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Differences in cognitive processes underlying the collaborative activities of children and chimpanzees

Grace E. Fletcher [a,*], Felix Warneken [a,b], Michael Tomasello [a]

[a] Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
[b] Department of Psychology, Harvard University, Cambridge, MA, United States

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ABSTRACT

We compared the performance of 3- and 5-year-old children with that of chimpanzees in two tasks requiring collaboration via complementary roles. In both tasks, children and chimpanzees were able to coordinate two complementary roles with peers and solve the problem cooperatively. This is the first experimental demonstration of the coordination of complementary roles in chimpanzees. In the second task, neither species was skillful at waiting for a partner to be positioned appropriately before beginning (although children did hesitate significantly longer when the partner was absent). The main difference between species in both tasks was in children's, but not chimpanzees', ability to profit from experience as a collaborator in one role when later reversing roles. This difference suggests that as they participate in a collaboration, young children integrate both roles into a single "birds-eye-view" representational format in a way that chimpanzees do not.

Humans collaborate with one another in various ways, often with complex behavioral coordination involving a division of labor among multiple partners toward a joint goal. Nonhuman animals engage in certain forms of collaborative activities as well, such as bees and ants coordinating their movements in elaborate ways to build nests and gather foods (Dugatkin, 1997), lionesses coordinating their actions to hunt mammals which could not be acquired otherwise (Packer & Ruttan, 1988), and chimpanzees coordinating actions while hunting monkeys (Boesch & Boesch, 1989). Yet it is likely that important underlying cognitive differences exist between human collaboration and that of other animals.

* Corresponding author at: Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103, Leipzig, Germany.
E-mail address: fnkymnky7@gmail.com (G.E. Fletcher).

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Boesch and Boesch (1989) claimed that chimpanzees' group hunting is comparable to human collaboration in that there exists a joint goal and complementary roles, such as chaser, blocker, and ambusher. Tomasello, Carpenter, Call, Behne, and Moll (2005), in contrast, proposed that chimpanzee group hunting is not human-like in the sense that it does not comprise humans' characteristic dual-structure, involving both a joint goal and complementary roles defining joint collaborative activities. Rather, chimpanzee group hunting can be more parsimoniously explained as each individual chimpanzee acting for itself, with behavioral coordination resulting from individuals reacting to others' hunters' behavior in an attempt to maximize their own chances of success. Thus, these chimpanzees collaborate in a broad sense because they achieve a goal that neither one could have achieved alone, but they do not necessarily engage therein as a joint collaborative activity. There is thus neither a joint goal, in the sense that "we" are hunting the monkey together, nor any specific roles in the sense that we each play our own part in pursuing that joint goal.

In experimental studies of chimpanzee collaboration, the most complex behavior so far demonstrated is two chimpanzees pulling an object in parallel (Chalmeau & Gallo, 1996; Crawford, 1937; Hirata & Fuwa, 2007; Melis, Hare, & Tomasello, 2006a, 2006b). Chimpanzees are fairly good at this activity, including waiting for a partner to approach the apparatus (Hirata & Fuwa, 2007) and actively recruiting a partner by opening a door so that the other can enter and both can pull together (Melis et al., 2006a). However, experiments aimed at addressing whether chimpanzees perform these actions with a joint goal in mind have yielded negative conclusions, based on the fact that when a collaboration is interrupted chimpanzees do not attempt to re-engage the partner, as human children do (Warneken, Chen, & Tomasello, 2006); moreover, when one lucky partner gets its reward first, chimpanzees do not follow through in their commitment to collaborate, as do human children (Greenberg, Hamann, Warneken, & Tomasello, 2010; Hamann, Warneken, & Tomasello, 2011).

A key issue not addressed in these studies is whether chimpanzees are able to engage in tasks with complementary roles and to understand these roles as part of a joint collaborative activity. Although studies testing human-raised chimpanzees in interactions with humans have shown that they can perform either of two different complementary actions when scaffolded by the human (Warneken et al., 2006), no experimental studies have investigated whether two chimpanzees can spontaneously (without training) collaborate with complementary roles on their own (see Povinelli, Nelson, & Boysen, 1992, regarding role comprehension in human-chimpanzee dyads and Savage-Rumabugh, Rumbaugh, & Boysen, 1978, regarding role comprehension in two extensively language-trained chimpanzees). Consequently, it is unclear whether in their collaborations chimpanzees can do such things as spontaneously divide labor into roles and engage in spontaneous role-reversal.

Several experimental studies of children's collaboration have found a major shift toward the end of the second year of life in the ability to coordinate roles successfully in joint games or problem-solving tasks in interactions with both adults and peers (Eckerman & Peterman, 2001). This coordination includes collaborative interactions with complementary roles, in which interactants perform different but interrelated actions, such as one child operating a lever so that another child may access it (Brownell & Carriger, 1991) or sending a toy down a tube so that the partner can catch it with a can (Warneken et al., 2006). Children by two years of age are attentive to the other's involvement in the task, as they try to re-engage a partner who is interrupting the activity and are able to perform both complementary roles.

A key unaddressed issue is the degree to which children represent the social situation from a 'bird's eye view' perspective, coordinating the behaviors successfully not just because they react appropriately to the concurrent behaviors of the partner, but because they represent both actions as part of an overarching joint collaborative activity with interrelated roles. Such understanding enables partners to engage in role-reversal, as carrying out one role entails mental representation of the other role. To date, experiments involving various tasks have addressed whether or not infants and young children are able simply to switch between two complementary roles. In simple and highly routinized interactions with adults, infants as young as 14 months switch roles in games such as peek-a-boo (Ratner & Bruner, 1978); when scaffolded by an adult, infants of the same age engage in role-reversal in novel tasks, such as one person holding out a plate so the other person can place a toy on top (Carpenter, Tomasello, & Striano, 2005). When interacting with peers in the absence of concurrent adult scaffolding, however, children as old as 3 years of age have trouble coordinating and switching between roles in problem-solving tasks requiring division of labor (Ashley & Tomasello, 1998). While these studies clearly show that young children are sometimes able to flexibly reverse roles in collaborative activities, especially with adults, they do not address whether and to what degree young children truly understand both roles of a collaboration simultaneously, enabling them to coordinate and reverse complementary roles.

In the studies presented here we therefore studied pairs of 3- and 5-year-old children and pairs of chimpanzees in tasks requiring them to coordinate two distinct and complementary action patterns in order to receive a reward. In the task used in Study 1, participants had to work toward the release of a reward by performing two complementary roles in an alternating sequence. To assess role-reversal, participants were given the opportunity to perform both roles. In two conditions (Cooperative & Role-Reversal), roles were predetermined and constrained, whereas in another condition (Division of Labor) performance was unconstrained. By employing forced roles which were then reversed, we were able to directly compare the performance of both partners during role-reversal, enabling us to assess whether 3 and 5 year old human children and chimpanzees had used their understanding of the other's role in performing their new role. In Study 2, the same pairs were introduced to a related but more complex problem-solving task in which two actions were temporally dependent upon one another, such that participants had to appropriately time their behavior with one another to successfully retrieve a reward. The same role conditions used in Study 1 were included. Again, our major question was the degree to which children and chimpanzees, in mastering a new role in a collaborative activity, benefitted from having played the other role in the activity previously.

1. Study 1a

In this study, we assessed 3 and 5-year-olds' skills in coordinating complementary roles in a peer cooperative problem-solving activity, including their ability to reverse roles and effectively divide the labor between them. Given previous research showing that infants between 12 and 18 months of age engage in collaborative games with complementary roles and by 24 months engage with peers in collaborative activities with joint goals (Brownell & Carriger, 1991; Hamann et al., 2011; Warneken et al., 2006), we hypothesized that both 3 and 5-year-olds would not only be able to solve a cooperative reward-acquisition task using complementary roles but also would engage in role-reversal, with the second child to perform a role showing a higher level of proficiency than the first child who had performed the same role.

1.1. Method

1.1.1. Participants

Participants were 56 children (28 dyads/14 dyads per age group) from two age groups. Mean age of one group was 3.6 years (range 3.4–3.8; $N = 28$; 14 girls) and mean age of the other 5.6 years (range 5.4–5.8; $N = 28$; 14 girls). Same-aged pairs were formed by pairing children who were friends or enjoyed playing together. Eight pairs were of mixed sex and 20 pairs were of the same sex (10 female and 10 male pairs).

Children were recruited from a database of parents who volunteered to participate in psychological studies. All children were seen in their regular kindergarten for a single testing session which lasted approximately 20–30 min. They were all native German speakers and came from heterogeneous socioeconomic backgrounds.

1.1.2. Materials

A collaboration apparatus (110 cm × 8 cm × 72 cm) required children to obtain a reward by performing complementary roles (Fig. 1). To successfully obtain the reward, one child had to initiate the trial by launching a red billiard ball down a ramp which rolled until it reached a spring-loaded door. At this point, the second child had to push back the door, thus revealing a hole through which the ball dropped. As the apparatus included three consecutive tiers, both children had to complete their role three times (Role A–Role B–Role A–Role B–Role A–Role B), after which the ball dropped through a tunnel thereby knocking off two rewards – one directed at each child. Rewards were marbles that each

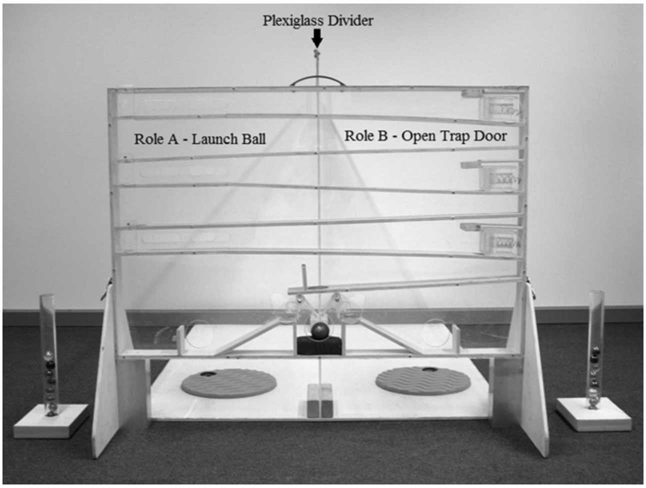

Fig. 1. Three-tiered "Marble-Run" game used in Study 1a. One member of pair rolls a ball down a ramp (left side of apparatus) and the other opens a spring-loaded door (right side of apparatus). A replica with minor modifications (dimension and material) was attached to the outside of two adjacent enclosures for use with chimpanzees in Study 1b.

child could collect by dropping them into their own clear tube, thereby creating a "Marble Tower". Piloting confirmed that collection of marbles to build the tower was sufficiently motivating. Aside from the marbles, children received no additional reward for participating.

As the children were tested in an open room located within their kindergarten, the apparatus was placed on the floor with a large plexiglass panel (130 cm × 100 cm) acting as a divider which ensured that each child remained on their assigned side of the apparatus. Children could perform their roles simply by inserting their fingers into holes on their side of the apparatus.

1.1.3. Design

Children participated in pairs and experienced the same three experimental conditions in a pre-determined order and always in the same sequence – Cooperative condition, Role-Reversal condition and Division-of-Labor condition – each followed by a Non-reward control condition.

Cooperative condition. In this condition, child A was located on the left half of the apparatus (initiation of ball rolling) while child B was located on the right half (opening of door trap). They could only obtain their individual rewards by completing their action in the proper sequence and on the proper level. It was impossible for a single child to perform both actions sequentially as the plexiglass divider was in place.

Role-Reversal condition. This condition is the same as the Cooperative condition, except that children exchanged places/roles (child A on right half and child B on left half of apparatus). Once again the plexiglass divider remained in place ensuring both children stayed on the assigned half of the apparatus.

Division-of-Labor condition. In contrast to the other two conditions, the plexiglass divider was removed. As before, one child had to initiate the rolling of the ball and the other had to open the door revealing the hole below. However there were no assigned roles.

Non-reward condition. In this condition, no marbles were present. This condition followed each experimental condition and was precisely the same in form as the experimental condition it followed.

Children experienced the sequence of conditions within a single testing session; length of the session depended upon how quickly the pairs were able to complete each condition (range was 15–30 min).

1.1.4. Procedure

Children were brought to an unoccupied room and introduced to the marble towers. They were prompted to put the marbles in the towers themselves. The experimenter then clarified that the marbles for the towers could only be collected from the apparatus and suggested that each child place themselves behind the apparatus, allowing children to choose their sides. Once the children were in place, the experimenter placed the marbles in the apparatus and then placed the ball on the lowest level, after which she demonstrated the functioning of the apparatus – initiating the rolling of the ball and then the opening of the trap door – using similar holes on the front side of the apparatus. The experimenter repeated this action three times, allowing the children to collect the marbles and place them in the respective marble towers.

The pair then completed as many trials as necessary to reach a criterion of three successful consecutive trials, at which point the pair was deemed proficient at the task. The experimenter then placed the ball on the middle level for four trials and then the top level for four trials, with pairs working their way up the apparatus. After the pair had completed the four trials from the top level of the apparatus, the first experimental condition (Cooperative condition) began. It consisted of four trials, with each participant allowed 30 s to complete their action. Pairs then underwent another four trials in which they no longer received marbles (Non-reward condition). If after 30 s one of the individuals did not complete their action, the trial was considered over, at which point the experimenter removed the ball from the apparatus.

Next, the pair exchanged places so that the roles each had to complete were reversed (Role-Reversal condition). This condition also consisted of four trials, with a 30-s maximum each to complete the respective action. Pairs then underwent another four trials in which they no longer received marbles (second Non-reward condition). Next, the plexiglass panel which separated the two halves was removed, allowing children to choose which action to complete on their own (Division-of-Labor condition). This condition again consisted of four trials, with a 30-s maximum each to complete the respective action. To be successful in this condition, the pair had to divide the labor between them but were free to do so however and how often they chose. Pairs then underwent another four trials in which they no longer received marbles (third Non-reward condition).

1.1.5. Coding

All sessions were videotaped and coded from tape by the first author. For each trial we coded (1) success (defined as releasing the reward at the bottom of the apparatus), (2) latencies from the beginning of a trial to the end of the trial, and (3) latencies from the beginning of Role B to the completion of Role B. All latencies were timed second by second. To assess interrater reliability, a second coder blind to the purpose of the study independently coded all of the conditions for 25% of all test pairings. The reliability for the category success was perfect ($K = 1.0$). For the trials to success and the latencies Pearson's r was calculated and reliability was excellent ($r = 1.0$).

1.2. Results

1.2.1. Main analyses

Both 3.6 and 5.6-year-olds solved the task successfully in 94% and 100%, respectively, of experimental trials, across all conditions. Summed across conditions, 5.6-year-olds completed significantly more trials when a reward was present than when it was absent, $t(13) = 2.14$, $p = .05$, while the 3.6-year-olds showed no difference between rewarded trials and non-rewarded trials (Fig. 2). Furthermore, 5.6-year-olds took significantly less time to complete rewarded trials (26.5 s) than unrewarded trials (29.5 s), $t(13) = 2.09$, $p = .05$, whereas the 3.6-year-olds were just as quick to complete a trial that was not rewarded (37.4 s) as one that was (35.0 s).

To assess children's ability to reverse roles, we conducted two analyses, one of performance in the Role-Reversal condition only and one of the difference between the proficiency of the first and second child in completing Role B (opening of the trap door). Both age groups were successful in completing the task after their roles had been reversed, with 11 of 14 3.6-year-old pairs and all 14 5.6-year-old pairs succeeding. A paired-samples t-test revealed that the 3.6 year olds did not show any decrease in the amount of time it took to complete Role B, with the second child requiring just as much time as the

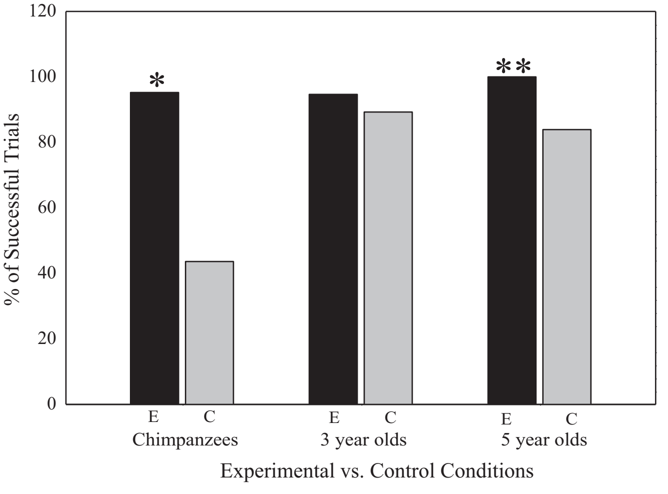

Fig. 2. Percentage of successful trials in experimental and control (Non-reward) conditions (Study 1). **p* < .01, ***p* < .05.

first child (roughly 3 s; *M* = 2.7, SD = 2.0). However, the 5.6-year-olds did show a significant decrease in the time required to complete Role B, $t(13) = 2.23$, $p < .05$, with the second child needing only half the amount of time required by the first child (*M* = 1.5 and *M* = 0.8 s, respectively; Table 1).

In the Division-of-Labor condition, when no roles were assigned and children could move freely about the apparatus, both age groups divided the labor appropriately and all pairs were successful in cooperatively solving the task. Furthermore, both age groups were equally swift to successfully complete a trial when they had to divide their labor on their own as when the roles were predetermined – among the younger group, *M* = 35.1 and *M* = 30.8, respectively; among the older group, *M* = 26.0 and *M* = 26.7 s, respectively.

1.2.2. Secondary analyses

Neither gender nor gender composition of the pair (same sex or mixed sex) among either age group had an effect on success rate in using complementary roles to cooperatively solve the task. However, there was an effect of gender in latency of the first child to complete Role B. At both ages, boys required less time to open the spring-loaded door (*M* = 1.5 s and *M* = 1.04 s for the younger and older groups, respectively) than their female counterparts (*M* = 2.9 s and *M* = 2.0 s for the younger and older groups respectively, $F(1,8) = 6.19$, $p < .05$; 5.6 year olds, $F(1,8) = 5.92$, $p < .05$). This gender difference disappeared once the pair reversed roles, with females and males of either age group requiring the same amount of time to complete Role B.

The only significant effect of age was in overall proficiency. During training, the 5.6-year-olds required significantly fewer trials to reach criterion of 3 consecutive trials with success (*M* = 4 trials) than did the 3.6-year-olds (*M* = 7 trials), $F(1,26) = 21.83$, $p < .001$. Additionally, the 5.6-year-olds were significantly faster to complete a trial (3.6 years *M* = 35 s; 5.6 years *M* = 26.5 s), $F(1, 26) = 16.75$, $p < .001$,

Table 1
Average duration (s) to perform Role B for 1st and 2nd members of pair (Study 1).

	1st individual	2nd individual	Paired *t*-test *p*-value	*N*
Chimpanzees	6.4 (SD 7.22)	3.5 (SD 3.17)	.188	14
3 year olds	2.8 (SD 1.69)	2.7 (SD 1.98)	.913	28
5 years olds	1.5 (SD 0.83)	0.8 (SD 1.44)	.043*	28

Note. Standard deviations appear in parentheses.
"*" refers to statistical significance.

and needed significantly less time to complete either Role A (3.6 years $M = 4.8$ s; 5.6 years $M = 3.2$ s), $F(1, 25) = 7.19$, $p = .01$, or Role B (3.6 years $M = 2.9$ s, 5.6 years $M = .8$ s), $F(1, 25) = 10.61$, $p < .005$. The 5.6-year-olds were significantly faster to complete a trial in each of the conditions (Cooperative condition, 10 s faster, $p < .001$; Role-Reversal condition 10 s faster, $p < .005$; Division-of-Labor condition, 5 s faster, $p = .05$), despite the fact that the 3.6-year-olds' performance improved from first to last condition, $t(12) = 3.21$, $p < .01$, whereas the 5.6-year-olds' performance remained the same across conditions ($M = 26.5$ s).

2. Study 1b

A number of studies have shown that chimpanzees are quite skilled at coordinating parallel roles in order to cooperatively solve a task (Chalmeau & Gallo, 1996; Crawford, 1937; Melis et al., 2006a, 2006b). Although chimpanzees are known to cooperatively hunt in the wild, to date there are no experiments in which two chimpanzees successfully use complementary roles in a collaborative interaction. Therefore, we used the same apparatus used with children in Study 1a to assess whether chimpanzees could coordinate complementary roles with a conspecific in a cooperative problem-solving activity, including an ability to reverse roles and appropriately divide the labor between them. Our methodological innovation was to have the chimpanzees collaborate from two separate rooms, each chimpanzee receiving its reward separately, so as to minimize food competition. Given chimpanzees' overall skill in coordinating behavior, we hypothesized that they would be able to solve a cooperative reward-acquisition task using complementary roles. However, due to findings suggesting that chimpanzees do not share joint goals (Greenberg et al., 2010; Warneken et al., 2006), it was not clear whether they would engage in role-reversal such that the second chimpanzee would show a higher level of proficiency than the first chimpanzee when completing the same role.

2.1. Method

2.1.1. Participants

Participants were 14 chimpanzees (11 females and 3 males) housed at the Wolfgang Köhler Primate Research Center at the Leipzig Zoo. Ten were housed together in one group and the remaining four were housed together in a separate group. As with the children in Study 1a, chimpanzee pairs were formed on the basis of their relationships with their conspecifics; only pairs that were positively affiliated and worked well together were selected. All chimpanzees had previously participated in experiments, including collaborative problem-solving tasks involving parallel roles. They ranged from 6 to 33 years of age.

2.1.2. Materials

A precise replica of the apparatus used in Study 1a was employed use with the chimpanzees (Fig. 1). All modifications were minor (e.g., change in materials and dimensions) and were done so as to make the apparatus more suitable for use with chimpanzees. The apparatus spanned two adjoining enclosures separated by a hydraulic door, thus ensuring each chimpanzee remained in their own enclosure. The apparatus was securely attached to the outside of their enclosures and the chimpanzees could complete their roles simply by inserting their fingers through the mesh straight into the apparatus. Chimpanzees were rewarded with either grapes or monkey chow biscuits, depending on the preference of the pair.

2.1.3. Design

All chimpanzees participated in pairs and experienced the same invariant sequence of three conditions as in Study 1a – Cooperative, Role-Reversal and Division-of-labor, each followed by a Non-reward control condition. Chimpanzees were generally tested over a two-day period within the same week, although some pairs completing all conditions in a single day.

2.1.4. Procedure

The experimental space included two large enclosures (3.85 m × 2.65 m × 2.4 m and 2.65 m × 2.75 m × 2.4 m) connected by a hydraulic door. Each pair was moved into the experimental space allowing both individuals to choose which enclosure to occupy, after which the hydraulic door was closed, separating the two chimpanzees. Like the children in Study 1a, chimpanzees received three demonstrations of how the apparatus functioned, each time allowing the chimpanzees to obtain the food reward themselves. After these demonstrations, each pair completed as many trials as necessary to reach a criterion of three successful consecutive trials at which point the pair was deemed proficient at the task. After showing their proficiency on the lowest level of the apparatus, the experimenter placed the ball on the middle level for four trials and then the top level for four trials, with pairs working their way up the apparatus. After the pair had completed the four trials from the top level of the apparatus, the first experimental condition (Cooperative condition) began.

The general procedure was nearly identical to that of the children. Whereas the children received four trials per condition, the chimpanzees received six trials per condition. We gave the chimpanzees more trials so as to ensure that they had enough chances to be successful and to allow for mistakes. Additionally, each chimpanzee had a total of 60 s in which to complete their action (rather than 30 s for children), as chimpanzees are not as dexterous as humans with their hands and fingers.

2.1.5. Coding

All sessions were videotaped and coded from tape by the first author. For each trial we coded (1) success (releasing the reward at the bottom of the apparatus), (2) latencies from beginning (insertion of ball into apparatus) to end of the trial, and (3) latencies from beginning to completion of Role B. All latencies were timed to the closest hundredth of a second. To assess interrater reliability, a second coder blind to the purpose of the study independently coded all of the conditions for 25% of all test pairings. Reliability for category success was perfect ($K = 1.0$). For latencies Pearson's r was calculated and reliability was again excellent ($r = 1.0$).

2.2. Results

All chimpanzee dyads performed the task successfully in 95% of all experimental trials (with no significant differences across Cooperative, Role-Reversal, and Division-of-Labor conditions). Additionally, they completed significantly more trials in the conditions in which they received a reward than the conditions without a reward, $t(6) = 3.43$, $p = .01$ (Fig. 2). Although chimpanzees completed over 40% of all non-rewarded trials (which is rather high, given their main motivator is food), they used significantly more time to complete the non-rewarded trials (95.6 s) than the rewarded ones (45.2 s), $t(4) = 3.08$, $p < .05$, as well as significantly more time to initiate the non-rewarded trials (13.8 s) than the rewarded ones (2.6 s), $t(4) = 2.63$, $p = .05$.

In the Role-Reversal condition, six of the seven pairs were able to successfully take the role of the other. However, a paired-samples t test revealed no significant decrease in the amount of time needed to complete Role B, despite the second chimpanzee requiring 50% less time to complete Role B (Table 1). In the Division-of-Labor condition, when no roles were assigned and the chimpanzees could move freely between the two enclosures, they divided the labor appropriately, and all pairs were successful in cooperatively solving the task. Furthermore, there was no significant difference in the amount of time the chimpanzees needed to complete a trial across conditions – 55.9 s in the Cooperative condition, 52.5 s in the Role-Reversal condition, and 40.9 s in the Division-of-Labor condition: 40.9 s.

2.3. Discussion

We evaluated the ability of 3- and 5-year-old children and chimpanzees to cooperatively solve a reward-acquisition task with complementary roles. Children of both age groups were able to perform complementary roles, showing both successful role-reversal and division of labor. However, there were marked differences between the two age groups, highlighting the development of particular skills during this time period. This is most readily in the Role-Reversal condition. Using the stringent criterion of role-reversal, we see a difference between 3- and 5-year-olds. Using the latency to complete Role B (opening of trap door), among 5-year-olds the second child completed Role B faster than the partner; suggesting that the second child learned from having seen the partner complete the role previously. In contrast, 3-year-olds required the same amount of time to complete Role B; suggesting that the second child did not learn from observing the partner. Furthermore, the second child's unimproved performance was not due to a lack of attention or physical inability to complete the action; rather they first tried to open the trapdoor by pushing it in the wrong direction, i.e., toward as opposed to away from the ball, but were eventually successful once they pushed the trap door in the proper direction. This suggests that the 3-year-olds understood that they were to act on the ball and the apparatus but they had not learned the precise manner of doing so from their partner.

These findings suggest that only the 5-year-olds represented both roles in a single mental representation. This is particularly interesting given findings in which children as young as one or two years of age seem to already possess this sort of representation (Carpenter et al., 2005; Warneken et al., 2006). However, in these studies children always collaborated in simple interactions which an adult scaffolded, whereas here children collaborated with peers to complete a complex task. Indeed These findings concur with those from Ashley and Tomasello (1998) in which 3-year-olds found it hard to coordinate complementary roles.

The chimpanzees too were able to coordinate complementary roles to cooperatively solve a reward-acquisition task, showing both basic role-reversal and division of labor. However, the performance of the chimpanzees differed from that of the children in one significant way. Although the chimpanzees did show role-reversal in the sense that each chimpanzee was successful in completing the role of the other without prior experience, they did not meet the more stringent criterion of role-reversal in which the second chimpanzee outperformed its partner when roles were reversed. While the overall performance of the second chimpanzee did improve by 50% over that of the first chimpanzee, this difference was not statistically significant, with only 4 of the 7 pairs showing a decrease in the time it took the second chimpanzee to perform Role B. Like the 3-year-old children, most of the chimpanzees had the problem of wanting to push the trap door in the wrong direction but were later able to successfully open the trap door. Other factors such as dexterity, inattentiveness, or inability to open the door did not influence their performance. This suggests that although chimpanzees are able to perform either role and flexibly switch between them, they do not seem to gain any insight into their partner's role through observation while cooperating, instead relying on their own behavioral repertoire and persistence.

While this is the first experimental study to show that chimpanzees – not just humans – can coordinate complementary roles, the task we presented them represented a very simple cooperative situation in which attention to the behavior of the partner was not essential for success. Specifically, although the chimpanzees were able to perform either role and flexibly switch between them, successful attainment of the goal could be attributed to their simply responding to the movement of the ball through the apparatus without necessarily ascribing any of the results to the actions of the partner. Thus we cannot claim that the chimpanzees understood the role of the partner (as opposed to the behavior of the ball) in solving the task. Therefore, in a second study, we introduced a similar, but more complex task to assess whether individuals actually attended to the other's behavior (rather than the outcome of the other's behavior alone). Specifically, one partner had to time their own action with that of the other by waiting to initiate Role A only when the other was ready to perform the subsequent Role B.

3. Study 2a

In this study, we presented the same pairs of 3- and 5-year-old children with a more complex problem-solving task in which they had to coordinate complementary roles that were temporally dependent upon one another, including the need to reverse roles and effectively divide the labor between them. Furthermore, we included an additional condition in which the second child was not directly available to collaborate so that the first child had to either wait for or recruit the partner to join them at the task. Therefore, in order to successfully solve the task, pairs had to take the behavior of their partner into account. Given children as young as 18 months will try to re-engage a wayward

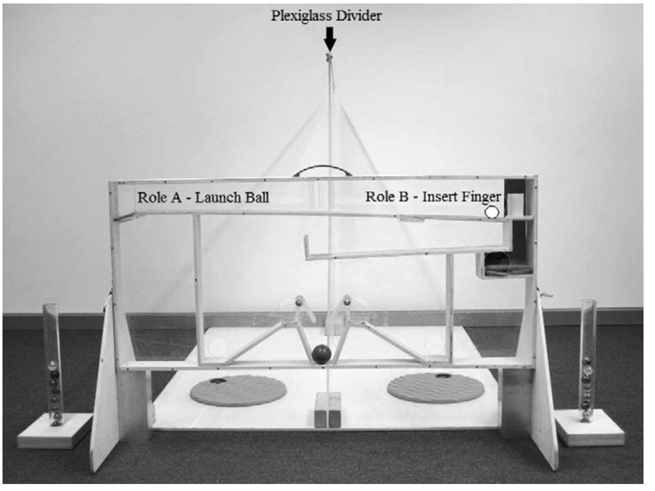

Fig. 3. One-tiered "Marble-Run" game used in Study 2a. One member of pair rolls a ball down the ramp (left side of apparatus) and the other inserts a finger to direct the ball toward the correct ramp (right side of apparatus). A replica with minor modifications (dimension and material) was attached to the outside of two adjacent enclosures for use with chimpanzees in Study 2b.

partner (Warneken et al., 2006), we hypothesized that both age groups would either wait for or recruit their partner to join them at the task.

3.1. Method

3.1.1. Participants

The same 56 children from Study 1 participated, usually the day after having completed Study 1 but no later than 14 days after completion of Study 1.

3.1.2. Materials

A new apparatus (110 cm × 6 cm × 50 cm) was designed which allowed for two participants to cooperatively solve a reward-acquisition task using temporally dependent complementary roles (Fig. 3). It was impossible for one child to perform both actions sequentially as a plexiglass divider precluded access. To obtain the reward, one child had to initiate the trial by launching a red billiard ball down a ramp (Role A) while the second child had to insert a finger into a hole located just before the entrance to an inaccessible and opaque compartment (Role B). Doing so kept the ball from entering the compartment and becoming irretrievable and also redirected the ball toward the tunnel, leading to release of the marbles. Children could collect marbles by dropping them into their own individual clear tube, thereby creating a "Marble Tower". They received no additional rewards. To occupy the partner in the Waiting conditions (see below), two puzzles were placed on the ground roughly 3 feet away.

3.1.3. Design

The apparatus was placed on the floor with a large plexiglass divider (130 cm × 100 cm) to ensure that each child remained on their assigned side of the apparatus. Children could fulfill their roles by inserting their fingers into holes on their side of the apparatus. All children were tested in pairs and experienced the same three experimental conditions in the same invariant order used in Study 1a – Cooperative condition, Role-Reversal condition and Division-of-Labor condition – interspersed with a Non-reward control condition following each experimental condition. Additionally, following the Role-Reversal condition and its accompanying Non-reward control condition, each child engaged in a Waiting condition. This allowed both children the opportunity to act in Role A while their partner waited. A non-reward condition did not follow the Waiting condition. After both children had experienced a Waiting condition, the pair moved on to the Division-of-Labor condition and its accompanying Non-reward condition.

In the *Cooperative* condition, child A was located at the left half of the apparatus (initiation of ball rolling) and child B at the right half (diverting ball with finger). The *Role-Reversal condition* was the same as the Cooperative condition except that the children exchanged places and thereby the roles they were to complete. The *Waiting-for-partner* conditions were essentially the same as the Cooperative and Role-Reversal conditions, except that the second child was not located in front of the apparatus and thus not ready to collaborate. Rather, while the first child was located at the right half of the apparatus ready to complete Role A, the second child sat a few feet away in sight of both the apparatus and partner, completing a puzzle. To be successful, the first child had to either wait 10 s for their partner to be allowed to join them or call themselves for their partner to join them. The *Division-of-Labor Condition* differed only in the absence of the divider, allowing partners to decide who would perform which role. In the *Non-reward* condition, no marbles were present.

Children completed all conditions within a single session, ranging from 30 to 45 min depending on the child's performance.

3.1.4. Procedure

On entering the experimental room, children were first asked if they remembered the "Marble Towers" from the day before and were then allowed to place themselves behind the apparatus. The experimenter first placed the marbles and then the ball in the apparatus, after which she demonstrated the functioning of the apparatus – initiating the rolling of the ball and then the insertion of a finger – using similar holes on the front side of the apparatus. A second demonstration was a demonstration of failure – the experimenter did not insert her finger into the hole, thus allowing the ball to roll into the inaccessible compartment and out of sight. A third demonstration was identical to the first. Children were allowed to take and collect the marbles themselves during these demonstrations.

Following the three demonstrations, the pair completed up to 16 trials to reach a criterion of three successful consecutive trials (with a minimum of four completed trials) at which point the pair was deemed proficient at the task. After reaching this criterion, the first experimental condition (Cooperative condition) began. Pairs were allowed 16 trials to reach the criterion of three successful consecutive trials (with a minimum of four completed trials), with each partner receiving 30 s to complete their action. After the pair had reached this second criterion or completed 16 trials, the Non-reward condition ensued. Pairs were given four trials to complete their actions but no longer received rewards for doing so. If after 30 s one of the individuals did not complete their action, the trial was considered unsuccessful, at which point the experimenter removed the ball from the apparatus.

The Role-Reversal condition followed. Again, 16 trials were allowed with each individual receiving 30 s to complete their respective action. After the pair reached criterion or had completed all 16 trials, the Non-reward condition followed, with pairs given another four trials to complete their actions.

At this point, both children were asked to come to the front of the apparatus to show the experimenter their marble towers. After engaging with the children for 30 s or so, the experimenter brought the nearby puzzles to the attention of the child who had originally completed Role B first. This child was then encouraged to g complete the puzzles. Once the second child was occupied with the puzzles, the experimenter suggested to the first child that s/he could continue to play with the marble apparatus. That child was then given 16 trials to complete the task; the experimenter simply placed the ball back into the apparatus for the child to complete the next trial without saying anything to either child. If the child waited to complete Role A for 10 s, the experimenter told the child doing the puzzles that they could go over and help by completing Role B. Children were not informed of this 10-s rule. If the child initiated a call to the second child to come help, the second child was free to do so and then returned to the puzzles. After the pair had reached a criterion of three consecutive successful trials or completed all 16 trials, the children were asked to switch places, such that the child who had just completed the puzzles was now located behind the apparatus to complete Role A and the other child could now complete the puzzles. The same procedure followed.

Finally, the children were both allowed to complete the puzzles, allowing the experimenter time to remove the plexiglass panel separating the two halves of the apparatus. Children were then allowed to choose which action to complete (Division-of-Labor condition). The pair was given trials with each

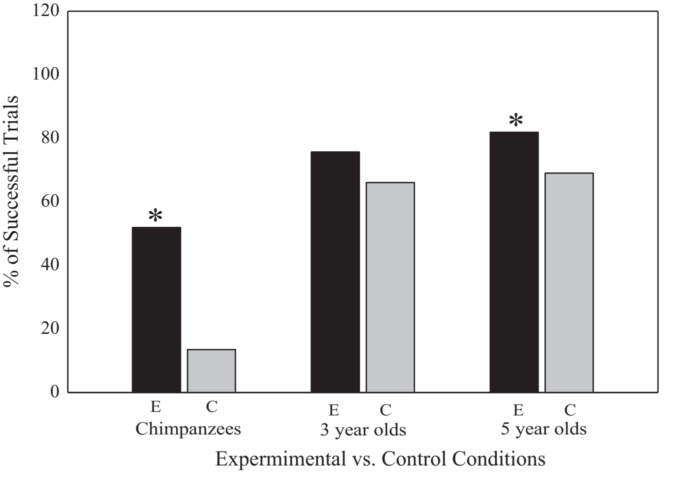

Fig. 4. Percentage of successful trials in experimental and control (Non-reward) conditions (Study 2). $^{*}p < .005$.

individual receiving 30 s to complete their action. The Non-reward condition followed and concluded the session.

3.1.5. Coding

All sessions were videotaped and coded from tape by the first author. For each trial we coded for success (defined as releasing the reward at the bottom of the apparatus). Whereas in Study 1a time to complete Role B was measured to assess role-reversal, here we compared number of trials to reach criterion in the Cooperative and Role-Reversal conditions, as Role B could only be coded as the child inserting a finger into the apparatus or not. We also coded amount of time children hesitated before initiating a trial (launching the ball) in the conditions in which the partner was readily available (Cooperative and Role-Reversal conditions), as well as in the conditions in which the partner was not readily available (Waiting conditions). Latencies were timed to the closest hundredth of a second. To assess interrater reliability, a second coder blind to the purpose of the study independently coded all of the conditions for 25% of all test pairings. Interrater agreement for both successes ($K = 1.0$), trials to criterion ($r = 1.0$), and latencies ($r = 0.99$) were excellent.

3.2. Results

3.2.1. Main analyses

Both 3.6- and 5.6-year-olds solved the task successfully in 75% and 81%, respectively, of all experimental trials (all conditions). Summed across conditions (Waiting conditions not included), the 5.6-year-olds completed significantly more trials when a reward was present, $t(13) = 3.61$, $p < .005$, while the 3.6-year-olds showed no difference between rewarded trials and non-rewarded trials (Fig. 4).

To assess role-reversal skills, first we examined performance in the Role-Reversal condition only. Thirteen of 14 3.6-year-old pairs and all 14 5.6-year-old pairs were successful in completing the task after their roles had been reversed. Second, we compared performance (number of trials to reach criterion) of the second child to have completed Role B (timely finger insertion) to the performance of the child who first completed that role. A paired-samples t-test revealed that for both 3.6- and 5.6-year-olds, the second child required fewer trials to reach criterion on Role B than the first child, $t(12) = 2.59$, $p < .05$ and $t(13) = 4.27$, $p = .001$, respectively (Table 2). In the Division-of-Labor condition, both age groups were able to successfully divide the labor between them and required no more trials (an average of 7 for 3.6-year-olds and 6 for 5.6-year-olds) to reach criterion than when the roles were determined for them.

Table 2
Average number of trials to reach criterion for 1st and 2nd members of pair (Study 2).

	1st individual	2nd individual	Paired *t*-test *p*-value	*N*
Chimpanzees	7.4 (SD 2.60)	11.00 (SD 4.30)	.171	14
3 year olds	14.71 (SD 5.99)	9.15 (SD 4.23)	.024*	28
5 years olds	11.71 (SD 3.36)	6.42 (SD 2.97)	.001*	28

Note. Standard deviations appear in parentheses.
"*" refers to statistical significance.

In the Waiting conditions, only four (of 28) 3.6-year-olds and six (of 28) 5.6-year-olds waited for or actively recruited their partner to join them in solving the task. They did, however, hesitate to initiate the trial when the partner was absent. As there was no variance in behavior after the initial trials, we compared only the first four trials of those conditions in which the partner was available (Cooperative and Role-Reversal) to the first four trials of those conditions in which the partner was unavailable (both Waiting conditions) for only those children who did not wait. Both the 3.6- and 5.6-year-olds hesitated significantly longer to initiate the trial when the partner was unavailable, $t(9) = 4.69$, $p < .01$ and $t(8) = 3.96$, $p < .005$, respectively (Table 3).

3.2.2. *Secondary analyses*

It was evident that having to use temporally dependent complementary roles provided both age groups with a challenge, with both groups completing significantly fewer trials in Study 2 than in Study 1, $t(13) = 4.92$, $p < .001$ and $t(13) = 5.49$, $p < .001$, respectively. However, one-way analysis of variance (ANOVA) showed no difference between the success rates of the younger and older groups (75% vs. 81%) when using temporally dependent complementary roles. Additionally, there was no effect of age in (a) trials to reach criterion in any condition (b) trials to reach criterion in Role B (timely finger insertion), or (c) the decrease in trials needed between first and second child. Age had a significant effect in the training phase, as the 5.6-year-olds required significantly fewer trials to reach criterion than the 3.6-year-olds (6 vs. 8.5), $F(1,26) = 3.91$, $p = .05$. In addition, across all cooperative conditions, there was only a significant age difference in the Role-Reversal condition, with the 5.6-year-olds completing a greater proportion of trials than the 3.6-year-olds (81.8% vs. 65.1%), $F(1,26) = 4.28$, $p < .05$.

4. Study 2b

In this study, we presented chimpanzees the same task presented to children in Study 2a. Other research (Melis et al., 2006a; Yamamoto & Tanaka, 2009) has shown that in parallel roles chimpanzees understand when they need a partner to complete a task and when they can solve the problem without a partner, suggesting that chimpanzees should wait for their partner in this task if they understand the cooperative nature of the task. However, it remains an open question whether chimpanzees show similar skills when engaging in complementary roles.

Table 3
Average duration (s) of hesitation to initiate action when partner absent (Study 2).

	Partner present	Partner absent	Paired *t*-test *p*-value	*N*
Chimpanzees	1.1 (SD 0.38)	2.5 (SD 1.85)	.082	14
3 year olds	1.4 (SD 0.45)	3.8 (SD 1.65)	.001*	24
5 years olds	1.4 (SD 0.46)	4.1 (SD 1.97)	.004*	22

Note. Included are only those participants who did initiate action in partner's absence. Standard deviations appear in parentheses.
"*" refers to statistical significance.

4.1. Method

4.1.1. Participants

Participants were the same 14 chimpanzees (11 females and 3 males) from Study 1, tested with the same partners.

4.1.2. Materials

A precise replica of the apparatus used with the children was constructed for use with the chimpanzees (Fig. 3). All modifications were minor (e.g., change in materials and dimensions) and were done to make the apparatus more suitable for use with chimpanzees. The apparatus spanned two adjoining enclosures separated by a hydraulic door, thus ensuring each chimpanzee remained in their own enclosure. The apparatus was securely attached to the outside of their enclosures and the chimpanzees could perform their roles simply by inserting their fingers through the mesh straight into the apparatus. Chimpanzees were rewarded with either grapes or monkey chow biscuits, depending on the preference of the pair.

4.1.3. Design

All chimpanzees participated in pairs and experienced the same invariant sequence of three conditions as in Study 2a. Chimpanzees were generally tested over a two-day period within the same week, although some pairs completing all conditions in a single day.

4.1.4. Procedure

The experimental space included the same two large enclosures connected by a hydraulic door: used in Study 1b. Each pair was moved into the experimental space allowing them to choose which enclosure to occupy after which the hydraulic door was closed separating the two chimpanzees. The experimenter demonstrated the apparatus three times, the second demonstration a demonstration of failure, as in Study 2a.

The general procedure was nearly identical to that in Study 2a. Whereas the children received 16 trials per experimental condition, the chimpanzees received 24 trials per experimental condition. We gave the chimpanzees more trials so as to ensure that they had enough chances to be successful and to allow for mistakes. Additionally, each chimpanzee had a total of 60 s in which to complete their action (rather than 30 s for children).

4.1.5. Coding

All sessions were videotaped and coded from tape by the first author. The procedure was the same as in Study 2a, again resulting in excellent interrater agreement for both successes ($K = 1.0$) and latencies ($r = 0.99$).

4.2. Results

Five of the seven chimpanzee pairs were successful in coordinating complementary roles temporally dependent upon another to solve the task in 52% of all experimental conditions. Across all experimental conditions (Waiting conditions not included), chimpanzees completed significantly more trials when a reward was present than absent, $t(6) = 4.86$, $p < .005$, with 13.4% of all non-rewarded trials being completed (Fig. 4).

In the Role-Reversal condition, five of seven chimpanzee pairs were successful. However, a paired-samples t test revealed no significant decrease in the amount of time needed to complete Role B (Table 2). However, the chimpanzees initially required significantly fewer trials to reach criterion on Role B then did the children, $F(1,31) = 6.31$, $p = .01$. Once roles were reversed, performance of the chimpanzees matched that of the children. In the Division-of-Labor condition, the chimpanzees required no greater number of trials to reach criterion than when the roles were determined for them (roughly 13 trials).

In the Waiting condition, only one of the 14 chimpanzees waited for their partner to join them in solving the task. As with the children, we compared those trials in which the partner was and was not available. As was no variance in their behavior after the initial trials, we compared the first four trials of those conditions in which the partner was available (Cooperative and Role-Reversal) to the first four trials of those conditions in which the partner was unavailable (both Waiting conditions). The chimpanzees did not show any significant difference in the time they took to initiate a trial (Table 3).

Like the children, having to use temporally dependent complementary roles posed chimpanzees a challenge – with the chimpanzees completing significantly fewer trials overall when performing temporally dependent complementary roles (51.9%) than when performing non-temporally dependent complementary roles (95.2%), $t(6) = 5.34$, $p < .005$.

It is possible that chimpanzees failed to wait for the partner because they had not sufficiently understood the functioning of the apparatus. Therefore, we gave all of the chimpanzees individual training with an apparatus that a single chimpanzee could manipulate bi-manually. Subsequently, we tested all chimpanzee individuals who had been successful in the individual version of the task. Thus, three of the original pairs were tested in the Waiting conditions again. Of the six individuals tested, only one was successful in waiting for the partner to become available when they had not been successful previously, indicating that failure to wait for the partner was not solely due to a lack of understanding of the apparatus.

4.3. Discussion

In Studies 2a and 2b, we elaborated on our first studies by increasing the complexity of the cooperative task with complementary roles temporally dependent upon one another. Both 3- and 5-year-olds were able to coordinate complementary roles temporally dependent upon one another, showing role-reversal and division of labor. As in Study 1a, we were also interested in whether children could successfully reverse roles such that the second child required less trials to be deemed competent (reached the criterion of three consecutive successful trials) than the first child. This proved to be the case in both age groups, with both groups requiring about the same number of trials to reach criterion.

This finding is surprising given there was a significant difference between age groups in Study 1a, where the roles were not temporally dependent upon one another. A possible explanation is that while the timing of one's action to another's is more complex within the social domain, the actual action the child is required to make (insertion and holding of finger in a hole) requires a less complex understanding in the physical domain compared to having to open a spring-loaded door as in Study 1a. This difference in cognitive demand (social vs. physical) may account for 3-year-olds' better performance in the Role-Reversal condition in Study 2a. In other words, the social-cognitive skills needed for success are already online at the age of 3 years, but the necessary physical-cognitive skills are still developing.

The social-cognitive skill of attending to the behavior of a partner therefore plays an important role in collaboration, and it is precisely this skill that we wanted to capture in the Waiting condition. Neither age group was successful in waiting or calling for their partner when doing so was required – only four 3-year-olds and six 5-year-olds did so, although they did hesitate to initiate the trial when their partner was absent.

This failure to wait or actively recruit their partner was surprising given studies which show that children in their second year of life already adjust their behavior in various joint activities, such as communicating to an adult play partner who is not taking their turn (Ross & Lollis, 1987), attempting to reengage an adult play partner who has stopped playing (Warneken et al., 2006), and attempting to achieve a goal only if a peer is available as a partner (Brownell, Ramani, & Zerwas, 2006). A possible explanation for failure to wait or recruit the partner is that children viewed their partner as inaccessible while doing the puzzle – "An adult has asked my partner to do a puzzle and I should therefore not interrupt them." This explanation is consistent with several studies on "normativity" which show that even very young children understand the normative structure of an activity – how things ought to be done. Additionally, throughout the Waiting condition, children of both ages made comments showing they knew they needed their partner (e.g., "Lilly is over there so it won't work;" "Someone needs to stick their finger in the hole"). Several children also told their partner to "hurry up" or "finish the puzzle faster." Such comments suggest that children considered the partner to be occupied and needing to complete the task before being able to collaborate again. Taken together with the fact that the children hesitated to initiate trials in which the partner was absent, we can safely propose that both 3.6- and 5.6-year-olds understood the importance of the partner in a cooperative problem-solving situation, but that the experimental situation constrained their behavior.

Like the children, chimpanzees were able to coordinate temporally dependent complementary roles, showing both basic role-reversal and division of labor. However, the behavior of the chimpanzees differed from that of the children in two ways. First, although the chimpanzees successfully completed a partner's role when roles were reversed, the second chimpanzee did not outperform its partner when completing the new role. Second, however, chimpanzees initially showed greater proficiency than children of both ages in Role B (timely insertion of finger), with the first chimpanzee requiring fewer trials (half as many as children) to reach criterion. Nonetheless, after roles were reversed, the performance of children of both ages matched that of the chimpanzees (same number of trials to reach criterion).

These findings suggest that chimpanzees possess an ability to understand and solve complex physical problems (see Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007, for support of this suggestion). Yet, unlike children, chimpanzees in the Waiting condition did not hesitate significantly longer to initiate those trials in which the partner was not readily available to collaborate, although there was a trend ($p = .08$) in this direction. While these results thus remain inconclusive, there is the possibility that our findings were influenced by chimpanzees' inability to inhibit actions toward a valued food item. The ability of chimpanzees to inhibit their prepotent response toward food items is, unfortunately, still not very clear. Findings in delay-of-gratification tasks demonstrate that chimpanzees are capable of inhibiting choosing an immediately available piece of food to later obtain a larger one (Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999; Dufour, Pelé, Sterck, & Thierry, 2007; Rosati, Stevens, Hare, & Hauser, 2007). Findings in a reverse contingency task are mixed, with some studies showing chimpanzees' extreme bias toward choosing the larger of two food rewards although doing so always results in their receiving the smaller reward (Boysen & Berntson, 1995; Boysen, Berntson, Hannan, & Cacioppo, 1996; Boysen, Berntson, & Mukobi, 2001), whereas others show that when the demands and/or the procedures are modified, chimpanzees are indeed able to master the task (Boysen, Mukobi, & Berntson, 1999; Uher & Call, 2008; Vlamings, Uher, & Call, 2006). Despite this unclear picture, if inhibition is one of the basic skills required for cooperating with others, the chimpanzees' limited inhibition is telling in and of itself.

5. Conclusions

In mature human collaboration, participants coordinate their behavior with that of the other by attending to both roles simultaneously, combining both roles into a single mental representation comprising the whole collaboration from an external viewpoint – allowing for the reversal of roles in tasks with complementary actions. When the collaborative task is not demanding, human children are able to coordinate simple complementary roles (with an adult partner) very early in development. The ability to coordinate one's behavior with others improves with age, so that by age 3–4, children cooperatively solve problems with their peers. One of our closest primate relatives, the chimpanzee, is also able to achieve coordination using complementary roles, as the present studies show. However, some qualitative differences appear across the two species in the extent to which the act is collaborative versus merely coordinated.

The first divergence in behavior emerged in the Role-Reversal condition. The children showed an ability to profit from experience as a collaborator in one role when later switching to the other role. This suggests that as they participate in a collaboration, young children integrate both roles into a single "birds-eye-view" representational format in a way that chimpanzees do not. The chimpanzees too were able to reverse roles with their partners, but after having done so, the second chimpanzee did not outperform its partner, suggesting that they did not learn about the second role while performing the first. One might thus conclude that although chimpanzees can perform either of two roles, they do not simultaneously attend to the partner's role in the same way children do. However, there are numerous studies providing evidence that chimpanzees do indeed learn socially (Whiten, Horner, & de Waal, 2005). If chimpanzees do extract knowledge from social encounters, why is this not reflected in the role-reversal measure? Current findings suggest that the way in which chimpanzees learn the properties of a task from a social partner (e.g., how to crack open a nut) differs qualitatively from the way humans do so. While humans imitatively learn (copying a demonstrator's precise *actions*), chimpanzees show emulative learning (copying the *results* of a demonstrator's actions; Tennie, Call, & Tomasello, 2009). Therefore, if chimpanzees are not specifically imitating a demonstrator's action, there is no reason to expect the observer to show improvement on the performance of the "demonstrator" in our task.

The second divergence in behavior emerged in the Waiting condition. Although like children, chimpanzees did not wait for the partner to become available to collaborate, their behavior did not differ as a result of the presence or absence of the partner. This suggests the possibility that the chimpanzees did not understand the necessity of their partner in performing the task. At least one study (Melis et al., 2006a) showed that chimpanzees do recognize when they need a partner to achieve their goal, even recruiting a partner more often in the trials in which a partner was necessary for success. However, chimpanzees in the Melis et al. (2006a) study received several training phases before the test in which individual chimpanzees learned to wait for increasing increments of time (5–30 s) for the release of the partner. In our study, the chimpanzees received only three demonstrations before beginning the test. Perhaps if the chimpanzees in our test had received training such as that given by Melis et al., the chimpanzees would have shown greater hesitation and/or actually waited for the partner to join them before initiating a trial. Also, compared to the complementary roles required by our apparatus, the physical relation between the parallel roles in the Melis et al. study was highly transparent and therefore more easily comprehensible (pulling on one end of the rope had an immediate effect on the other end).

While there is still much that requires further exploration, the current literature leads toward a picture of chimpanzee collaboration which on the surface seems similar to human collaboration but after further investigation proves itself to be different in some respects. Several studies have shown that chimpanzees (and other primates) are capable of working together toward a goal and that the chances of their success are correlated to social aspects such as tolerance between partners and divisibility of food resources. Despite their ability to work together, however, chimpanzees may not make use of the same cognitive processes as human cooperators do. Human collaboration requires a joint goal and joint effort to obtain that goal; the concept of "we-ness" is then integral to collaboration. It is precisely this concept of "we-ness" that chimpanzees seem to do without. Their lack of attention to the role of their partner in the present studies suggests that chimpanzees coordinate by flexibly synchronizing their actions toward a goal, but they do this by both independently pursuing the reward and responding to the *result* of the partner's actions. Future studies should attempt to clarify further the distinction between surface behavior and underlying cognitive processes, thereby allowing us to better understand chimpanzee collaboration and how it is not only different from but similar to human collaboration.

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