

Spontaneous Triadic Engagement in Bonobos (*Pan paniscus*) and Chimpanzees (*Pan troglodytes*)

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Humans are believed to have evolved a unique motivation to participate in joint activities that first develops during infancy and supports the development of shared intentionality. We conducted five experiments with bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) (Total $n = 119$) to assess their motivation to spontaneously participate in joint activities with a conspecific or a human. We found that even the youngest subjects preferred to interact together with a human and a toy rather than engaging in an identical game alone. In addition, we found that subjects could spontaneously interact with a human in a turn-taking game involving passing a ball back and forth and used behaviors to elicit additional interaction when the game was disrupted. However, when paired with a conspecific, subjects preferred to interact with an object individually rather than together. Our results indicate that nonhuman apes are motivated to engage in triadic activities if they occur spontaneously with humans and require a minimum amount of coordination. These findings leave open the question of whether these activities are coordinated through shared intentions.

Keywords: chimpanzee, bonobo, shared intentionality, triadic interaction, social motivation

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Human cooperation is unusual for its frequency and complexity (Hare, 2011; Hill, Barton, & Hurtado, 2009; Tomasello, 2009). Some developmental psychologists have proposed that human cooperation has its foundation in unique social motivation and intention-reading skills that develop within the first years of life (Tomasello, Carpenter, Call, Behne, & Moll, 2005; Trevarthen, 1982). Human children are not only motivated to understand the intentions of others but are also driven to actively share their own

intentions with others (Gilbert, 1992; Searle, 1995; Tomasello, 1999; Trevarthen & Hubley, 1978; Tuomela, 1995). This foundation allows humans to develop levels of collaboration that require joint commitment and coordination through overt communication about shared goals (Gräfenhain, Behne, Carpenter, & Tomasello, 2009; Gustafson, Green, & West, 1979; Ratner & Bruner, 1978; Warneken, Chen, & Tomasello, 2006).

The shared intentionality hypothesis (Tomasello & Carpenter, 2007; Tomasello et al., 2005) was proposed based in part on experiments demonstrating that children are spontaneously motivated to engage in joint activities with others. For example, Warneken et al. (2006) gave children the opportunity to engage in cooperative social activities with an experimenter. If this adult partner interrupted the joint activity, many children made attempts to reengage him as if attempting to reinstate a shared goal. Such reengagement attempts seem to be made with some understanding of the partner's intentions. Children were more likely to attempt such reengagements when partners were unable rather than unwilling to cooperate (Warneken et al., 2012). Similarly, children were more likely to attempt reengagement if the experimenter announced a prior commitment to the activity (Gräfenhain et al., 2009). Lastly, these results cannot be explained as the child using the experimenter as a "social tool" to accomplish a nonshared goal. Children were just as likely to reengage the experimenter when the child could complete the activity herself as when the activity required a second individual (Warneken, Gräfenhain, & Tomasello, 2012). Therefore, it seems that children represent the shared intentions underlying these activities and are motivated to share these experiences from early in human ontogeny.

The hypothesis that humans possess a species-unique motivation and skill for shared activity has been tested comparatively by examining the behavior of chimpanzees. In both field and exper-

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imental studies chimpanzees have been shown to cooperate skillfully with conspecifics (Boesch, 2002; Hare, Melis, Woods, Hastings, & Wrangham, 2007; Hirata, 2003; Melis, Hare, & Tomasello, 2006a; Melis, Hare, & Tomasello, 2009; Mitani, Merriwether, & Zhang, 2000; Watts & Mitani, 2001; Yamamoto, Humle, & Tanaka, 2009). However, the extent to which these behaviors are driven by shared intentions remains unknown. To evaluate this question, Warneken et al. (2006) presented chimpanzees and human children with a series of social games that required cooperation with a partner. Compared with the children, the chimpanzees had little interest in joint activities that did not result in a concrete goal (i.e., food). The chimpanzees also showed no evidence of reengagement attempts when the experimenter disrupted the activity (Warneken et al., 2006). They did not wait near the play area nor did they encourage the experimenter to continue playing by touching him or gesturing. Instead, they most often disengaged and attempted to solve the task individually (see also Hirata, Morimura, & Fuwa, 2010). Based on these differences between humans and chimpanzees several authors have concluded that shared intentionality and the motivation that leads to its development may be a uniquely human trait (Burkart, Hrdy, & Van Schaik, 2009; Tomasello, 2009; Tomasello & Herrmann, 2010).

However, several limitations in the studies by Warneken et al. (2006) suggest that additional nonhuman ape research is warranted. First, the cooperative tasks were relatively complex, and only one subject showed any form of coordination in the majority of games. This may be partially attributable to the fact that subjects were not familiarized with the apparatus beforehand. Consequently, subjects may have been attracted to the novelty of the apparatus, rather than the potential for joint activity (chimpanzees are neophilic relative to human children; Herrmann, Hare, Cisewski, & Tomasello, 2011). Further, with minimal evidence for coordination in these tasks, it is possible that subjects' lack of response to the interruptions was simply because no robust social activity had been established to interrupt. Therefore, the hypothesis that chimpanzees are not motivated by triadic social games requires additional experiments using activities carefully chosen for this species. Several observational studies from captivity and the wild suggest that great ape species do participate in bouts of triadic play (Gómez, 2010; Ingmanson, 1996; Plooi, 1978; Tanner & Byrne, 2010) when the games are simple in nature (e.g., play with a stick, piece of fabric, or ball). For example, Gómez (2010) reports a series of triadic interactions in which a gorilla repeatedly exchanged a ball with a human in a turn-taking sequence. Thus, it is important to identify appropriate social games for these species before experimentally testing subjects' behavior when the game is interrupted.

Lastly, Warneken et al. (2006) tested a small sample of chimpanzees ($n = 3$), and no bonobos (who are equally related to humans) were studied. Bonobos are more tolerant than chimpanzees when cofeeding (Boesch, Hohmann, & Marchant, 2002; Hashimoto, 1997; Kano, 1992), allowing them to cooperate more flexibly with a wider range of individuals—including strangers (Hare & Kwetuenda, 2010; Hare et al., 2007). They have also been observed to engage in a number of triadic activities for which there is no evidence in chimpanzees (Palagi, 2006; Pika & Zuberbuhler, 2008). Thus, bonobos are an especially important species to consider for this topic.

In a series of five experiments we tested whether a large sample of bonobos and chimpanzees spontaneously participate in joint instrumental activities. We also examined the effect of the subjects' age, sex, and species on behavior. We predicted that if the motivation for triadic social activities is unique to humans, non-human apes would show little interest in joint engagement with objects or turn-taking games and would opt to play individually when possible. Further, if shared intentions are unique to humans we predicted that apes would show no attempts to reinstate a joint activity, disrupted by a human experimenter.

Experiment 1

We first tested whether a group of young bonobos and chimpanzees prefer to interact with an object together with a human, or alone. Two sets of identical objects were presented and a human experimenter played with one of the objects. If a subject approached the experimenter, she attempted to play together with the subject and object. Between trials we varied the objects available and the familiarity of the experimenter.

Method

Subjects and apparatus. Fourteen bonobos (*Pan paniscus*; 8 male, 6 female, mean age = 3.8 years, range = 2–5) and 16 chimpanzees (*Pan troglodytes*; 9 male, 7 female, mean age = 3.5 years, range = 1–5) participated (Table S1). All chimpanzee subjects live in semifree ranging conditions at the Tchimpounga Chimpanzee Sanctuary, Pointe Noire, Republic of Congo. All bonobo subjects live in semifree ranging conditions at Lola ya Bonobo sanctuary, Democratic Republic of Congo. The majority of apes at both sanctuaries are orphans of the bushmeat trade who have been reintroduced to species-typical social groups and environments (large forested enclosures) at the sanctuary (Cox, Rosen, Montgomery, & Seal, 2000; Farmer, 2002). All apes are familiar with humans through routine feeding and medical care but spend the majority of their time in conspecific groups with limited human contact. For a description of these populations see Wobber and Hare (2011).

In all experiments apes were tested in familiar dormitory rooms, and experimenters interacted with the subjects through the mesh walls of these enclosures (subjects and experimenters were not in the same enclosure). We used 30 cm × 30 cm green plastic squares and 2-m nylon ropes as the objects with which apes were allowed to interact. Both of these specific objects were unfamiliar to apes at the time of testing, although rope and plastic are common materials at the sanctuaries.

Procedure. In each session two identical objects (green plastic squares or rope) were positioned ~ 2m apart. Once these objects were in place subjects were allowed 2 minutes to habituate to the experimental setup. In test trials, subjects were first centered with a food reward, delivered by an individual who did not otherwise participate in the trial. Then the experimenter approached and played with one of the objects for 1 minute. The experimenter manipulated the object playfully (e.g., by rattling it against the enclosure or juggling it between her hands) and mimicked ape laughter (as in MacLean & Hare, 2012) but did not actively solicit the subject's attention; the apes were allowed to behave freely. If the ape approached the experimenter, the exper-

inenter attempted to play with the object together with the subject (e.g., by swinging one end of the rope playfully, or wiggling or tapping the plastic square while the subject held the object). On half of the trials, the experimenter was familiar to the ape (sanctuary staff) and on the other half the human was a stranger (a visiting researcher). The identity of the experimenter (familiar, stranger) was alternated between trials and the condition for the first trial was counterbalanced across subjects. The location of the object that the experimenter played with was counterbalanced within subjects and the location of the object that the experimenter played with on the first trial was counterbalanced between subjects. Each subject participated in four consecutive trials with the nylon ropes and four consecutive trials with the plastic squares—the order of which was counterbalanced between subjects.

Scoring and analysis. All trials were coded from video. We recorded (1) the first object the subject touched and (2) the amount of time that subjects spent within arm's reach of each object. We calculated (3) the percentage of time that subjects spent within arm's reach of the object the human was playing with as a function of the total time they spent within arm's reach of either object. We compared the object that subjects first touched to chance using one-sample *t* tests. The time that each subject spent near the two objects was compared by paired-sample *t* tests. To explore the effects of species, sex, and age on performance we included these variables as factors (Species, Sex) or covariates (Age) in General Linear Models with measures 2 and 3 (described above) as the dependent measures. Analyses of sex differences are reported in the supplementary online materials (SOM). Forty-one percent of chimpanzee trials and 43% of bonobo trials were coded by a second individual naïve to purpose of the study in order to assess interrater reliability. All reliability scores were excellent (object first touched: $\kappa = .85$; time at object near human: Pearson's $r = .97$; time at object away from human: Pearson's $r = .93$). Statistical values for supplemental results are shown in the SOM and Table S2.

Results

Overall preferences. Overall, apes of both species preferred to interact with the object that the human was playing with (and the human) rather than interacting with an identical object alone. Chimpanzees and bonobos spent an average of $70 \pm 5\%$ and $66 \pm$

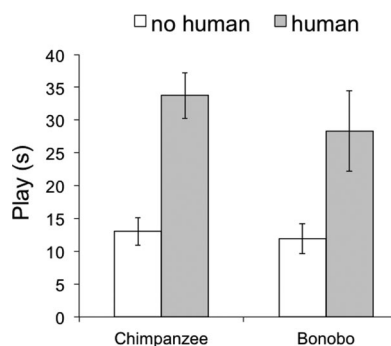


Figure 1. The amount of time that subjects spent within arm's reach of an object a human was playing with versus an identical object elsewhere in the enclosure.

6% of their total time respectively near the object that the human was playing with (see Figure 1), and 29/30 subjects spent some time in proximity to the object the human was playing with across trials. Within-subjects *t* tests for each species indicated that both chimpanzees ($t_{15} = 4.24, p < .01$) and bonobos ($t_{13} = 2.42, p < .05$) spent significantly more time within arm's reach of the object that the human was playing with than the other object. Analysis of the location of subjects' first touches revealed a similar pattern. Both chimpanzees and bonobos first touched the object that the human was playing with more frequently than expected by chance (chimpanzees: $77 \pm 3.7\%, t_{15} = 7.40, p < .01$; bonobos¹: $70 \pm 7.4\%, t_{12} = 2.73, p < .05$). The identity (stranger or familiar) of the individual who played with the subject had no effect on either species' behavior (mean percent time near familiar: $64 \pm 5\%$; mean percent time near stranger: $67 \pm 5\%$; Table S2).

Species, sex, and age effects. There was no effect of species on the percentage of time that subjects spent near the object the human was playing with ($F_{1,24} = 2.13, p = .16$).¹ Although we tested only infants and juveniles in this experiment, age significantly predicted subjects' behavior. Specifically, increases in age were associated with an increased amount of time near the object that the human played with ($F_{1,25} = 7.63, p = .01$). However, the proportion of time that subjects were near the object that the human played with (controlling for total time spent near either object) did not vary as a function of age ($F_{1,24} = 2.96, p = .10$).¹ Therefore, older subjects likely spent more time near the human simply as a byproduct of more time interacting with the objects. SOM and Table 1 show that males interacted together with the experimenters longer and for a larger percentage of the testing time than did females.

Discussion

Subjects of both species preferred to interact with an object a human was playing with rather than an identical object alone. Both species were more likely to first touch the object near the human experimenter and spent a greater proportion of time near this object. The identity of the experimenter did not affect subject's preferences. Finally, for subadult apes, older subjects showed an increased tendency to interact with objects for longer time periods. Therefore, both young bonobos and chimpanzees showed a strong motivation to interact together with an object together with a human, rather than alone.

Experiment 2

Experiment 1 showed that young bonobos and chimpanzees prefer to interact with an object together with a human, rather than alone. Experiment 2 measured whether these species have similar preferences for joint activity with a conspecific. Pairs of chimpanzees and bonobos were given the opportunity to interact with a rope either jointly or individually. Given that subjects preferred to interact with the same object as a human in Experiment 1, we also varied whether a human joined the activity.

¹ One bonobo was excluded from this analysis because she did not touch either object on any trial.

Table 1
Species and Age Group Differences in Experiments 1–3

Experiment	Condition	Measure	Species difference	Sex difference	Age difference
1	—	Time playing near human	—	M > F	*
2	Conspecific	Percent time touching same rope	—	—	Young > Old
3	Conspecific	Percent time touching same rope	C > B	—	—
	Human	Percent time touching same rope	C > B	—	Young > Old

Note. M = Male; F = Female; C = Chimpanzee; B = Bonobo.

* All subjects were subadult.

Method

Subjects and apparatus. All subjects lived at the sanctuaries described in Experiment 1. Thirty-eight chimpanzees (20 males, 18 females) and 30 bonobos (16 males, 14 females) participated (Table S1). Apes were tested in male–male (MM), male–female (MF), and female–female (FF) pairs. No individuals were used in multiple pairs. To explore the effects of age we divided pairs of both species into a younger group (both apes ≤ 8 years; 18 chimpanzees mean age: 5.6 ± 0.4 years; 16 bonobos, mean age: 5.7 ± 0.4 years) and older group (both apes ≥ 8 years; 20 chimpanzees, mean age: 14.0 ± 0.7 years; 14 bonobos, mean age: 15.3 ± 1.5 years) with multiple instances of each pair type (MM, MF, FF) in both age groups for both species (chimpanzee pairs—younger: 2 FF, 4 MM, 3 MF, older: 4 FF, 3 MM, 3 MF; bonobo pairs—younger: 2 FF, 4 MM, 2 MF; older: 3 FF, 2 MM, 2 MF). Individual apes within each pair lived in the same social group at the sanctuary and were familiar with one another before the experiment. The same pairs were tested in both the conspecific and human conditions, which were always administered in this order. Three nylon ropes (3 m long) were attached to the enclosure mesh 1 m apart from one another and ~ 1 m above the ground. The center of each rope was tied to the enclosure such that each rope was divided into two segments of equal length.

Procedure. Once the ropes were installed, subjects were allowed to enter the room. We measured subjects' interaction with the objects in two conditions. In the conspecific condition, subjects were allowed 1 min to behave freely in the presence of their conspecific partner. In the human condition, the experimenter played with the center rope and subjects (along with their partner) were allowed one minute to behave freely in the room. The experimenter manipulated one end of the center rope playfully (e.g., by pulling the rope, tossing it in the air, or waving the rope in circles) while mimicking ape laughter. If a subject approached the rope the experimenter was playing with he attempted to play with the rope together with the subject but did not otherwise solicit the subject's attention.

Scoring and analysis. All sessions were coded from video. On a second-by-second basis, we measured the amount of time that each subject made physical contact (hands, feet, mouth) with each of the ropes. From these observations we calculated the amount of time that subjects spent simultaneously touching the same rope as their partner (or the human) as well as the total amount of time that they spent touching any of the ropes. To control for differences in the absolute amount of time that subjects touched the ropes, we determined the percentage of time that subjects touched the same rope as their partner(s). This percentage was used as the

dependent measure for analysis. Data were analyzed using a General Linear Model with Species, Age Group, Sex, and Pair Composition (MM, MF, FF) as explanatory variables in the model. Analyses of total time touching the ropes as well as sex differences and pair composition are reported in the SOM. A second coder naïve to the purpose of the study coded the behavior of one individual in 26% of chimpanzee pairs and 27% of bonobo pairs to assess interrater reliability. The scores of these coders were highly correlated (Pearson correlation = .96, $p < .01$).

Results – Conspecific Condition

Apes interacted with the ropes (mean time touching rope = 35 ± 2 s) but relatively rarely together. Overall subjects spent an average of only 5% of their time touching the same rope as their conspecific partner, and only 29% of subjects spent any time simultaneously handling the same rope with their partner. The percent of time touching the same rope varied significantly as a function of age ($F_{1,48} = 13.32$, $p < .01$). Individuals in the younger age group spent a greater percentage of time touching the same rope ($10 \pm 3\%$) than individuals in the older group ($0.8 \pm 0.3\%$). There were no species differences ($F_{1,48} = 2.15$, $p = .15$).

Results – Human Condition

The total amount of time touching the ropes did not differ between the conspecific and human conditions (Conspecific: 34.8 ± 2.4 s; Human: 30.2 ± 2.6 s; $F_{1,52} = 0.01$, $p = .53$). However, subjects spent a much greater percentage of time touching the same rope as the human ($46 \pm 5\%$) than they did touching the same rope as their partner in the conspecific condition ($5 \pm 1\%$; $F_{1,40} = 35.19$, $p < .01$). Overall 57% of subjects spent some time touching the same rope as the human. Subjects also spent a greater percentage of time simultaneously touching the same rope as their conspecific partner in this condition, compared with when a human was not present (Conspecific: $5 \pm 1\%$; Human: $14 \pm 3\%$; $F_{1,40} = 18.86$, $p < .01$). There were no effects of species ($F_{1,42} = 0.82$, $p = .37$) or age group ($F_{1,42} = 0.16$, $p = .69$) on the percentage of time that subjects manipulated the same rope as the human.

Discussion

Subjects were always paired with a conspecific and had the opportunity to interact alone or together with one of three ropes. Overall subjects spent little time interacting together with the ropes and younger individuals were more likely to exhibit joint activity with a conspecific than adults, echoing the results of past obser-

vational studies (Mendoza-Granados & Sommer, 1995; Nishida & Wallauer, 2003; Takeshita & Walraven, 1996). Subjects were more interested in interacting together with the ropes when a human was present, possibly as a byproduct of the human structuring the activity by presenting himself as a willing play partner, or perhaps simply because of the movement of the rope that the human manipulated. Because all subjects participated in these conditions in the same order, it is also possible that order effects contributed to the difference between conditions.

The finding that apes spent little time simultaneously interacting with the same rope suggests that social tolerance levels may limit joint instrumental activities. For example many reports of triadic play in apes describe activities in which one individual possesses an object that she tries to keep away from the other, and it is uncommon for apes to spend prolonged periods simultaneously interacting with the same object (Ramsey & Mcgregew, 2005; Tanner & Byrne, 2010). Further, experimental studies of ape cooperation have highlighted the constraining role of social tolerance in collaborative activities (Hare et al., 2007; Melis, Hare, & Tomasello, 2006b). However, the current study cannot differentiate between low levels of joint engagement caused by constraints on tolerance, or a lack of motivation for joint activities with conspecifics. We address these two possibilities in Experiment 3.

Experiment 3

Experiment 3 was designed to test whether subjects infrequently interacted together with the ropes as a result of a lack of motivation (i.e., subjects did not wish to interact together) or as a result of tolerance constraints (i.e., subjects were averse to sharing a resource). Here, a single rope was provided to a pair of bonobos or chimpanzees. In some trials a human also played with this rope as in Experiment 2. If subjects were unmotivated (but capable) of interacting together with objects in Experiment 2, we predicted that joint activity would increase when subjects were limited to a single object. However, if low tolerance precluded subjects from interacting together in Experiment 2 (i.e., subjects could not share the same physical resource), we predicted them to show similarly limited interaction when only one rope was available.

Method

Subjects and apparatus. All subjects lived at the sanctuaries described in Experiment 1. Forty-two chimpanzees (23 males, 19 females) and 32 bonobos (16 males, 16 females) participated (Table S1). Apes were tested in male–male (MM), male–female (MF), and female–female (FF) pairs. No individuals were used in multiple pairs. As in Experiment 2, we divided pairs of both species into a younger group (both apes ≤ 8 years; 20 chimpanzees—mean age: 6.0 ± 0.4 years, 20 bonobos—mean age: 5.4 ± 0.4 years) and older group (both apes ≥ 8 years; 22 chimpanzees—mean age: 15.0 ± 0.7 years, 12 bonobos - 13.9 ± 1.6 years) with multiple instances of each pair type (MM, MF, FF) in both age groups for both species (chimpanzees pairs—younger: 3 FF, 4 MM, 3 MF, older: 3 FF, 4 MM, 4 MF; bonobo pairs—younger: 3 FF, 4 MM, 3 MF, older: 3 FF, 2MM, 1MF – because of demographic limitations there was only one MF pair in the older group of bonobos). Individual apes within each pair lived in the same social group at the sanctuary and were familiar with one another

before the experiment. The same pairs were tested in both the conspecific and human conditions, which were always administered in this order. The center of one nylon rope (3 m) was attached to the enclosure mesh ~ 1 m above the ground such that it was divided into two segments of equal length.

Procedure, scoring, and analysis. The procedure, scoring and analysis were identical to Experiment 2 except that only 1 rope was available.

Results – Conspecific Condition

Subjects spent a much higher percentage of time touching the same rope as their conspecific partner in Experiment 3 ($M = 52\%$) than Experiment 2 (Figure 2; $M = 5\%$; $t_{129} = -9.28$, $p < .01$).² Compared with only 29% of subjects in Experiment 2, 77% of subjects spent time simultaneously touching the rope with their partner when only 1 rope was available to the pair. As shown in Figure 3, the percent of time that subjects simultaneously touched the rope was significantly higher in chimpanzees ($63 \pm 6\%$) than bonobos ($44 \pm 9\%$; $F_{1,51} = 9.84$, $p < .01$). The younger and older age groups did not differ in the percentage of time that subjects touched the rope simultaneously (Young: $59 \pm 6\%$, Old: $51 \pm 9\%$; $F_{1,51} = 2.10$, $p = .15$).

Results – Human Condition

The majority of subjects (77%) spent some time interacting with the object together with the human, and 55% of subjects manipulated the rope simultaneously with their conspecific partner in this condition. The percent of time that subjects spent simultaneously touching the rope with their conspecific partner was significantly higher in chimpanzees ($49 \pm 6\%$) than bonobos ($29 \pm 9\%$; $F_{1,44} = 15.89$, $p < .01$), mirroring the results of the conspecific condition. Across species, individuals in the younger age group spent a significantly greater percentage of time touching the rope simultaneously ($52 \pm 6\%$) than individuals in the older age group ($25 \pm 7\%$; $F_{1,44} = 17.82$, $p < .01$).

Discussion

These results suggest that it is a lack of motivation for joint interaction, and not tolerance that constrained joint activity in Experiment 2. With only one rope available, individuals of both species tolerated a conspecific handling the same rope simultaneously. Indeed, subjects spent approximately half of the trial handling the rope simultaneously even when a human was not present. In addition, the observed species difference also suggests that tolerance does not constrain object-based interactions in the same way it affects activities involving food. Specifically, chimpanzees—whose low social tolerance constrains cooperation for food (Melis et al., 2006b)—interacted together more than bonobos, who exhibit greater tolerance in cofeeding contexts (Hare et al., 2007). Finally, as in Experiment 2, the youngest individuals were again the most likely to interact with the object jointly.

² The percent time touching the rope simultaneously was similar for subjects that had (mean = $47 \pm 7\%$) or had not (mean = $55 \pm 6\%$) participated in Experiment 2 ($t_{65} = 0.8$, $p = 0.38$).

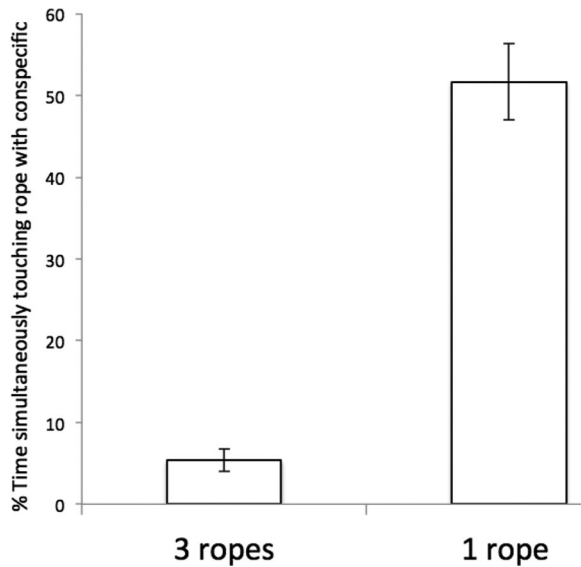


Figure 2. The percent of time that subjects simultaneously touched the same rope as their conspecific partner. Chimpanzees and bonobos spent a much greater proportion of time interacting with the rope together when there was only one rope to be shared (Experiment 3) than when multiple ropes were available (Experiment 2).

Experiment 4

Experiments 1–3 showed that chimpanzees and bonobos are motivated by, and capable of triadic activities in some simple

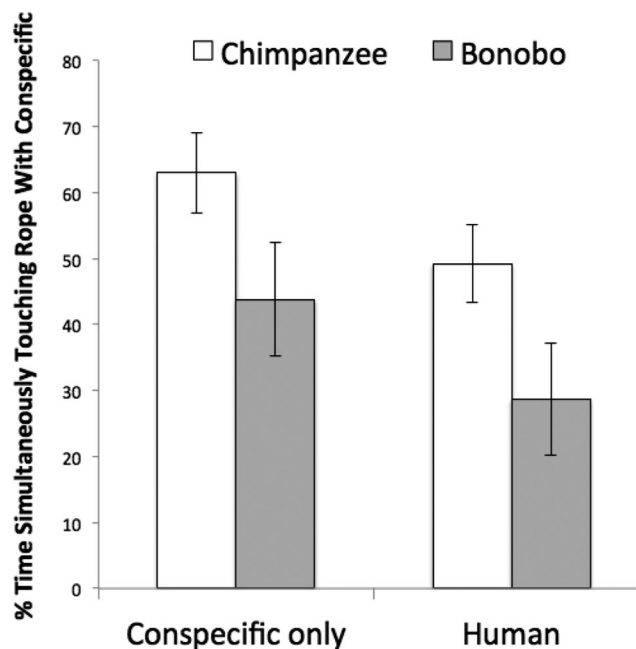


Figure 3. The percent of time that chimpanzees and bonobos simultaneously touched the rope with their conspecific partner in Experiment 3. Chimpanzees spent a greater proportion of time touching the rope together than bonobos (1) when the activity included only conspecifics, and (2) when a human presented himself as a play partner.

contexts. However, Experiments 1–3 cannot address whether non-human apes represent shared intentions toward joint activities in the manner characteristic of human children. Therefore in Experiments 4 and 5 we used interruption periods similar to Warneken et al. (2006) and observed apes' reactions to a disruption of the social activity. In Experiment 4 a human played jointly with an individual ape; then the experimenter interrupted the activity to observe whether subjects would try to reengage the experimenter.

Method

Subjects and apparatus. All subjects lived at the sanctuaries described in Experiment 1. Fourteen chimpanzees (7 females, 7 males, mean age 4.2 ± 1.1 year, range = 3–7) and 8 bonobos (2 female, 6 male; mean age 4.8 ± 1.7 years range = 4–6) participated. An additional 2 chimpanzees and 6 bonobos were tested but excluded from analysis because of poor video quality that precluded coding these sessions.

Procedure, scoring, and analysis. Each subject was tested in two social games, the ball game and the stick game. The

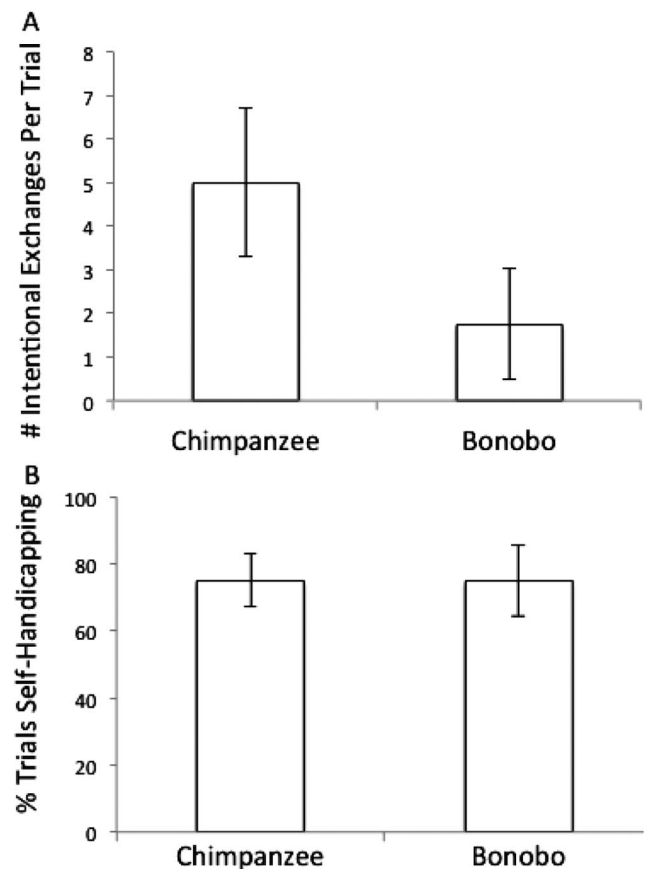


Figure 4. Participation in the social games from Experiment 4. A, The average number of times per trial that chimpanzees hit, pushed, or threw the ball back to the experimenter. B, The percent of trials that subjects self-handicapped during the stick game. Unlike previous studies in which chimpanzees showed little interest in social games designed for human children, apes in these studies actively participated in triadic social games with a human partner.

order in which these games occurred was counterbalanced across subjects. We conducted four trials of both games, each of which was followed by a 30-second period, during which the experimenter disrupted the social game. In the ball game, the experimenter attempted to engage subjects in a game of catch with a soccer ball. During the 1-min trials, the experimenter knelt ~ 1 m from the subjects, threw the ball to the subject (subjects could reach the ball by extending their arms out of the enclosure), and then reached his hands out and verbally encouraged the subject to return the ball. If the subject returned the ball, the experimenter reinitiated this sequence. If the subject directed the ball elsewhere, or tried to retain possession of the ball, the experimenter retrieved the ball and restarted the sequence by again throwing the ball to the subject. In the stick game, the experimenter poked and tickled the subject through the enclosure mesh with a small stick in a playful manner. Following each 1-min trial, the experimenter turned sideways to the subject, placed the object (ball or stick) on the ground beside him and remained passive for 30 seconds.

From video, we coded behaviors during the 1-min trials and the 30-s interruption periods. In the ball game, we coded the number of times that subjects exchanged the ball with the experimenter (1) unintentionally or (2) intentionally. We defined exchanges as incidents in which the experimenter delivered the ball to the subject, the ball touched the subject's hands or feet, and the ball came back to the experimenter (unintentionally or intentionally). Exchanges were categorized as intentional if the subject redirected the ball to the experimenter using a hitting, pushing, or throwing motion. All other cases in which the subject lost possession of the ball, hit, pushed, or threw the ball elsewhere, were coded as unintentional exchanges.

In the stick game, we coded whether subjects self-handicapped during the trial. Self-handicapping is a behavior in which one play partner intentionally puts him or herself at a disadvantage while engaged in a social game (Bauer & Smuts, 2007; Bekoff & Byers, 1998; Nishida, Kano, Goodall, McGrew, & Nakamura, 1999; Petrù, Spinka, Charvatova, & Lhota, 2009). Here, we defined self-handicapping as the subject turning her back while being poked or tickled and attempting to grab the stick from behind her body as an indication of subjects adopting complementary roles during social play.

During the interruption periods of both games we coded (1) whether the subject touched the object (ball or stick) and (2) whether the subject touched the experimenter. During the stick game we also coded whether subjects touched the experimenter with the stick during the interruption as a possible indication of reciprocating roles in the game. Because of limitations in the video quality we were unable to code more subtle behaviors such as gaze alternation. All trials were coded from video by a primary coder. A second coder scored 36% of trials in the ball game, and 27% of trials in the stick game, to assess interrater reliability. All measures had good interrater reliability (Ball game - number intentional exchanges, Pearson correlation = 0.90; number unintentional exchanges, Pearson correlation = 0.87; touch object, $\kappa = 0.93$; touch experimenter, $\kappa = 0.80$; Stick game—self-handicap, $\kappa = 0.75$; touch object, $\kappa = 0.91$; touch experimenter, $\kappa = 0.78$; touch experimenter with stick, $\kappa = \text{N/A}$, 100% agreement).

Results

Both chimpanzees and bonobos participated in the ball game. 100% of subjects manipulated the ball when it was thrown to them, and 59% of subjects scored at least one intentional exchange with the experimenter. On average chimpanzees intentionally exchanged the ball 5 ± 1.7 times per trial versus 22 ± 3 times per trial for unintentional exchanges. Bonobos intentionally exchanged the ball an average of 2 ± 1 times per trial versus 13 ± 5 times time per trial for unintentional exchanges (Figure 4). Although chimpanzees intentionally exchanged the ball more frequently than bonobos, the relative percentage of intentional exchanges was similar between the two species (chimpanzees: $15 \pm 4\%$; bonobos: $12 \pm 11\%$; $t_{20} = 0.23$, $p = .82$).

During the interruption period, both species made physical contact with the experimenter (chimpanzees: 32% trials; bonobos: 28% trials), the ball (chimpanzees: 75% trials; bonobos: 41% trials), and occasionally both the ball and the experimenter (chimpanzees: 27% trials; bonobos 13% trials) possibly as attempts to reinstate the game. Overall, chimpanzees were more likely to touch the ball than the experimenter during the interruption period ($\chi^2 = 9.6$, $p < .01$). Bonobos touched the ball and the experimenter approximately equally during the interruption periods ($\chi^2 = 0.73$, $p = .39$). Direct comparisons of the two species revealed that chimpanzees were more likely to touch the ball during the interruption than bonobos ($t_{20} = 2.6$, $p = .02$) but that both species touched the experimenter, and both the ball and the experimenter (during the same interruption period) at similar frequencies (touch human: $t_{20} = 0.27$, $p = .79$; ball and human: $t_{20} = 1.26$, $p = .22$).

Both species also actively participated in the stick game, frequently self-handicapping while the experimenter attempted to poke or tickle them with the stick. 96% of subjects exhibited self-handicapping on at least one trial. On average, chimpanzees self-handicapped on $75 \pm 8\%$ of trials and bonobos self-handicapped on $75 \pm 11\%$ of trials (Figure 4). When the game was interrupted, apes of both species touched the experimenter (chimpanzees: 64% trials; bonobos: 69% trials), the stick (chimpanzees: 16% trials; bonobos: 25% trials) and sometimes both (chimpanzees: 11% trials; bonobos: 22% trials), possibly in an attempt to continue the activity. Both chimpanzees and bonobos were more likely to touch the experimenter, than the object during the interruption period (chimpanzees: $\chi^2_1 = 18.7$, $p < .01$; bonobos: $\chi^2_1 = 7.35$, $p < .01$). Direct comparisons of the two species revealed no differences in the percent of trials that subjects touched the experimenter, the stick, or both during the interruption period (touch experimenter: $t_{20} = 0.32$, $p = .75$; touch stick: $t_{20} = 0.78$, $p = .20$; touch both: $t_{20} = 0.12$, $p = .25$). Lastly, 4 chimpanzees, but no bonobos touched the experimenter with the stick (one trial each) during the interruption.

Discussion

In this experiment chimpanzees and bonobos engaged in object-based social games with a human experimenter either by passing a ball back and forth (similar to human children in Ratner & Bruner, 1978; Gustafson et al., 1979) or by self-handicapping to facilitate object play. In addition, during interruption periods both species frequently touched the experimenter rather than simply attempting to participate in the game individually as in Warneken (2006).

Therefore chimpanzees and bonobos are motivated by (and capable of) some object-oriented social games, and they direct behaviors toward their social partner when the game is interrupted. However, few subjects ever attempted to reverse roles in the stick game (e.g., by tickling or poking the experimenter with the stick during the interruptions).

By replicating the paradigm used by Warneken et al. (2006), we did not run a baseline condition (i.e., a dyadic interaction). This makes subjects' behavior during the interruption periods difficult to interpret. Subjects' tendency to touch the experimenter and objects may have been an attempt to reinstate the activity. However, subjects' actions may also reflect alternative intentions (e.g., simple interest in the object or experimenter unrelated to the previously established social activity). Thus, while we attained positive results, there was no unambiguous behavior that would conclusively indicate active reengagement attempts. Therefore in the final study we replicated Experiment 4 but also included a control condition that did not include triadic interaction with an object.

Experiment 5

In Experiment 5 we replicated Experiment 4, adding a control condition in which the experimenter interacted with the subject dyadically (but in the presence of the object) before the interruption period.

Method

Subjects and apparatus. Eight chimpanzees (6 males, 2 females, mean age = 5.6 ± 0.5 years, range = 4–8) and 16 bonobos (9 males, 7 females, mean age = 7.2 ± 0.7 years, range = 3–12) participated (Table S1). Five of the chimpanzees and three of the bonobos had previously participated in Experiment 4 (approximately 1 year beforehand).

Procedure, scoring, and analysis. The procedure was identical to the ball game in Experiment 4 except that we now included four control trials in which the experimenter played socially with the subject (e.g., by patting or grasping the subject's hands or feet in a playful manner while mimicking ape laughter) without incorporating the object. During control trials the ball was positioned to the side of the experimenter and was thus visible, and physically accessible to the subject, as in test trials. We conducted four test and four control trials per subject, administered in two consecutive blocks, the order of which was counterbalanced between subjects. All trials were 90 seconds in length. Following the procedure of Experiment 4, every trial (test and control) was followed by a 30-second interruption period during which the experimenter turned sideways to the subject, placed the ball on the ground beside him, and remained passive for 30 seconds. We coded the same measures during the test trials and interruption as in Experiment 4. A second coder naïve to the purpose of the study scored 27% of video to assess interrater reliability. All dependent measures had good interrater reliability (number intentional exchanges: Pearson correlation = 0.99; unintentional exchanges: Pearson correlation = 0.96; touch object: $\kappa = 0.96$, touch experimenter: $\kappa = 0.92$).

Results

As in Experiment 4, subjects of both species actively participated in the game. 87% of subjects manipulated the ball when it was thrown to them, and 38% of subjects scored at least one intentional exchange with the experimenter. Chimpanzees intentionally exchanged the ball with the experimenter an average of 13 ± 4 times per trial and unintentionally exchanged the ball 31 ± 4 times per trial. Bonobos intentionally exchanged the ball on far fewer trials (1 ± 0.7) and unintentionally exchanged the ball 23 ± 5 times per trial. The percent of exchanges characterized as intentional was significantly higher in chimpanzees than bonobos ($t_{8,83} = 2.6, p = .03$).

To address whether subjects' behavior during the interruption period differed following the test or control trials, we made within-subjects comparisons for each of the dependent measures recorded during the interruptions. For chimpanzees, the number of interruption periods that subjects touched the experimenter, or the ball was unrelated to whether the interruption followed a test or control trial (touch ball—control: 3.5 ± 0.3 , test: 2.9 ± 0.3 ; $t_7 = 1.9, p = .10$; touch experimenter—control: 3.1 ± 0.4 , test: 2.3 ± 0.5 ; $t_7 = 1.22, p = .26$). Surprisingly, chimpanzees were more likely to touch both the experimenter and the ball (during the same interruption) following control trials than test trials (control = 2.6 ± 0.4 , Test 1.3 ± 0.5 ; $t_7 = 2.43, p = .05$). For bonobos, none of these measures differed between interruptions following test or control trials (touch ball—control: 1.5 ± 0.4 , test: $1.4 \pm .04$; $t_{15} = 0.37, p = .71$; touch experimenter—control: 1.1 ± 0.3 , test: 0.6 ± 0.2 ; $t_{15} = 1.26, p = .23$; touch both—control: 0.4 ± 0.2 , test: 0.1 ± 0.1 ; $t_{15} = 1.17, p = .26$).

To assess overall patterns during the interruption periods, and to directly compare chimpanzees and bonobos, we conducted repeated-measures ANOVAs with species and condition (test, control) as factors. Analysis of the number of interruption periods that subjects touched the ball revealed a main effect of species ($F_{1,22} = 16.74, p < .01$) indicating that chimpanzees touched the ball more frequently than bonobos across conditions (chimpanzee: 3.2 ± 0.3 , bonobo: 1.5 ± 0.2). There was no main effect of condition ($F_{1,22} = 1.17, p = .29$), or condition by species interaction ($F_{1,22} = 0.34, p = .57$). Analysis of the number of interruption periods that subjects touched the experimenter showed the same pattern. Overall, chimpanzees touched the experimenter more frequently than bonobos (chimpanzee: 2.7 ± 0.2 , bonobo: 0.9 ± 0.2 ; $F_{1,22} = 41.81, p < .01$), and there was no effect of condition ($F_{1,22} = 3.32, p = .08$), or condition by species interaction ($F_{1,22} = 0.25, p = .62$). Lastly, analysis of the number of interruptions that subjects touched both the ball and the experimenter revealed a main effect of condition ($F_{1,22} = 10.73, p < .01$), species ($F_{1,22} = 36.24, p < .01$), and a condition by species interaction ($F_{1,22} = 5.14, p = .03$). Specifically there was an overall pattern for subjects to touch both the ball and the experimenter more frequently following the control (1.5 ± 0.2) than test trials (0.7 ± 0.2), and this difference was larger in chimpanzees than bonobos.

Discussion

This experiment largely replicated the findings of Experiment 4 showing that nonhuman apes will engage in triadic joint activities with a human. Chimpanzees showed the strongest motivation and

capacity for joint activity, exchanging the ball more readily than bonobos. The inclusion of a control condition suggested that subjects' behaviors during the interruption of the triadic game were not solely for the purpose of restarting joint interaction with the object. Instead, subjects were just as likely to show these same behaviors after a bout of dyadic as opposed to triadic activity. This suggests that subjects were using these behaviors to engage the experimenter more generally and were not specific to the previously established social activity.

However, these findings also point out the difficulty of interpreting nonhuman apes' behavior in these kinds of tasks. Without verbal exchanges expressing joint commitment, it is unclear what nonverbal behaviors would indicate shared intentions in a nonhuman species (but for possible approaches see Greenberg, Hamann, Warneken, & Tomasello, 2010; Hamann, Warneken, Greenberg, & Tomasello, 2011).

General Discussion

In these five studies, chimpanzees and bonobos demonstrated the capacity and interest for a variety of triadic social activities. These findings are consistent with observational studies of these species (Gómez, 2010; Goodall, 1986; Kano, 1992; Nishida et al., 1999; Ramsey & McGrew, 2005; Tanner & Byrne, 2010), and indicate that the results of Warneken et al. (2006) should be interpreted with caution. Specifically, the lack of interest in social games reported by Warneken et al. may have been specific to the nature of the activities, which were designed for human children. Here, we used relatively simple social games, based on those reported to occur spontaneously in observational studies of apes (Gómez, 2010; Ramsey & McGrew, 2005; Tanner & Byrne, 2010), and observed near-universal participation. In addition, subjects of both species showed interest and skill at participating in a turn-taking game similarly to human children (Gustafson et al., 1979; Ratner & Bruner, 1978), and some chimpanzee subjects touched the experimenter with the stick during the interruption periods, a possible indication of reciprocating roles.

Nonetheless, our findings support the hypothesis that humans may differ from other apes in terms of our motivation to *share* social activities. Although bonobos and chimpanzees were tolerant enough to interact jointly with an object, they did not prefer to do so when the interaction was with a conspecific. These findings complement recent work comparing human children and chimpanzees on cooperative tasks; compared with children who preferred to work together, chimpanzees showed no preference between individual and collaborative solutions to a food-acquisition task (Rekers, Haun, & Tomasello, 2011).

Our findings may be interpreted to support the hypothesis that nonhuman apes do not have the inherent social motivation to support the development of shared intentions (Tomasello et al., 2005). However, it is unknown to what degree the apparent gulf between humans and other apes is also affected by ontogenetic factors. To our knowledge, all studies of shared intentions in humans have been conducted in postindustrialized nations, and little is known about the development of these social-cognitive abilities cross-culturally (Tomasello, 2011). However, the growing field of cross-cultural developmental psychology suggests that the basic sociocognitive abilities of human children show remarkably similar trajectories despite enormous differences in the ontogenetic

environment (Callaghan et al., 2011; Shahaeian, Peterson, Slaughter, & Wellman, 2011). Similarly, although apes raised in human environments differ behaviorally from wild apes, "enculturated" apes never develop many of the sociocognitive skills believed to underlie shared intentions in humans (Call, 2009; Carpenter, Tomasello, & Savage-Rumbaugh, 1995; Gómez, 2010; Greenfield & Savage-Rumbaugh, 1991). Therefore, uniquely human biology, in conjunction with species-typical ontogeny, supports the development of skills for shared intentionality.

In previous studies of ape cooperation, tolerance has been shown to constrain a dyad's ability to collaborate (Hare et al., 2007; Melis et al., 2006b). Nevertheless, it is unlikely that social intolerance is the predominant explanation for the low levels of conspecific interaction that we observed. Both species were capable of handling an object jointly even though they did not spontaneously prefer this option. Therefore, object-based interactions are simply not constrained by tolerance in the same way as cooperation to obtain food (Hare et al., 2007). This finding has implications for the evolution of human cooperation and culture, because greater social tolerance has been suggested as one important precursor to human-like social systems (Hare, 2007; Tomasello, 2011). Our results indicate that these evolutionary shifts in social tolerance may have been specific to the cooperative acquisition and sharing of food, practices that are common across human societies (Hill et al., 2009; Hill, Kaplan, Lancaster, & Hurtado, 2000).

Another important factor shaping coordinated social activity is the identity of the social partner. The experiments in which young children have shown the most coordination toward shared activities have incorporated an adult, who helps to scaffold the cooperative activity (Bakeman & Adamson, 1984; Warneken et al., 2006). Our data suggest that this is also the context in which nonhuman apes are most likely to engage in coordinated collaborative behavior. Bakeman and Adamson (1984) directly compared infants' abilities to engage in joint activities with a parent, or a peer, and reported that joint engagement was much more common when infants interacted with their mothers. Therefore careful comparisons of pairs of apes and human children tested under similar circumstances will be important for future research on this topic.

The experiments reported here complement earlier studies of triadic interactions in great apes, which have described the behavior of smaller samples in great detail. By testing a large, demographically diverse sample of apes we were able to compare behavior across species, sexes, and age groups. These comparisons provide an important measure of inter- and intraspecific variation not previously described. However, by virtue of our sample size and design, it was impractical to evaluate behavior with the level of detail employed in more intensive investigations (e.g., Gómez, 2010; Pika & Zuberbühler, 2008; Tanner & Byrne, 2010). Because each of these approaches has tradeoffs with regard to scope and detail, we anticipate that they will play complementary roles in future research on this topic.

Lastly, measuring the spontaneous behavior of subjects may not be the most powerful way to assess an understanding of shared intentions in nonhumans (for other approaches see Greenberg et al., 2010; Hamann et al., 2011). Future tests may benefit by incorporating the more recent procedures developed by Warneken et al. (2012) to determine whether nonhuman apes respond differ-

ently to play partners who disrupt the activity because they are unable versus unwilling to participate. Given the motivational results above, this paradigm will be most powerfully adopted with a large group of young bonobos and chimpanzees. In addition, the social tasks reported here could easily be incorporated into such a design to assure that ape subjects are interested and motivated by the social games. Finally, recent advances in noninvasive eye tracking (e.g., Kano & Tomonaga, 2011; Myowa-Yamakoshi, Scola, & Hirata, 2012) may also help to characterize subtle behaviors such as gaze alternation, and looking to the experimenter's face during the disrupted social activities.

Taken together, these experiments support the hypothesis that our species' capacity for cooperation emerged from preexisting capabilities for coordinated action, likely present in the last common ancestor of bonobos, chimpanzees, and humans. Building on these capacities, humans have evolved unique motivations for collaboration, supported by a psychological system for understanding, and sharing intentions with others. The extent to which these capacities are shared with other primates remains an important topic for empirical study.

References

- Bakeman, R., & Adamson, L. B. (1984). Coordinating attention to people and objects in mother-infant and peer-infant interaction. *Child Development, 55*, 1278–1289. doi:10.2307/1129997
- Bauer, E. B., & Smuts, B. B. (2007). Cooperation and competition during dyadic play in domestic dogs, *canis familiaris*. *Animal Behaviour, 73*, 489–499. doi:10.1016/j.anbehav.2006.09.006
- Bekoff, M., & Byers, J. A. (1998). *Animal play: Evolutionary, comparative, and ecological perspectives*. Cambridge, UK: Cambridge University Press. doi:10.1017/CBO9780511608575
- Boesch, C. (2002). Cooperative hunting roles among tai chimpanzees. *Human Nature, 13*, 27–46. doi:10.1007/s12110-002-1013-6
- Boesch, C., Hohmann, G., & Marchant, L. F. (Eds.). (2002). *Behavioural diversity in chimpanzees and bonobos*. Cambridge, UK: Cambridge University Press. doi:10.1017/CBO9780511606397
- Burkart, J. M., Hrdy, S. B., & Van Schaik, C. P. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology, 18*, 175–186. doi:10.1002/evan.20222
- Call, J. (2009). Contrasting the social cognition of humans and nonhuman apes: The shared intentionality hypothesis. *Topics in Cognitive Science, 1*, 368–379. doi:10.1111/j.1756-8765.2009.01025.x
- Callaghan, T. C., Moll, H., Rakoczy, H., Warneken, F., Liszkowski, U., Behne, T., & Tomasello, M. (2011). *Early social cognition in three cultural contexts*. New York, NY: Wiley-Blackwell.
- Carpenter, M., Tomasello, M., & Savage-Rumbaugh, S. (1995). Joint attention and imitative learning in children, chimpanzees, and enculturated chimpanzees. *Social Development, 4*, 217–237. doi:10.1111/j.1467-9507.1995.tb00063.x
- Cox, D., Rosen, N., Montgomery, C., & Seal, U. (2000). *Chimpanzee sanctuary guidelines and management workshop: Report*. Apple Valley, MN: Conservation Breeding Specialist Group.
- Farmer, K. H. (2002). Pan-African sanctuary alliance: Status and range of activities for great ape conservation. *American Journal of Primatology, 58*, 117–132. doi:10.1002/ajp.10054
- Gilbert, M. (1992). *On social facts*. Princeton, NJ: Princeton University Press.
- Gómez, J. C. (2010). The ontogeny of triadic cooperative interactions with humans in an infant gorilla. *Interaction Studies: Social Behaviour and Communication in Biological and Artificial Systems, 11*, 353–379. doi:10.1075/isis.11.3.02gom
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Belknap Press of Harvard University Press.
- Gräfenhain, M., Behne, T., Carpenter, M., & Tomasello, M. (2009). Young children's understanding of joint commitments. *Developmental Psychology, 45*, 1430–1443. doi:10.1037/a0016122
- Greenberg, J. R., Hamann, K., Warneken, F., & Tomasello, M. (2010). Chimpanzee helping in collaborative and noncollaborative contexts. *Animal Behaviour, 80*, 873–880. doi:10.1016/j.anbehav.2010.08.008
- Greenfield, P., & Savage-Rumbaugh, E. S. (1991). Imitation, grammatical development, and the invention of protogrammar by an ape. In N. A. Krasnegor, D. M. Rumbaugh, R. L. Schiefelbusch & M. Studdert-Kennedy (Eds.), *Biological and behavioral determinants of language development* (pp. 235–258). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Gustafson, G. E., Green, J. A., & West, M. J. (1979). The infant's changing role in mother-infant games: The growth of social skills. *Infant Behavior & Development, 2*, 301–308. doi:10.1016/S0163-6383(79)80039-9
- Hamann, K., Warneken, F., Greenberg, J. R., & Tomasello, M. (2011). Collaboration encourages equal sharing in children but not in chimpanzees. *Nature, 476*, 328–331.
- Hare, B. (2007). From nonhuman to human mind - what changed and why? *Current Directions in Psychological Science, 16*, 60–64. doi:10.1111/j.1467-8721.2007.00476.x
- Hare, B. (2011). From hominoid to hominid mind: What changed and why? *Annual Review of Anthropology, 40*, 293–309. doi:10.1146/annurev-anthro-081309-145726
- Hare, B., & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology, 20*, R230–R231. doi:10.1016/j.cub.2009.12.038
- Hare, B., Melis, A. P., Woods, V., Hastings, S., & Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology, 17*, 619–623. doi:10.1016/j.cub.2007.02.040
- Hashimoto, C. (1997). Context and development of sexual behavior of wild bonobos (*pan paniscus*) at Wamba, Zaire. *International Journal of Primatology, 18*, 1–21. doi:10.1023/A:1026384922066
- Herrmann, E., Hare, B., Cissewski, J., & Tomasello, M. (2011). A comparison of temperament in nonhuman apes and human infants. *Developmental Science, 14*, 1393–1405. doi:10.1111/j.1467-7687.2011.01082.x
- Hill, K., Barton, M., & Hurtado, A. M. (2009). The emergence of human uniqueness: Characters underlying behavioral modernity. *Evolutionary Anthropology, 18*, 187–200. doi:10.1002/evan.20224
- Hill, K., Kaplan, H., Lancaster, J., & Hurtado, A. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology, 9*, 156–185. doi:10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.0.CO;2-7
- Hirata, S. (2003). Cooperation in chimpanzees. *Hattatsu, 95*, 103–111.
- Hirata, S., Morimura, N., & Fuwa, K. (2010). Intentional communication and comprehension of the partner's role in experimental cooperative tasks. In E. Lonsdorf, S. Ross, T. Matsuzawa & J. Goodall (Eds.), *The mind of the chimpanzee: Ecological and experimental perspectives* (pp. 251–265). Chicago, IL: University of Chicago Press.
- Ingmanson, E. (1996). Tool using behaviour in wild pan paniscus: Social and ecological considerations. In A. Russon, K. Bard, & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 190–210). Cambridge, UK: Cambridge University Press.
- Kano, F., & Tomonaga, M. (2011). Perceptual mechanism underlying gaze guidance in chimpanzees and humans. *Animal Cognition, 14*, 377–386. doi:10.1007/s10071-010-0372-3
- Kano, T. (1992). *The last ape: Pygmy chimpanzee behavior and ecology*. Stanford, CA: Stanford University Press.
- MacLean, E. L., & Hare, B. (2012). Bonobos and chimpanzees infer the target of another's attention. *Animal Behaviour, 83*, 345–353. doi:10.1016/j.anbehav.2011.10.026

- Melis, A. P., Hare, B., & Tomasello, M. (2006a). Chimpanzees recruit the best collaborators. *Science*, *311*(5765), 1297–1300. doi:10.1126/science.1123007
- Melis, A. P., Hare, B., & Tomasello, M. (2006b). Engineering cooperation in chimpanzees: Tolerance constraints on cooperation. *Animal Behaviour*, *72*, 275–286. doi:10.1016/j.anbehav.2005.09.018
- Melis, A. P., Hare, B., & Tomasello, M. (2009). Chimpanzees coordinate in a negotiation game. *Evolution and Human Behavior*, *30*, 381–392. doi:10.1016/j.evolhumbehav.2009.05.003
- Mendoza-Granados, D. & Sommer, V. (1995). Play in chimpanzees of the Arnhem zoo: Self-serving compromises. *Primates*, *36*, 57–68. doi:10.1007/BF02381915
- Mitani, J. C., Merriwether, D. A., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, *59*, 885–893. doi:10.1006/anbe.1999.1389
- Myowa-Yamakoshi, M., Scola, C., & Hirata, S. (2012). Humans and chimpanzees attend differently to goal-directed actions. *Nature Communications*, *3*, 693. doi:10.1038/ncomms1695
- Nishida, T., Kano, T., Goodall, J., McGrew, W. C., & Nakamura, M. (1999). Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science*, *107*, 141–188. doi:10.1537/ase.107.141
- Nishida, T., & Wallauer, W. (2003). Leaf-pile pulling: An unusual play pattern in wild chimpanzees. *American Journal of Primatology*, *60*, 167–173. doi:10.1002/ajp.10099
- Palagi, E. (2006). Social play in bonobos (*pan paniscus*) and chimpanzees (*pan troglodytes*): Implications for natural social systems and interindividual relationships. *American Journal of Physical Anthropology*, *129*, 418–426. doi:10.1002/ajpa.20289
- Petrù, M., Spinka, M., Charvatova, V., & Lhota, S. (2009). Revisiting play elements and self-handicapping in play: A comparative ethogram of five old world monkey species. *Journal of Comparative Psychology*, *123*, 250–263. doi:10.1037/a0016217
- Pika, S., & Zuberbühler, K. (2008). Social games between bonobos and humans: Evidence for shared intentionality? *American Journal of Primatology*, *70*, 207–210. doi:10.1002/ajp.20469
- Plooi, F. X. (1978). Some basic traits of language in wild chimpanzees? In A. Lock (Ed.), *Action, gesture and symbol* (pp. 111–131). London, UK: Academic Press.
- Ramsey, J. K., & McGrew, W. C. (2005). Object play in great apes. Studies in nature and captivity. In A. Pellegrini, & P. Smith (Eds.), *The nature of play: Great apes and humans* (pp. 89–112). New York, NY: Guilford.
- Ratner, N., & Bruner, J. (1978). Games, social exchange and the acquisition of language. *Journal of Child Language*, *5*, 391–401. doi:10.1017/S0305000900002063
- Rekers, Y., Haun, D., & Tomasello, M. (2011). Children, but not chimpanzees, prefer to collaborate. *Current Biology*, *21*, 1756–1758. doi:10.1016/j.cub.2011.08.066
- Searle, J. R. (1995). *The construction of social reality*. New York, NY: Free Press.
- Shahaian, A., Peterson, C. C., Slaughter, V., & Wellman, H. M. (2011). Culture and the sequence of steps in theory of mind development. *Developmental Psychology*, *47*, 1239. doi:10.1037/a0023899
- Takeshita, H., & Walraven, V. (1996). A comparative study of the variety and complexity of object manipulation in captive chimpanzees (pan troglodytes) and bonobos (pan paniscus). *Primates*, *37*, 423–441. doi:10.1007/BF02381377
- Tanner, J. E., & Byrne, R. W. (2010). Triadic and collaborative play by gorillas in social games with objects. *Animal Cognition*, *13*, 591–607. doi:10.1007/s10071-009-0308-y
- Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Tomasello, M. (2009). *Why we cooperate*. Cambridge, MA: MIT Press.
- Tomasello, M. (2011). Human culture in evolutionary perspective. In M. Gelfand (Ed.), *Advances in culture and psychology*. Oxford, UK: Oxford University Press.
- Tomasello, M., & Carpenter, M. (2007). Shared intentionality. *Developmental Science*, *10*, 121–125. doi:10.1111/j.1467-7687.2007.00573.x
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, *28*, 675–691. doi:10.1017/S0140525X05000129
- Tomasello, M., & Herrmann, E. (2010). Ape and human cognition: What's the difference? *Current Directions in Psychological Science*, *19*, 3–8. doi:10.1177/0963721409359300
- Trevarthen, C. (1982). The primary motives for cooperative understanding. In G. Butterworth, & P. Light (Eds.), *Social cognition: Studies of the development of understanding* (pp. 77–103). London, UK: Harvester Press.
- Trevarthen, C., & Hubble, P. (1978). Secondary intersubjectivity: Confidence, confiding, and acts of meaning in the first year. In A. Lock (Ed.), *Action, gesture and symbol: The emergence of language* (pp. 183–229). London, UK: Academic Press.
- Tuomela, R. (1995). *The importance of us: A philosophical study of basic social notions: A philosophical study of basic social notions*. Stanford, CA: Stanford University Press.
- Warneken, F., Chen, F., & Tomasello, M. (2006). Cooperative activities in young children and chimpanzees. *Child Development*, *77*, 640–663. doi:10.1111/j.1467-8624.2006.00895.x
- Warneken, F., Gräfenhain, M., & Tomasello, M. (2012). Collaborative partner or social tool? New evidence for young children's understanding of joint intentions in collaborative activities. *Developmental Science*, *15*, 54–61. doi:10.1111/j.1467-7687.2011.01107.x
- Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, *138*, 299–327. doi:10.1163/15685390152032488
- Wobber, V., & Hare, B. (2011). Psychological health of orphan bonobos and chimpanzees in African sanctuaries. *Plos One*, *6*, e17147. doi:10.1371/journal.pone.0017147
- Yamamoto, S., Humle, T., & Tanaka, M. (2009). Chimpanzees help each other upon request. *Plos One*, *4*, e7416. doi:10.1371/journal.pone.0007416

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