and/or discussion between them. The monopolizers are pairs in which one child obtained the rewards in at least 75% of the trials. The unsuccessful dyads were unable to find any kind of solution to the dilemma during the first block of trials. Although, overall, more dominant children did not monopolize more rewards than less dominant ones, in 8 out of the 12 monopolizing dyads it was the dominant individual who monopolized the majority of the rewards.

Age	Perfect Turn-taking	Turn-taking developers	Struggling pairs	Monopolizing	Unsuccessful
5-year-olds	8 (2)	6 (5)	4 (1)	5 (1)	0
3.5-year-olds	0	2 (2)	7 (1)	7	8

On average chimpanzees succeeded in delivering the reward to someone in 64% of the trials (see Figure 2). As opposed to the 3.5-year-olds, all 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 study progressed (Estimate ± SE = -0.62 ± 0.187, Z= -3.305, p < 0.001). A closer look at the chimpanzees' behavior in the unsuccessful trials revealed that in 42% of these trials subjects were at the apparatus but could not agree which side to pull, whereas in the remaining trials (58%) one or both subjects left the apparatus (31% and 27% of the trials respectively). No chimpanzee pair developed a consistent turn-taking strategy. The average of alternating turns exhibited by the chimpanzees was 6.1% (Range: 0-23%, Figure 2). The dyad that alternated the most, alternated 10 times in total (four of them in consecutive trials, see Figure 5 and supplemental material for examples of other dyads), but this turn-taking pattern was observed at the beginning of the study and did not stabilize over time; by the end of the study it was the same individual who obtained the rewards in all trials. A GLMM confirmed that instead of alternating, the same individual tended to obtain the rewards on several consecutive trials (Significant effect of previous trial, Estimate ± SE= 4.505 ± 1.15, Z= 3.917, p< 0.001).
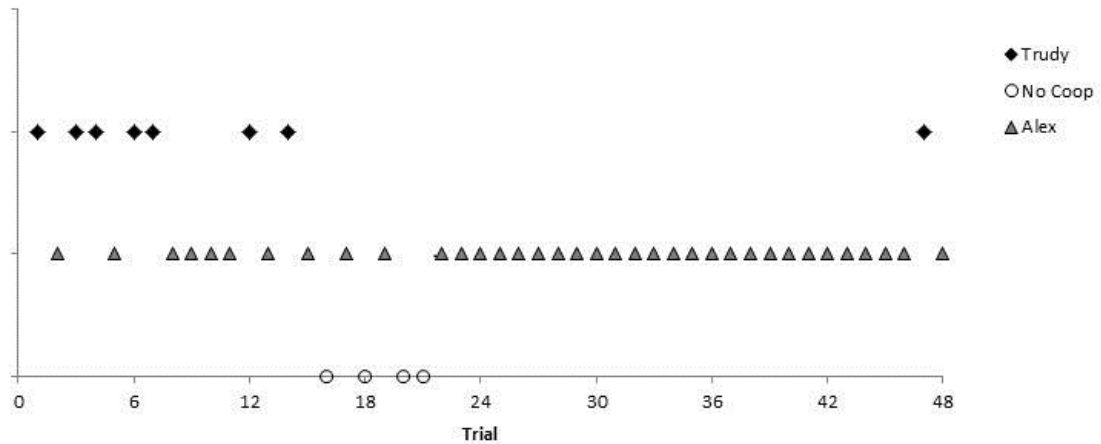
Figure 5. Trial by trial outcome of the dyad that alternated the most (Trudy-Alex). Markers indicate who got the reward. The two subjects alternated the most in the first session, but this pattern did not stabilize with increasing number of trials.

Dominants did not get more food than subordinates, and dyads did not cooperate faster or slower as the study progressed (Latency to pull: Mean= 23s, Range=14-35s, see video in Supplemental material). Although 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 subjects' likelihood of obtaining the reward (see supplemental material for details on these additional analyses).

To attempt to maximize conditions for the chimpanzees, we conducted a follow-up study in which alternation could take place within, rather than between, trials. That is, we blocked the food-trap hole in the center of the apparatus, so that after obtaining one of the rewards, dyads could immediately pull the other tray and obtain the partner's reward. On average subjects cooperated in 59% of the trials (Range=21%-94%). However, as in the main condition, chimpanzees did not develop a turn-taking strategy. On average subjects reciprocated their

partner (pulling the 2nd 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. Similar to 3-year-olds, the chimpanzees did not develop a turn-taking strategy even though they participated in a higher number of trials and had more opportunities to learn than the children. Although chimpanzees initially were successful fairly often, 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 forego 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 children at both ages demanded pulling to their side, only 5-year-olds seemed to take into consideration the outcome of the previous trial; demanding less and complying with the 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 5-year-olds explicitly proposed to take turns, referring to future trials, either immediate ones as in "next one for me, ok?" or in general terms "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 5-year-olds are able to develop such a turn-taking strategy shows that learning such a rule is not simple. It is unlikely

that 3-year-olds and chimpanzees did not understand their partner's desires, since children talked and chimpanzees pulled towards their preferred side and used attention getters. It is also unlikely that 3-year-olds and chimpanzees found it difficult to change their response from trial to trial, since they did it in the pretests when there was no conflict of interests between partners. We can also conclude that language is neither sufficient nor necessary to establish a turn-taking strategy, since children made verbal demands at similar levels at both ages 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.

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 3 and 5 years may be particularly important for the emergence of a turn-taking strategy, such as ability to think about temporal sequences (linking a present action to past and future ones), patience to wait one's turn or delay of gratification, and fairness considerations (McCormack & Atance, 2011; Rochat, Dias, Guo, Broesch, Passos-Ferreira, Winning, & Berg, 2009).

Children at 3.5 years of age are capable of behaving more prosocially towards previously prosocial individuals (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 & Warneken (2015), suggesting that the capacity to anticipate how one's own behavior might influence the 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 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 (10-1 vs. 5-5), some dyads were capable of compromising by accepting the lower (5-5) payoff to maintain cooperation with a partner (Melis, Hare & Tomasello, 2009). The current task required foregoing completely a potential immediate benefit and hoping for future return, something which may be more challenging for chimpanzees than children, due to their more limited skills in inhibitory control and their more limited skills for 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-year-olds were not able to cooperate at all, both 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 subjects of both species were willing to do something for the partner (e.g. Brownell et al. 2009, Melis et al. 2011). And finally, and especially in the children's case, it is also possible that children found the pulling task rewarding in itself. The important outcome, though, is that since neither chimpanzees nor young children developed an equitable turn-taking strategy, overall cooperation levels among these participants were lower than among 5-year-olds.

There is naturalistic evidence suggesting that chimpanzees engage in long-term reciprocal interactions, alternating being the donors and recipients of prosocial actions (Mitani, 2006; de Waal, 1997; Gomes, Mundry, & Boesch, 2009). However, it is unlikely that they engage in reciprocal interactions motivated by the prospect of payback and future selfish benefits (something which is sometimes implied as an alternative explanation for animals' altruistic behaviours, confusing proximate and ultimate levels of explanation, see de Waal, 2008 for a discussion on the topic). Similar to 3.5-year-olds, their reciprocal interactions could be based on 1) a basic motivation to altruistically help others in certain situations (Warneken et al. 2007, Yamamoto, Humle & Tanaka, 2009; Melis, Warneken, Schneider, Jensen, Call & Tomasello, 2011) and 2) skills that allow individuals to keep track of past interactions with others either via an *emotional bookkeeping* system or a more cognitively advanced mechanism as in *calculated reciprocity* (de Waal, 2008; Schino & Aureli, 2009; see also Melis, Hare & Tomasello, 2008).

This study shows that humans, on top of that, at around 5 years of age, come to understand the necessity to forego an immediate benefit to maintain a collaborative interaction with a partner, learning about the mutual benefits of taking turns. This is extremely advantageous not just to 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, not necessarily motivated by a concern for the welfare of others but in 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 which may be lacking in chimpanzees. Future human developmental studies will need to investigate further the specific cognitive skills that enable turn-taking.

References

Boesch, C. and H. Boesch-Achermann, (2000). *The Chimpanzees of the Tai Forest.* (Oxford
Univ. Press.

Boysen ST, Berntson GG, Hannan MB, Cacioppo JT (1996). Quantity-based interference and
symbolic representations in chimpanzees (Pan troglodytes*). Journal of Experimental
Psychology: Animal Behavior Processes, 22*, 76–86.

Brosnan, S. F. & de Waal, F. B. M. (2014). Evolution of responses to (un)fairness. *Science.*
doi:10.1126/science.1251776.

Brosnan, Sarah Frances; Silk, Joan B.; Henrich, Joseph; Mareno, Mary Catherine; Lambeth,
Susan P.; & Schapiro, Steven J. (2009). Chimpanzees (Pan troglodytes) do not develop
contingent reciprocity in an experimental task. *Animal Cognition*, *12*(4), 587-597.

Carlson, S.M., Davis, A.C. & Leach, J.G. (2005). Less is more. Executive Function and
Symbolic Representation on Young Children. *Psychological Science,16*, 609-616.

de Waal, F. B. M. (2000). Attitudinal reciprocity in food sharing among brown capuchin
monkeys. *Animal Behaviour, 60*: 253-361.

de Waal, F. B. M. (2007). The chimpanzee's service economy: food for grooming. *Evolution and
Human Behavior, 18*, 375-386.

de Waal, F. B. M. (2008). Putting the Altruism Back into Altruism: The Evolution of Empathy.
Annual Review of Psychology, 59, 279–300.

Dufour, V. & Sterck, E. H. M. (2008). Chimpanzees fail to plan in an exchange task but succeed
in a tool-using procedure. *Behavioural Processes*, *79*, 19-27.

Evers, E., de Vries, H., Spruijt, B. M., & Sterck, E. H. M. (2015). Emotional Bookkeeping and High Partner Selectivity Are Necessary for the Emergence of Partner-Specific Reciprocal Affiliation in an Agent-Based Model of Primate Groups. *PLoS ONE*, *10*(3), e0118921.

Gilby, I. C. (2006). Meat Sharing among the Gombe Chimpanzees: Harassment and Reciprocal Exchange." *Animal Behaviour*, *71*, 953-963.

Gomes, C. M., R. Mundry and C. Boesch. Long-term reciprocation of grooming in wild West African chimpanzees (2009). *Proccedings of the Royal Society, Series B: Biological Sciences*, *276,* 699-706.

Hamann, K., F. Warneken, J. R. Greenberg and M. Tomasello. (2011). Collaboration Encourages Equal Sharing in Children but Not in Chimpanzees. *Nature, 476*, 328-31.

Hare, B., A. P. Melis, V. Woods, S. Hastings and R. Wrangham. (2007) Tolerance Allows Bonobos to Outperform Chimpanzees on a Cooperative Task. *Current Biology, 17*, 619-23.

House, B., Henrich, J., Sarnecka, B., & Silk, J.B. (2013). The development of contingent reciprocity in children. *Evolution and Human Behavior*, *34*, 86–93.

Levitt, M. J., Weber, R. A., Clark, M. C., & McDonnell, P. (1985). Reciprocity of exchange in toddler sharing behavior. *Developmental Psychology, 21*, 122–123.

McCormack, T., & Atance, C. M. (2011). Planning in young children: A review and synthesis. *Developmental Review*, *31*, 1–31.

Melis, A.P. and Tomasello, M. (2013). Chimpanzees' strategic helping in a collaborative task. *Biology Letters, 13*.

Melis, A.P., B. Hare, and M. Tomasello, (2006a). Chimpanzees recruit the best collaborators. *Science*, *311*, 1297-300.

Melis, A. P., B. Hare and Tomasello, M. (2006b). Engineering Cooperation in Chimpanzees: Tolerance Constraints on Cooperation. *Animal Behaviour, 72*, 275–286.

Melis, A.P., Hare, B., & Tomasello, M. (2009). Chimpanzees coordinate in a negotiation game. *Evolution and Human Behavior, 30*, 381-392.

Mitani, J. C. (2006). Reciprocal exchange in chimpanzees and other primates. In: *Cooperation in Primates and Humans. Mechanisms and Evolution* (Ed. by P. M. Kappeler & C. P. van Schaik), pp.107-119 (Berlin: Springer-Verlag).

Muller, M.N. and J.C. Mitani, (2005). Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior, 35*, 275-331.

Neill, D. B. Cooperation and coordination in the Turn-Taking Dilemma (2003). *Proceedings of the Ninth Conference on Theoretical Aspects of Rationality and Knowledge*: 231-244.

Nowak, M.A. and Sigmund, K. (1994). "The alternating prisoner's dilemma," *Journal of Theoretical Biology, 168*, 219-226.

Rawls, J. (1971) *A theory of justice* (Harvard University Press).

Robbins, E. & Rochat, P. (2011). Emerging signs of strong reciprocity in human ontogeny. *Frontiers in Psychology, 2(353)*, 1-14.

Rochat, P., Dias, M.D.G., Guo, L., Broesch, T., Passos-Ferreira, C., Winning, A. & Berg, B. (2009). Fairness in distributive justice by 3- and 5-year-olds across seven cultures. *Journal of Cross-Cultural Psychology, 40*, 416–442.

Schino, G., & Aureli, F. (2009). Reciprocal altruism in primates: Partner choice, cognition, and emotions. *Advances in the Study of Behavior, 39*, 45–69.

Sebastian-Enesco, C. & Warneken, M. (2015). The shadow of the future: 5-Year-olds, but not 3-year-olds, adjust their sharing in anticipation of reciprocation. *Journal of Experimental Child Psychology*, *129*, 40–54.

Stevens, J. R. & Hauser, M. D. (2004). Why be nice? Psychological constraints on the evolution of cooperation. *Trends in Cognitive Sciences*, *8*, 60-65.

Tomasello, M. (2009) Why We Cooperate (MIT Press).

Warneken, F., & Tomasello, M. (2013). The emergence of contingent reciprocity in young children. *Journal of Experimental Child Psychology*, *116*, 338–350.

Warneken, F., M. Grafenhain and M. Tomasello. (2012). Collaborative Partner or Social Tool? New Evidence for Young Children's Understanding of Joint Intentions in Collaborative Activities. *Developmental Science, 15*, 54-61.

Warneken, F., Hare, B., Melis, A. P., Hanus, D. & Tomasello, M. (2007) Spontaneous altruism by chimpanzees and young children. *PLoS Biology*, 5, 184.doi:10.1371/journal.pbio.0050184

Yamamoto S, Tanaka M. (2009a) Do chimpanzees (*Pan troglodytes*) spontaneously take turns in a reciprocal cooperation task? *Journal of Comparative Psychology. 123*, 242–249.

Yamamoto S, Tanaka M. (2009b) Selfish strategies develop in social problem situations in chimpanzee (*Pan troglodytes*) mother–infant pairs. *Animal Cognition*, *12(1),* S27-S36.

Yamamoto S, Humle, T. & Tanaka M. (2009).) Chimpanzees help each other upon request *PLoS ONE, 4 (*10): e7416