Abstract

Cooperative behaviors such as helping, sharing, and collaboration are important components of human social life. Here, we summarize recent experiments that provide insight into both the ontogenetic and phylogenetic origins of these behaviors. Specifically, by combining a developmental and comparative approach, these experiments investigate the emergence of these behaviors in human ontogeny, and highlight similarities as well as differences with those of chimpanzees and bonobos. We review altruistic and mutualistic behaviors as two broad classes of cooperative behaviors that are underlain by different motivational and cognitive processes, emphasizing the importance of investigating proximate mechanisms to gain a comprehensive understanding of human cooperation.

Key Words: Cooperation, altruism, mutualism, joint intentions, human children, chimpanzees, bonobos

Introduction

Cooperation is a hallmark of human social life, ranging from simple acts of helping another individual to large-scale collective practices in which multiple people pool their efforts to achieve goals that lie beyond the means of any one individual. Cooperative behaviors have been investigated concerning the fitness costs and benefits that these behaviors entail for the individuals involved, raising several issues about the circumstances under which they can evolve by natural selection. These questions have been a challenge for biology, and altruistic behaviors, in particular, have been somewhat mysterious phenomena until seminal figures such as Hamilton and Trivers provided explanations of how these behaviors can evolve by natural selection (Hamilton, 1964; Trivers, 1971). However, cooperative behaviors have not only been challenging for evolutionary theory in trying to explain its emergence by natural selection, but also raise important and challenging questions for psychological research, as cooperative behaviors are often based on complex cognitive and motivational processes. This appears to be especially true for human cooperative behaviors, because humans develop the skills to perform a variety of cooperative behaviors that are probably unparalleled anywhere else in the animal kingdom. As Sober put it poignantly, “a mindless organism can be an evolutionary altruist” (2002, p. 17), referring to the evolutionarily relevant fitness payoff. However, a mindless altruist will be constrained to cooperate in a very limited set of situations, lacking the flexibility to deal with new exigencies and take advantage of novel opportunities. Humans, on the other hand, possess proximate (psychological) processes to perform variable cooperative behaviors that are special and, perhaps, unique in the animal kingdom. For example, a skillful helper must be able to represent the goal that another person is trying but failing to achieve and, in addition, have the
motivation to act on behalf of the other (Warneken & Tomasello, 2006); to engage in contingent reciprocal altruism, an individual has to be able to select individuals who are likely to return the favor in the future and, in addition, have the ability to forego an immediate benefit (Stevens & Hauser, 2004; Trivers, 1971). Finally, participants in a mutualistic collaborative activity have to represent a collective goal and integrate their individual actions by dividing up the labor and aligning their own interests with those of others (Tomasello, Carpenter, Call, Behne, & Moll, 2005).

Therefore, to gain a comprehensive understanding of cooperative behaviors, we have to investigate the psychological processes involved in different cooperative behaviors. By studying these processes, we can gain a better understanding of the factors that both enable and constrain cooperative behaviors. In particular, as we will argue in this chapter, what might appear trivial in terms of the fitness costs and benefits (such as conspecifics engaging in mutualistic behaviors) is not at all trivial concerning the psychological mechanisms necessary to engage therein, potentially explaining differences in the occurrence of cooperative behaviors across species.

In our review, we will focus on the ontogeny of cooperation in human children in comparison to the behaviors of our closest living evolutionary relatives—chimpanzees and bonobos. The goal is to provide insight into the ontogenetic emergence of cooperative behaviors in humans and differentiate between those aspects of cooperative behaviors that potentially already characterized the last common ancestor from those aspects that are unique to the human lineage. Another reason for this focus is simply that a significant body of empirical evidence has been gathered on these species in recent years, occasionally even allowing direct comparisons between humans and mainly chimpanzees. As our focus is on the proximate psychological mechanisms that underlie these behaviors, we will constrain ourselves to experimental studies. For reviews of naturalistic observations of cooperative behaviors (which are often also the motivator for more controlled laboratory studies to get at the underlying psychology), see in particular Muller and Mitani (2005) and Boesch (chapter 26 of this volume). We will begin our review with human children, and then move on to compare their behavior with the behavior of chimpanzees and bonobos.

We use cooperation (or “cooperative behaviors”) as an umbrella term for all social behaviors among conspecifics that provide a benefit to another individual (the recipient) or are beneficial to both the actor and the recipient. These can be broken down into two broad classes of cooperation based on their influence on the immediate payoff for actor and recipient: (1) altruistic or investing behaviors in which only the recipient obtains immediate benefits, and the actor’s motivation is to invest toward another person’s goal, problem, need, emotion, and so forth, and (2) mutualistic behavior in which two or more individuals coordinate their actions to produce outcomes from which both individuals benefit immediately, such as obtaining a common resource or producing an effect that one individual would not be able to produce on his or her own (Melis & Semmann, 2010).

Altruistic Behaviors

Children

Altruistic behaviors come in many forms. People share food, donate money to strangers, comfort people in distress, hold doors open for delivery men, help old ladies across the street, and give directions to those who are lost in the inner city jungle. Warneken and Tomasello (2009a) provided the following typology to classify the various altruistic behavior under study in psychology and related disciplines (mainly based on the commodity that is provided): Comforting others by providing emotional support to a person in distress, sharing valuable goods such as food, informing others by providing the piece of information that others are lacking, and helping others to achieve goals by acting for them. Traditionally, developmental psychology has focused on comforting (or empathic intervention) in the study of young children. However, in recent years, several studies have been conducted about the latter three types of altruistic behaviors, occasionally complemented by comparative studies with chimpanzees (and sometimes, but rarely, bonobos). Therefore, in our review of altruistic behaviors, we will focus on these recent studies on sharing, helping, and informing.

SHARING IN CHILDREN

Sharing of resources by definition involves an immediate cost, because the donor has to give up a resource to benefit another individual. Correspondingly, sharing is one of the most extensively studied types of altruistic behaviors in both humans and other animals. Despite the importance of this behavior and the large body of research on sharing in adult humans (by anthropologists and behavioral economists alike), surprisingly few
Schematic studies have been conducted with young children. Thus, to what extent are children able to detect the need of a potential recipient and have the motivation to share a resource on the other's behalf? One piece of evidence on sharing in young children comes from a study by Brownell and colleagues (Brownell, Svetlova, & Nichols, 2009), demonstrating that 2-year-olds begin to be responsive to another person's desire. Specifically, toddlers could either pull the rope of an apparatus that would deliver a snack to themselves and a snack to a bystander (1/1-option) or pull another rope delivering food only to themselves (1/0-option; an apparatus adapted from Silk et al. 2005 for use with chimpanzees). Therefore, children could deliver food to the other individual at no extra cost to themselves. Results showed that whereas 18-month-old children chose between these two options randomly, 25-month-old children chose the 1/1-option that rewarded both themselves and the bystander. Importantly, the older children showed this tendency only in condition in which the bystander had verbalized a desire for the food (“I like crackers.”), which suggests that, in this type of situation, children need explicit cues from the recipient to note their need. Implicit communication from the recipient appears to be critical to elicit sharing in these young children. It also indicates that a child’s failure to share might not necessarily be due to a lack of motivation, but the social-cognitive ability to attribute need to other individuals. Thus, at least when need is expressed directly, children begin to share resources with others shortly after their second birthday.

Studies with older children, often using variations of the Dictator and the Ultimatum Games, indicate an increase of altruistic choices, as well as an emerging use of equality (Gummerum, Hanoch, & Keller, 2009). For example, in Moore (2009), 4- to 5-year-old children chose equal rewards for themselves and another befriended child rather than taking a selfish option with a higher payoff for themselves. Toward school age, costly sharing increases, including situations in which children “interact” with anonymous others. Blake and Rand (2010) point out that their own experiment and other studies using the Dictator Game indicate that children's tendency to at least something increases steadily over development between 3 and 9 years of age. Moreover, the experiments in which children allocate actual resources, as well as studies using hypothetical situations, converge on the finding that between 5 and 7 years of age, children most often share according to equality, even if the alternative would be to obtain a larger reward for themselves (Blake & Rand, 2010; Damon, 1977; Fehr, Bernhard, & Rockenbach, 2008; Hook & Cook, 1979).

The aforementioned studies typically involve windfall situations in which children divide up a resource that is just given to them to share. Using a slightly different approach based on the notion that resource sharing is often preceded by joint work to obtain the resource in the first place, Warneken and colleagues conducted a study that indicates that children as young as 3 years of age appear to have a sense of equality (Warneken, Lohse, Melis, & Tomasello, 2011). Specifically, 3-year-old peers had to solve a collaborative problem-solving task to obtain four items of a certain resource (e.g., food or stickers). The main finding was that children shared the resource equally most of the time after this collaboration condition. Hamann, Warneken, Greenberg, and Tomasello (2011) directly compared a collaboration and a windfall condition with 3-year-olds, in which one child ended up with three toys and the other child with only one toy. The “lucky” child was more likely to share one of the three toys with the “unlucky” child after they had worked together (collaboration condition) than when the rewards were just in front of them (windfall). Moreover, in another experiment children either worked individually on a task or collaborated, in both cases resulting in an uneven outcome of three versus one toy. Children were more likely to rectify the situation and produce equal outcomes in the collaboration condition as compared to the individual work condition. This indicates that equality begins to play a role quite early in development, at least in collaborative situations in which children work toward a common resource. Equal sharing appears to be facilitated if it occurs as part of a joint activity with joint effort.

Taken together, from early on in their ontogeny, children begin to share resources with others. For young children, it appears critical that the recipient is present and makes her desire explicit, but toward middle childhood, children begin to share resources also with absent individuals. Toward school age, children express a sense of equality that they uphold even if it entails self-sacrifice in windfall situations. Evidence for an early emerging sense of equality comes from studies in which children collaborate to obtain a resource, dividing the resource equally if both partners have worked on the task together.

INFORMING IN CHILDREN

Another important form of altruistic behavior is apparent in the gestural communication of young
children: infants will point to things that other people are searching for. These behaviors come at almost zero cost (as the children neither have to put a lot of effort in producing a gesture nor do they give up a valuable resource), but they exemplify the social cognitive capacities that young infants bring to bear to act on behalf of others. Specifically, several experiments have demonstrated that, from the time that infants begin to point at around 1 year of age, they already use this newly acquired prelinguistic device for altruistic purposes. For example, in one study a protagonist sat at a desk and used an object such as a hole puncher, then left the scene, upon which an “evil” experimenter approached and put the hole puncher and another irrelevant distractor object in two different locations behind the desk (Liszowski, Carpenter, Striano, & Tomasello, 2006). When the protagonist returned and sat down at the desk, she lifted her arms and looked around in bewilderment. Results showed that infants pointed more often to the location of the hole puncher than to the distractor object, indicating that infants understood which of the two objects the protagonist was looking for and displayed the altruistic motivation to help her in her search by so-called informative pointing. A follow-up study showed that these young infants more frequently point to an object that disappeared without the protagonist witnessing it over an object that she saw falling, indicating that they take into account the protagonist’s state of knowledge and ignorance when pointing for them (Liszowski, Carpenter, & Tomasello, 2008). Therefore, human infants not only point imperatively to have other people bring them things or do something for them, but also to point out relevant information to others when those others need it to accomplish their goals. This behavior is interesting because it highlights the social-cognitive capacity to respond appropriately to the people who express ignorance about certain aspects of the world that the child is knowledgeable of. Thus, young children use their ability to detect epistemic states to intervene altruistically by sharing information.

**INSTRUMENTAL HELPING IN CHILDREN**

Human altruistic behaviors are not only expressed in the tendency to share material resources, share information, or comforting others to alter their emotional state, but also in such mundane acts as picking up a dropped object, holding a door open, or trying to fix something if others fail. These behaviors differ from sharing and informing in that, rather than giving a resource or communicating, the helper assists instrumentally by contributing to the other person’s goal fulfillment with her own actions. Thus, in order to help in these situations, the helper has to be able to detect the goal that the person is trying but failing to achieve (the object being out of reach, trying to enter through a door, etc.) and have the altruistic motivation to act on behalf of the other’s goal (rather than for one’s own goal or an immediate benefit to oneself).

Concerning the social-cognitive component for instrumental helping, it is well known that by at least 12 to 18 months of age, children are able to represent other people’s behaviors in terms of their intentions. For example, children distinguish accidental from purposeful actions (for an overview see Tomasello et al., 2005) and infer the goal a person was trying to achieve, even if all they see is the person’s failure (thus witnessing the unintended rather than the intended outcome; Meltzoff, 1995). Therefore, already in the second year of life, infants appear to possess the social-cognitive skills necessary to engage in instrumental helping. Concerning the motivational component for instrumental helping, these young children also intervene on behalf of others’ negative emotional states (such as comforting a person in distress; for an overview see Eisenberg, Fabes, & Spinrad, 2006) and engage in informative pointing (as described earlier). Thus, will young children put these two things together and also help instrumentally by assisting them to achieve an unfulfilled goal?

A series of studies demonstrated that young children are quite sophisticated helpers. In a first experimental study, Warneken and Tomasello (2006) presented 18-month-old infants with 10 different situations in which an adult experimenter was having trouble achieving a variety of goals. For example, the experimenter used clothespins to hang towels on a line when he accidentally dropped a clothespin on the floor and was unsuccessfully reaching for it. In another helping situation, the experimenter was trying to put a stack of magazines into a cabinet, but he could not open the doors because his hands were full. The main finding from this study was that young children provided help spontaneously, without receiving a concrete reward, without being asked to do so, and without being praised for their effort. They helped in various situations, requiring them to intervene in different ways, such as picking up out-of-reach objects, completing a failed action after the experimenter’s failed attempt to stack books on top of each other, opening the doors of a cabinet to let the experimenter put magazines inside or bringing out the experimenter’s goal by different means, such
shifting the flap of a novel box rather than copying the experimenter’s failed attempt to squeeze a hand through a tiny hole on the box to retrieve his spoon that had fallen inside. Importantly, children performed these behaviors almost exclusively in situations in which help was needed, and not in matched control conditions with the same basic situation, but with no indication that it constituted a problem for the experimenter (such as the experimenter throwing a clothespin on the floor on purpose or trying to put magazines on top of the cabinet rather than inside). These behaviors can, to some extent, already be observed in 14-month-old children, although these younger infants helped reliably only by handing over out-of-reach objects, possibly because in these cases it was easier to determine the goal, and the intervention was more straightforward and easier to perform than in the other types of tasks such as the closed doors of a cabinet or opening a novel box (Warneken & Tomasello, 2007). Further evidence for this comes from a study by Svetlova, Nichols, and Brownell (2010), in which children from 1.5 to 2.5 years of age were more likely to help with concrete goals, such as a person reaching for an object, than in tasks that supposedly require more inferential steps in how to intervene (a person shivering and thus needing a blanket). Moreover, Svetlova and colleagues found that whereas in tasks with more concrete goals, such as the out-of-reach situations, children helped without direct communicative cues from the recipient, explicit communication was necessary to elicit helping in the more complex tasks, especially for the younger children in the sample. Taken together, these experiments indicate that, soon after their first birthdays, children begin to spontaneously help others in simple situations such as helping another person gain an out-of-reach object, and become increasingly more sophisticated over the second year of life, being able to infer goals from situational cues and without direct communication from the recipient.

Children are even able to help when they have to infer another’s goal from what the person does or does not know about the situation. Specifically, in an experiment by Buttelmann, Carpenter, and Tomasello (2009), a protagonist first put a toy into box A, and the toy was then moved to box B, either while the protagonist was absent (ignorant condition) or while the protagonist was present (knowledge condition). When the protagonist subsequently did but failed to open box A and gave up, children 18 months and older did not open box A (the previous location of the toy), but box B (where the toy actually was). Thus, children did not just blindly join into the protagonist’s action to open box A, but inferred that he was actually trying to get at the toy, which was now in a new location. Importantly, children tested in the knowledge condition helped the protagonist to open box A, presumably because they thought that he must have another goal in mind because he was not going for the location of the toy where he had seen it being moved. Therefore, this experiment shows that young children, in fact, help others with the goals they are trying to achieve (and not just complete an action such as failing to open something), and they are able to infer this goal based upon the other person’s knowledge state.

Taken together, these studies highlight the fairly sophisticated social-cognitive skills young children utilize to help instrumentally in various contexts. However, what is the motivational basis of their helping behaviors? The helping behaviors just described are of rather low cost (picking up an object, opening a box). Moreover, it is possible that children are driven by the expectation of external rewards, and helping is only instrumental in achieving this selfish goal.

Concerning the issue of costs, several recent experiments show that children are actually willing to put quite some effort into helping and are willing to forego opportunity costs when others are in trouble. Specifically, in one study, 18-month-old toddlers continued to help over two sessions with 20 helping trials in total, including situations in which they had to cross the testing room and surmount an array of obstacles each time to pick up an object for another person. In other experiments, young children helped in the vast majority of trials even though they had to disengage from a fun activity (a novel toy with flashy lights and sounds) or climb over obstacles to help the experimenter (Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Warneken & Tomasello, 2008). Young children are thus motivated to help, even if it involves opportunity costs or effort to do so.

Concerning the issue of external rewards, in one experiment, Warneken and colleagues (2007) varied whether 18-month-old children would receive a reward for helping (a little toy for picking up an out-of-reach object). We also manipulated whether the helper was reaching for the out-of-reach object. These two manipulations thus enabled us to determine whether children would help predominately because of a selfish goal to receive a concrete reward or because of their altruistic goal to help the person when that person indicated a desire for the object. Results showed that children gave the object
when the person was reaching for it, and they did so irrespective of receiving a reward for their helping. Rewarding was neither necessary nor did it increase the rate of helping over repeated trials. Therefore, what elicited children’s helping was the other person’s unfulfilled goal, and not an immediate reward for themselves. Given the results that children are willing to help under these circumstances, one might pose the question whether children are intrinsically motivated to help others. To investigate this possibility, Warneken and Tomasello (2008) made use of a curious feature of intrinsically motivated behaviors: It is a well-established phenomenon in social psychology that intrinsic rewards can be undermined by salient extrinsic rewards (Deci, 1971; Lepper, Greene, & Nisbett, 1973). For example, one of the classic studies by Lepper and colleagues showed that those children who liked to draw were less likely to draw in a free-play period after they had received a reward for drawing as compared to a group of children who had never drawn in order to receive a reward (Lepper, et al., 1973). The dominant interpretation of this finding is that children’s original intrinsic motivation had been supplanted by an extrinsic one, reducing their tendency to engage in these behaviors spontaneously. Warneken and Tomasello (2008) found that the same applies to the helping behaviors of 20-month-old children. Specifically, those children who, during an initial treatment phase, had been rewarded for helping were less likely to help in a subsequent test phase without rewards than children who had not received a reward (see also Fabes, Fulitz, Eisenberg, May-Plumlee, & Christopher (1989) for school-aged children). This finding provides further evidence for the notion that children help spontaneously because of an intrinsic motivation rather than because they are driven by expectation of extrinsic rewards. External rewards are not only superfluous; they can have a detrimental effect on young children’s altruistic motivation.

In sum, this series of studies demonstrate that the ontogenetic origins of altruistic helping are apparent in early childhood. Infants as young as 14 months of age display spontaneous, unrewarded helping behaviors when another person is unable to achieve his goal. Throughout the second year of life, children become increasingly more flexible in their ability to read the other’s intentions and intervene in different kinds of situations. Human infants use their emerging mind-reading capabilities, not only for their own ends, but also to help others. They are willing to help multiple times and continue to help when the costs for helping are raised. Further experiments confirm that infants are actually motivated by the other’s goal and not an immediate benefit for themselves, since rewarding is neither necessary nor does it increase the rate of helping. On the contrary, children appear to have an initial inclination to help, but extrinsic rewards may diminish it.

These results can be taken as preliminary evidence that humans have a biologically based predisposition to develop altruistic behaviors. More specifically, already in the second year of life, children begin to display a panoply of altruistic behaviors encompassing empathic intervention, informing, helping, and, to some extent, sharing. This highlights the social-cognitive capacities that young children utilize to act altruistically on behalf of others. These findings also challenge the hypothesis that socialization practices in the form of internalized social norms (e.g., Henrich et al., 2005) or external reinforcement through adults (e.g., Bar-Tal, 1982; Dovidio et al., 2006) are the main or only factor leading to altruistic behaviors in children. It seems more plausible to assume that socialization practices operate in concert with a biological predisposition to care about others (see, e.g., Hoffman, 2000 and Warneken & Tomasello, 2009a for details).

This raises the question to what extent these psychological processes are present in our closest evolutionary relatives as well. Comparing the behavior of human children to those of chimpanzees and bonobos is important for at least two reasons. First, it enables us to draw inferences about the phylogenetic origins, that is, whether these processes in human-specific characteristics that emerged after Homo and Pan split or whether they might have been present already in our common ancestor. Second, the presence or absence of these processes can provide insight into the factors that constitute altruistic behaviors in humans. If the altruistic behaviors that we observe in human children necessarily require human-specific socialization practices, such as the transmission and enforcement of norms or external reinforcement through adults, we would not expect to find similar behaviors in our closest evolutionary relatives. If, on the other hand, other great apes display similar tendencies to engage in these basic forms of altruistic behavior, it would provide further evidence for the notion that socialization practices are not the original source of human altruism.

**Altruistic Behaviors in Chimpanzees**

Natural observations suggest that chimpanzees occasionally act on behalf of others. However, the
recent years, several experimental studies have investigated, under controlled conditions, chimpanzees’ tendency and ability to act on behalf of others in situations in which potential helpers could not obtain any immediate benefits or these were kept constant across control conditions. Here, as in our chapter on children, we use the typology proposed by Warnken and Tomasello (2009a) and review what these studies have revealed so far regarding chimpanzees’ ability and propensity to share, help, and inform others.

**SHARING IN CHIMPANZEE**

The general conclusion from studies investigating chimpanzees’ propensity to deliver food rewards to conspecifics seems to be that chimpanzees are indifferent to the welfare of their partners, because subjects did not deliver food to their partner, even if this would come at no cost to themselves (Jensen, Hare, Call, & Tomasello, 2006; Silk, et al., 2005; Vonk, et al., 2008; Yamamoto & Tanaka, 2010). The main method employed in these studies was to let chimpanzees choose between an option that would deliver a food-piece to themselves and another food-piece to a conspecific (1/1 - mutualistic option) or an option that would deliver food only to themselves (1/0 - selfish option). Therefore, delivering food to the partner (positioned in an adjacent room) did not entail any additional costs for the actor. In most of the studies, the two options were presented in form of two out-of-reach trays that subjects had to choose from and pull (Jensen, et al., 2006, experiment 1; Silk, et al., 2005; Vonk, et al., 2008, experiment 2). Surprisingly, chimpanzees chose randomly between the two options. In an attempt to help subjects pay attention to the partner’s reward and overcome potential inhibitory problems when seeing the food rewards in front of them, Yamamoto and Tanaka (2010) modified this paradigm and developed a new task using buttons, whose associations with rewards were less intuitive. However, subjects developed a preference for the mutualistic option in the pretest phase, and carried this preference over to the test, choosing this option equally often in both the partner present and the control (partner absent) conditions. Although theoretically sound, since in these studies chimpanzees could help the partner at no cost for themselves, paradigms in which the potential helpers are occupied obtaining food for themselves bear different difficulties and do not (easily) elicit cooperative behavior in chimpanzees.
Jensen et al. (2006) and Vonk et al. (2008) also conducted experiments, in which the potential helpers were not occupied obtaining food for themselves because the rewards for the actors were eliminated, or actors could first obtain their own food and later provide food to their partners. Overall, subjects behaved similarly in partner-present and control-partner-absent conditions, so that, again, the conclusion from these experiments was not very different from that of previous ones. Only in Jensen et al. (2006, experiment 3) were there some signs of altruism. First, at an individual level, two of the six actors preferentially pulled for the partner, and second, there were more first-trial choices of the partner rope in the test (partner present) than in the control (partner absent).

A recent study by Melis and colleagues (2010), in which rewards for the actors were also eliminated, showed that, under certain circumstances, chimpanzees were willing to actively provide food to others. The main factor eliciting helping in this study was the recipients’ attempts to either get the food or get the attention of the potential helper (see earlier section, “Informing in Children,” for more details). This suggests that food per se does not hinder chimpanzees from acting altruistically as long as partners actively signal their goals and/or desires and the altruistic act does not interfere with the actor’s selfish goals.

The results of Melis et al. (2010) however, do not challenge the conclusion that chimpanzees are not particularly inclined to actively share resources with others (e.g., Warneken & Tomasello, 2009b) since in the majority of naturally occurring situations, sharing food with others does interfere with individuals’ own selfish goals. Natural food sharing situations are, by definition, those in which potential altruists have access to food themselves. Even in mutualistic cooperative situations, in which both individuals could potentially benefit, chimpanzees are particularly competitive over food. In problem-solving tasks, in which two individuals need to work together to access food otherwise inaccessible for all, cooperation is enormously constrained by chimpanzees’ difficulties to share the spoils at the end, and dominants’ tendency to monopolize all food rewards (Hare, Melis, Woods, Hastings, & Wrangham, 2007; Melis, Hare, & Tomasello, 2006a). Interestingly, this is not the case among bonobos, who seem to be more socially tolerant over food, cooperating and sharing the food at the end, even when the food items are clumped in one position and could be easily monopolized (Hare et al., 2007; see also Hare & Kwetuenda, 2010).

Thus, humans’ higher tolerance levels around food and more active forms of food sharing are likely newly evolved traits, which probably played a key role in the evolution of human cooperation.

**INSTRUMENTAL HELPING IN CHIMPANZEEZE**

Recent studies have shown that, under certain circumstances chimpanzees act on others’ behalf assisting them to achieve their goals. In a first study, Warneken and Tomasello (2006) adapted the helping tasks originally used with human infants and found that human-raised chimpanzees helped their human caregiver even in the absence of an external reward. Specifically, they handed her objects she was unsuccessfully reaching for (and did not do so in the control condition in which she was not reaching for them). These chimpanzees were thus able to determine the human’s goal and had the motivation to help her with the goal. However, they did not help reliably in the other types of tasks (opening a door for the other; using different means to open the novel box for the other, etc.). As in the case of the 14-month-old children (Warneken & Tomasello, 2007), this might reflect a difference in the complexity of the goal structure between the different types of tasks, and a certain limitation in chimpanzees’ ability to infer others’ goals. It has to be noted, though, that the subjects were human-raised chimpanzees who helped a caregiver with whom they maintained a close relationship. Therefore, it remains a possibility that they helped the caregiver as a consequence of their daily reinforcement of compliant behavior. Therefore, in a follow-up study (Warneken et al., 2007), a human tested a group of semifree ranging chimpanzees who had not interacted with them before the experiment (no training, no feeding, no previous testing). The chimpanzees in this study behaved like the chimpanzees from Warneken and Tomasello (2006) and helped just like human infants tested in a similar situation. They helped over consecutive trials by handing the out-of-reach object when the experimenter was struggling with an outstretched arm to reach it, and they did so irrespective of being rewarded. Moreover, they continued helping when the costs of helping were slightly increased and subjects were required to climb up into a raceway to pick up the out-of-reach object (Warneken et al., 2007, experiment 2). Taken together, this shows that semifree ranging chimpanzees are also willing and able to help a human stranger obtaining out-of-reach objects, even when helping is made effortful and they receive no immediate benefit for themselves.
However, these positive instances of helping tool consisted in chimpanzees bringing objects to humans, which is something for which they are often rewarded. Furthermore, the most ecologically valid question of whether chimpanzees would help other chimpanzees remained unanswered. Therefore, Warneken et al. (2007, experiment 3) created a novel situation in which chimpanzees could help a conspecific by employing a recently learned skill (see Figure 21.1). In this study one chimpanzee (the recipient) was faced with the problem that a door leading to a room with a piece of food was closed with a chain that he could not release. Only if the other chimpanzee (the subject) released this chain from another room could the recipient enter. Results showed that chimpanzees released the chain significantly more often in the test condition, when the recipient was unsuccessfully trying to enter the room, than in control conditions in which releasing the chain would either not help the recipient because the recipient was trying to go somewhere else or no recipient was present. This shows that recipients’ unsuccessful attempts to open the door provided the subjects with the necessary cues to help them detect the recipients’ goal. Furthermore, in a later study on reciprocity that used the same paradigm, chimpanzees released the chain significantly more often for a conspecific, who had previously helped them, than in the control condition, but equally often for an “unhelpful” conspecific (who had previously eaten the food himself) and in the control (Melis, Hare, & Tomasello, 2008). Thus, these experiments show that chimpanzees are able to use a novel skill to help conspecifics in a novel situation.

The role of the recipient’s cues eliciting helping behavior has been demonstrated in two further studies. Tanamoto, Humle, and Tanaka (2009) found that chimpanzees altruistically helped a conspecific partner transferring a tool the conspecific needed to access food, almost exclusively in situations preceded by recipients’ communicative cues. This included recipients’ behaviors aimed at reaching the tool (e.g., arm poking) and/or drawing the potential helper’s attention towards it (e.g., clapping hands, looking at helper). Chimpanzees virtually never handed over the tool proactively without such a cue. Melis and colleagues (Melis, Warneken, Jensen, et al., 2010) have replicated and extended this finding by showing that, in the presence of recipient’s cues, chimpanzees are willing and able to help a conspecific partner to obtain food and nonfood items. In this study, the potential helper could release a bag with a reward in it that would slide down a ramp toward a recipient. To test whether the presence of food might impede helping, it was varied whether the bag contained food or a token (that the recipient could later exchange for food). Chimpanzees released the bag more often when the recipient was actively trying to access the reward (e.g., by pulling a rope attached to the bag) or communicated toward the potential helper than when the recipient remained passive. However, the tendency to help was not diminished with food rewards (as compared to tokens). Thus, the main factor predicting helping was again the communicative cues (intentional or not) of the recipient.

This series of studies show that, under certain circumstances, and as long as it does not interfere with their immediate selfish goals, chimpanzees act on behalf of others helping them to achieve their goals, including accessing food. However, they seem to engage in instrumental helping in a (re)active rather than proactive way.

INFORMING IN CHIMPANZEES

Despite the low costs of the behavior itself and being an extremely common form of altruism in humans, there is no evidence for altruistic informing in our closest primate relatives. When chimpanzees communicate with others (humans) they seem to do it in an imperative way and for selfish purposes. That is, captive chimpanzees who use pointing-like gestures in interactions with humans, point imperatively, that is, to signal what they want the human to do, whereas there is no evidence that
they do so to provide information altruistically that another individual needs (Leavens, Hopkins, & Bard, 2005; Rivas, 2005; Tomasello, 2008). Bullinger et al. (2011) directly compared two situations in which a human was searching for a misplaced tool and varied whether the chimpanzees needed the tool to access food for itself or if only the human experimenter needed the tool to access food for herself. Chimpanzees pointed reliably only to the tool that they needed for themselves, but rarely did so when the experimenter needed the tool to retrieve a reward for herself. This shows that they produce gestures for selfish but not for altruistic purposes.

It is not quite clear why chimpanzees engage in instrumental helping behaviors but do not seem to perform communicative acts to help others. One hypothesis is that this difference is due to cognitive demands. As mentioned earlier, informing others requires that individuals distinguish between their own knowledge state and the ignorance of others. One possibility is that this is something beyond the cognitive capacities of chimpanzees, and that, even when chimpanzees point reliably to what they need for themselves (as in Bullinger et al., 2011), they are not aiming at changing the ignorance state of the partner (by providing the partner with the necessary information) but, instead, they are just aiming at influencing the partner’s behavior. However, this lean explanation seems to contrast with the results from competitive situations, in which chimpanzees seem to be using information about the attentional and knowledge states of others to outwit them (Hare, Call, & Tomasello, 2001; Kaminski, Call, & Tomasello, 2008). This account can, therefore, not fully explain the finding that chimpanzees do not seem to point informatively for others.

Surprisingly, chimpanzees even seem to have difficulty comprehending pointing gestures when it would be useful to them. A large number of experiments demonstrate that chimpanzees fail to use gestural cues in object-choice paradigms in which an experimenter is using a pointing gesture to indicate the location of the hidden food (see Call & Tomasello, 2005 for an overview). However, if the same situation is framed as a competitive one, and one individual (chimpanzee or human) reaches toward one of the possible locations, chimpanzees have no difficulty inferring that the piece of food must be hidden in that specific location (Hare & Tomasello, 2004). This led Tomasello (2008) to the hypothesis that chimpanzees appear to be unable to comprehend the helpful communicative intent of others. At the same time, chimpanzees do understand on a practical level that other humans can be helpful (or at least useful). This is highlighted in examples such as imperative pointing (to have a human give them something), imperative giving (like handing a container so that the human opens it, Tomasello, 2008) or direct physical contact in which the ape pulls a human toward a location to take action, such as pulling a heavy concrete block (Hirata, Morimura, & Fuwa, 2010). Therefore, although the exact reason is rather unclear, the experimental evidence highlights that chimpanzees appear to have a fundamental lack of understanding about gestures as devices that can be used to convey helpful information, both when they are in the role of the sender or the receiver.

The reported studies provide insight into both the ontogenetic and phylogenetic origins of human altruistic behavior. Young children engage in a variety of altruistic behaviors, highlighting the sophisticated social-cognitive capacities that children are equipped with and use not only for one’s own end, but also sometimes on behalf of others. Also, chimpanzees engage in some forms of altruism, especially instrumental helping. Although there are certain similarities between chimpanzees and humans, the altruistic behaviors of chimpanzees appear to be far more restricted, reflected both in the fact that they engage in some but not all the forms of altruism that we report and the fact that salient cues are important. Nevertheless, these findings indicate that human altruistic behaviors have deep evolutionary roots, predating cultural norms and socialization practices. Thus, it appears that human socialization practices can build upon this biological predisposition, rather than being its origin.

The research just described also shows the importance of investigating the proximate mechanisms underlying social behaviors in humans and other primates. Shifting the focus from the question about the presence of absence of altruistic behaviors, research should address the circumstances in which these tendencies are expressed, determining the psychological factors that enable and constrain these tendencies. This is true for cases in which an agent creates benefit for another individual, and—as we will argue in the remainder of this chapter—it is equally true for behaviors in which social agents create benefits for themselves as well.

**Mutualistic Cooperation**

In mutualistic forms of cooperation, two or more individuals coordinate their actions to produce...
outcomes from which all individuals can benefit, from an evolutionary perspective, these behaviors do not pose a problem as long as all agents can increase their fitness. Moreover, the motivational basis of mutual cooperation can be totally selfish: agents should be willing to cooperate if the only possibility to achieve an otherwise unobtainable goal is to do work together. However, even if mutualistic interactions in their perhaps most basic form—two individuals working toward an immediate benefit—are not at all trivial, as they can require sophisticated cognitive and behavioral skills. Specifically, individuals have to be able to create the opportunity for mutualistic benefits in the first place (Calcott, 2008). Individuals have to be able to identify that a social solution to a given problem will succeed, whereas a purely individual effort is likely to fail. It gets even more difficult when individuals have to work toward a goal that is not perceptually present, that is, in a situation in which collaborators have to initiate a collaborative act toward a temporally and spatially distant goal (Brinck & Gärdenfors, 2003). In addition to the question about when and how to cooperate, individuals have to make choices about the appropriate collaborator, especially when there are individual differences in skill and the situation poses temptations for defection (as is the case especially in group-level cooperation). Thus, even though seemingly straightforward concerning the potential payoffs for individuals engaging in acts of mutualism, these acts often require certain cognitive and behavioral capacities that might constrain the flexibility with which different species engage in mutualistic interactions.

One essential feature of human collaborative activities is that they are based upon joint intentions: participants perform their individual actions as part of a collective activity with a joint goal. As John Searle has put it: “When I am engaged in collective action, I am doing what I am doing as part of our doing what we are doing.” (Searle, 2005, p. 6). Using the conceptual distinctions made by analytic philosophers such as John Searle and Michael Bratman (1992), Tomasello et al. (2005) distilled the following three criteria to empirically assess the emergence of joint collaborative activities in humans and other animals. First, participants must be mutually responsive to each other, so that each participant’s action is at least in part influenced by the actions of the other. Second, participants must be able to represent each other’s actions as aimed at a joint goal. Third, they must be committed to the joint goal by mutually adjusting their own behavior to that of the partner, including mutual support if one participant faces problems to perform her part. Bearing these criteria in mind, to what extent do young children and chimpanzees engage in social interactions that can be qualified as collaborative activities with a joint goal? This question is difficult to answer empirically, in particular because we have to distinguish between cases of mere social coordination (in which each individual coordinates their own behavior with others, but because each one pursues her individual goal irrespective of the other person’s goals) and genuine collaborative activities (in which each participant’s action is performed as part of a collective plan). Therefore, in this section on collaboration, we will first summarize the available experimental evidence on the ability of children and chimpanzees to coordinate their actions in tasks that require that two individuals work together to achieve an otherwise unobtainable goal. As a next step, then, we will focus more specifically on the question to what extent these instances can be characterized as genuine collaborative activities based upon joint intentions.

**Mutualistic Cooperation in Children**

When do children begin to collaborate with others? How do they represent the social situation and their involvement therein? It has long been documented that young children engage with others socially in dyadic interactions and also triadically around objects. However, it is still a matter of debate to what extent children view certain games and problem-solving tasks as genuinely collaborative interactions in which two agents coordinate their individual actions in light of a joint goal. Thus, in addition to measuring children’s capacity to behaviorally coordinate their actions, recent research offers new empirical tools to assess children’s representation of the social situation and their motivation to engage therein.

The first instances of coordinated social interaction appear already in the first year of life in dyadic interactions such as peek-a-boo. These behaviors follow a highly practiced script and are highly scaffolded by adults (e.g., Ratner & Bruner, 1978). During the second year of life, children begin to socially coordinate with others in a more flexible way and across an increasing number of situations. For example, from around 14 to 18 months of age, children begin to coordinate their actions with an adult in situations that require the joint engagement and coordination of two people, such as one person pushing an “elevator” mechanism on one side.
of an apparatus so that another person can retrieve a reward on the other side, or two people lifting and shaking a “trampoline” to make a toy bounce on it (Warneken, Chen, & Tomasello, 2006; Warneken & Tomasello, 2007). Importantly, these young children engage in role reversal, switching between two complementary roles, such as one person pushing so that the other person can retrieve the reward or vice versa (Carpenter, Tomasello, & Striano, 2005; Warneken, et al., 2006; Warneken, et al., 2007). This indicates that children are not just responding to the other person’s action and rigidly perform one role (such as a dog playing fetch), but appear to be able to represent both roles as interconnected parts of a social activity in a bird’s-eye-view perspective, performing whatever role is necessary to successfully engage in the activity.

Toddlers collaborate, not only with adults, but also with their peers. This is noteworthy for at least two reasons: First, although interactions with adults are interesting in their own right and seem to constitute the first steps toward successful collaboration, these situations are highly structured by the adults, whereas, in peer interactions, children are left to their own devices, enabling researchers to assess their skill level independent of adult scaffolding. Second, it provides insight into how children of similar status (as compared to the inherent hierarchy of adult-child interaction) negotiate how the interaction should unfold and how resources are distributed in mutualistic tasks in which two individuals work toward an otherwise unobtainable resource. Concerning behavioral coordination, peers begin to successfully coordinate their actions with each other during the second half of the second year of life (Eckerman & Peterman, 2001). This includes coordinated attempts to initiate social interactions with peers, such as taking turns to act on an object (Eckerman, Davis, & Didow, 1989), or synchronizing one’s own action with that of a peer, such as two children simultaneously pulling two handles protruding from a music box to make a puppet sing (Brownell, Ramani, & Zerwas, 2006). In tasks that require the temporal and spatial coordination of two actions, children younger than 2 years usually fail, and it is only during the third year of life that children become proficient at tasks such as pulling handles simultaneously or performing complementary roles, such as one child manipulating a lever so that another child can retrieve an object (Ashley & Tomasello, 1998; Brownell & Carriger, 1990, 1991; Brownell, et al., 2006). Thus, what we can conclude from these studies is that children begin to coordinate their actions successfully with adults in the second year of life, probably facilitated by the adult’s expertise. Shortly thereafter, children begin to collaborate successfully with peers, with major improvements in coordination during the third year of life.

Are these instances of collaboration in young children based upon a representation of joint intentions? Specifically, do children view their own and the other person’s behaviors as being aimed at a joint goal, including the mutual commitment to support each other’s actions in light of the joint goal? To address these issues, Warneken, Chen, and Tomasello (2006) utilized a method first devised by Ross and Lollis (1987) for collaborative tasks requiring the joint engagement of two people: While the child and experimenter were collaborating on a task, the experimenter suddenly stopped participating in the middle of the activity. Children at 18 and 24 months of age (Warneken, et al., 2006) and to some extent 14-month-olds (Warneken & Tomasello, 2007) frequently tried to reengage the recalcitrant partner with referential gestures, such as looking at the experimenter and pointing to the apparatus or offering him the toy needed to perform his role. At the very least, these reengagement attempts demonstrate that children understand the other person’s involvement in the task, otherwise they would blindly continue with their own action. Moreover, it has been interpreted as an indicator for children’s attempt to reestablish the joint goal by drawing the partner’s attention to the joint activity. One interpretive problem of the result is that children might have just responded to the behavioral outcome; that is, they may have tried to reactivate the experimenter as a “social tool” just to be able to continue their own individual action. However, two pieces of evidence speak against this interpretation. In a follow-up study by Warneken, Gräfenhain, and Tomasello (in press), the experimenter interrupted a collaborative activity either because she was unwilling (e.g., purposefully placing a toy car on the ground that she needed to play the game) or because she was unable (she dropped the toy car by accident). Importantly, children at 21 and 27 months of age were more likely to try to reengage her by helping or communicating when she was unable than when she was unwilling, showing that children respond not only to the behavioral outcome, but to the intention having lead to it. Children treat the other person not just as a social tool but as an agent with intentions to either collaborate or not. In a slightly more complex design,
Gräfenhain, Behne, Carpenter and Tomasello (2009) showed that 3-year-olds respond differently to interruptions by an experimenter depending on the prior commitment during the initiation of a game. Specifically, children were more likely to reengage an experimenter who had previously expressed the commitment to collaborate (“Let’s play together!”) as compared to an experimenter who performed similar actions without expressing a prior commitment. The other piece of evidence against the notion that children just view the other person as a necessary accompaniment to their own individual goal is that they also reengage the partner in social games in which the other person’s involvement is not physically necessary for the child to perform her own action. Specifically, toddlers not only reduce these reengagement attempts when, for example, the experimenter has to push a mechanism so that the child can retrieve a reward (physically independent actions), but also in games in which both child and experimenter have levers in front of them that they can push to make a toy rabbit appear (physically independent actions) (Gräfenhain, et al., 2009; Warneken, et al., in press). Thus, after the game has been introduced as a social one in which both act in synchrony, children seem to insist on the social nature of the task rather than just performing their own actions irrespective of those by the partner. A further experiment by Gräfenhain and colleagues added a twist to the commitment and interruption paradigm: this time it was the child itself who interrupted the activity (Gräfenhain, et al., 2009, experiment 2 with 3- and 4-year-olds). Specifically, while the child was playing a game with the first experimenter, a second experimenter started to play a more attractive game in another part of the room, enticing the child to leave the first experimenter. Once again, the manipulation was whether the child had formed a commitment to play the first game together with the experimenter (commitment condition) or whether the child was just playing in parallel (noncommitment condition). Three-year-old children were more likely to acknowledge their having to the first experimenter in the commitment than the noncommitment condition. For example, while they were on their way to the new game, they would announce that they cannot continue because they would like to play the other game now or look back to the first experimenter, acknowledging that they are now playing the other game.

The mutual commitment during collaborative activities becomes apparent also in interaction among peers. One crucial feature of collaborative activities is that a joint goal is only satisfied for one partner if it is also satisfied for the other partner: each partner should be committed to collaborate until each partner is successful (Tuomela, 2007). Hamann, Warneken, and Tomasello (in press) operationalized this criterion by having peers collaborate on a task that required that both worked jointly. Specifically, as shown in the photos of Figure 21.2, peers had to lift a long bar (too long to be moved by one child) upward within a large box until rewards that were attached to the bar were in front of different holes on the box, making the rewards accessible to the children. The decisive moment was when one “lucky” child could already retrieve her reward when the stick was lifted halfway, whereas the rewards of the “unlucky” child became available only after the bar had been lifted all the way up to the upper end of the box. Results showed that 3-year-olds would continue to collaborate even though they had already obtained their reward. Interestingly, children differentiated between this collaborative condition and a baseline condition in which the “lucky” child could directly retrieve her reward without prior collaboration, and the “unlucky” child needed the lucky child to help obtain hers: children were more likely to help in the collaborative condition than the baseline condition. Thus, at least 3-year-olds (but not 2-year-olds) differentiated between noncollaborative and collaborative contexts, being more likely to provide support when the other’s failure was part of a joint collaborative activity. This indicates that around 3 years of age, children begin to appreciate the commitment for mutual support that characterizes collaboration.

Taken together, these studies show that children are active participants in the collaborative activities, not only adjusting their behaviors to those of adults, but actively trying to engage others in the task. Children’s attempts to reengage partners, including the responsiveness to the other’s intention and prior commitment to collaborate indicate that, during the second and third year of life, children already begin to represent these interactions as genuinely collaborative activities with a joint goal. These results thus highlight that joint intentions are already present early in human ontogeny, providing the foundation for human-specific collective interactions. However, to what extent are joint intentions actually human-unique, as proposed, most prominently, by Tomasello et al. (2005)? What kind of mutualistic activities are chimpanzees and bonobos able to engage in, and what psychological capacities might subserve these behaviors?
Mutualistic Cooperation in Chimpanzees

Chimpanzees’ motivation to collaborate in instrumental food-retrieval tasks is not as straightforward as one might predict from a payoffs’ perspective and the potential for mutual benefits. In fact, pioneering studies of chimpanzees’ collaborative problem-solving behavior found positive instances of coordinated behavior among only a very limited number of individuals (Chalmeau, 1994; Povinelli & O’Neill, 2000) or after extremely long training procedures, such as training individuals to pull following a verbal command given by the human experimenter (Chalmeau, 1994; Crawford, 1937; Povinelli & O’Neill, 2000; see Melis, Warneken, & Hare, 2010 for more details on these initial studies).

One interpretation of these results was that cognitive constraints prevented individuals from acting together with the partner. For example, Povinelli and O’Neill (2000) concluded that chimpanzees’ failure to cooperate was largely because either naive individuals were unable to imitate the experienced individuals, or experienced individuals were unable to teach the naive individuals. However, research conducted with other primate species suggested that successful cooperation might not only require a certain level of cognitive capacities, but also tolerance between potential cooperative partners (e.g., Tonkean macaques: Petit, Desportes, & Thierry, 1992; capuchin monkeys: de Waal & Davis, 2003). Furthermore, a study by Chalmeau and colleagues showed that the cooperative behavior of their chimpanzees was limited by social constraints on the subordinates (Chalmeau, 1994; Chalmeau & Gallo, 1996). Specifically, the most dominant individual monopolized the apparatus, thereby preventing others from potentially cooperating while eating any food that was retrieved through joint effort. This suggested that, in cooperative problem-solving experiments, chimpanzees treated the situations as competitive ones, and that low levels of social tolerance, in particular in food retrieval contexts, could be affecting chimpanzees’ ability to cooperate with others.

Building on these findings, Melis and colleagues (Melis, et al., 2006a; Melis, Hare, & Tomasello, 2006b) systematically varied the tolerance levels by pairing individuals either with a low-tolerance or a high-tolerance partner. Pairs of chimpanzees were presented with an out-of-reach baited tray, which required that they both pulled simultaneously (see Figure 21.3). Strikingly, when subjects were paired with partners with whom they could not share food, they never succeeded pulling the tray (and this was even the case when the food rewards on the tray were in two separated dishes and, thus, each individual had a fair chance to obtain food). However, all subjects immediately succeeded when they were paired with a tolerant partner with whom they could share food and co-feed. This shows that, after lifting tolerance constraints, chimpanzees can spontaneously and without training act together with a partner. However, as mentioned earlier, when food items were clumped in one position and could be easily monopolized, chimpanzee cooperation started falling apart. Interestingly, this does not appear to be the case of bonobos, who
succeed in the same plank-pulling task equally often when the rewards are clumped in one location or dispersed. This indicates that the greater overall tolerance level in bonobos does not put the same constraints on cooperation as in chimpanzees (Hare et al., 2007; see also Hare & Kvetuenda, 2010). The same study has recently been conducted with 3-year-old human children, and the results show that peers cooperate at very high levels when rewards are clumped and are easily monopoppable, suggesting that tolerance constraints in children are not as severe as among chimpanzees (Würneken et al., 2011). This also suggests that we share with bonobos a more social tolerant nature over food.

Taken together, these studies show that under the right circumstances, chimpanzees are able to produce mutualistic outcomes. However, what level of understanding do chimpanzees bring to the situation? Is there any evidence that chimpanzees perform these actions based on joint intentions? In other words, do individuals intentionally coordinate their actions with those of their partners based upon a joint plan of action toward a joint goal? Tomasello et al. (2005) proposed that human collaboration fundamentally differs from chimpanzee mutualism because the former is based on joint intentions, whereas the latter is either the by-product of individual efforts or because one individual assists the other as a social tool to achieve their own individual ends. On the other hand, Boesch argues that chimpanzee group hunting is an example of group-level activity with joint intentions (Boesch, 2005; Boesch & Boesch, 1989). This remains a controversial issue, especially because of the general problem that these claims require researchers to make inferences about the underlying cognitive representations of nonverbal animals. Nevertheless, recent experiments have started to address this issue.

Experiments show that chimpanzees do not blindly perform their individual actions, but intentionally coordinate with each other, having a clear understanding that they need a partner to succeed. Specifically, in Melis et al. (2006a; 2006b) most individuals learned within a few trials to wait for each other in the plank-pull task, delaying their own pulling of the rope until the partner was in position. The task required true synchronization, because otherwise the rope slipped out of the apparatus (see Hirata & Fuwa, 2006 for details on the apparatus). In addition, in a more difficult test situation, individuals could choose to recruit a partner by opening a door to allow the partner to enter the testing area. Subjects recruited the partner significantly more often when the task required cooperation than when the task could be individually solved, showing an understanding of the role of their partner to succeed. Furthermore, when given the choice between two different collaborative partners, they preferentially recruited the more skilful partner. Altogether these results demonstrate that chimpanzee cooperation is not just the by-product of independent individual actions that happen to converge, but that individuals do intentionally coordinate their behavior with that of partners and choose collaboration as a means to reach goals they cannot otherwise achieve. However, this does not
mean that their coordinated actions are based on joint intentions, as is the case in humans, because it is possible that in all these interactions chimpanzees view their partners as social tools to reach their own individual goals.

An important measure that has been used to assess whether chimpanzees view the social interaction as a collaborative act with a joint goal are reengagement attempts. Specifically, one study by Warneken, Chen, and Tomasello (2006) used the same method as with human children described earlier: a human experimenter who had previously worked successfully on a mutualistic task stopped playing her role during certain predetermined interruption periods. Chimpanzees consistently attempted to solve the task by their own means or disengaged completely from the task, and they never produced any communicative signals to influence their partners' behaviors (although the same chimpanzees did produce such signals in other noncollaborative contexts; Tomasello & Carpenter, 2005). On the other hand, another study by Hirata and Fuwa (2006) showed that chimpanzees took a previously proficient, but now recalcitrant human experimenter by the hand and guided him to a large stone covering food that could only be moved if both chimpanzee and human pulled together (for similar observations with bonobos in social interactions around objects broadly construed, see Pika & Zuberbühler, 2007). Thus, it remains an open question to what extent chimpanzees do or do not try to reengage social partners who disengage from the task. At least in interaction with humans, they appear to sometimes reengage an individual whose participation is necessary for the chimpanzee to perform her own action or achieve a food reward. However, it remains a possibility that chimpanzees perform these behaviors because they use the other as a social tool. In particular, it is not yet known whether chimpanzees will act differently depending on whether the other individual interrupted intentionally or unintentionally, an important criterion in deciding whether chimpanzees actually view the other individual as a collaborative partner or a mere social tool. Human children make this distinction from an early age, but it is not clear whether it characterizes chimpanzee cooperation as well.

Beyond tests of collaboration in human-chimpanzee pairs, important insights come from studies on conspecific collaboration. First, strikingly few communicative attempts occurred in a study in which pairs of chimpanzees were required to agree on pulling from one (and only one) of two potential cooperation trays (Melis, Hare, & Tomasello, 2009). The study created a conflict of interest between partners, with the dominant individual aiming to obtain one tray, and the subordinate the second tray. Subjects typically waited for the partner to join them in front of their preferred option. Sometimes they would even approach the partner and monitor the partner. However, there were surprisingly few instances of clear intentional communication between them or any efforts to influence the partner's behavior, which was surprising, because any type of communicative efforts could have facilitated or accelerated the negotiation process (e.g., Crawford, 1937; Hirata & Fuwa, 2006; Hirai et al., 2010, for positive instances of communication). This clearly marks a limitation in chimpanzees’ ability to regulate and influence a cooperative activity, and also casts doubts on the idea that they form shared goals with their partners.

Second, Greenberg and colleagues used a noncommunicative measure to assess how chimpanzees conceive of collaborative activities (Greenberg, Hamann, Warneken, & Tomasello, 2010). This study operationalized the criterion that partners in a collaborative activity should be mutually committed to ensure that both partners succeed (similar to the aforementioned studies with children by Hamann et al., 2011). Participants should be displeased with the situation if only one, but not both, partners achieve their ends. Specifically, in a variation of the plank-pull task, two chimpanzees had to pull together to access food rewards in a collaborative condition, both chimpanzees together pulled a board with two rewards; one "lucky" individual already received the reward once the board had been pulled half way to the middle position; whereas the other "unlucky" chimpanzee would be rewarded only after both chimpanzees had pulled it all the way to the end. In a noncollaborative condition, the board was already sitting in the middle position at the beginning of the trial, so that one individual could retrieve the reward without prior collaboration ("lucky"), whereas the "unlucky" chimpanzee needed the other’s help to pull the board to the end. Interestingly, results showed that the "lucky" individual helped the "unlucky" individual in approximately one-third of trials by jointly pulling the board with the partner toward the end, even though the "lucky" partner would not receive a reward for its help. However, this help was provided equally often in both the collaborative and the noncollaborative condition. Thus, chimpanzees
were willing to help their partners, but in contrast to human children, collaboration did not seem to facilitate helping. This finding provides further evidence for the notion that chimpanzees are able to represent individual actions and occasionally help others with their individual goals, but they do not engage in genuine collaborative interactions with joint goals and the ensuing commitment for mutual support.

Last but not least, even if chimpanzees are willing and able to join efforts when the situation demands it, they do not seem particularly motivated to act together with partners unless this is the only way to access their goals. This stands in contrast to human children who appear to find collaborative acts rewarding in themselves, because they often choose to play together when they could do so alone (Gräfenhain, et al., 2009; Warneken, et al., in press). Specifically, when chimpanzees were given the choice between working either individually or collaboratively with a tolerant partner (with both options resulting in equal payoffs for the subjects), chimpanzees preferably chose the nonsocial option. However, they preferred the social-collaborative option as soon as its payoffs were minimally increased, showing that they are strategic and cognizant of their cooperative options, but they do not seem to be particularly inclined to act together with others at least in food-retrieval contexts (Bullinger, Melis, & Tomasello, 2011). Thus, this supports the hypothesis that they view their partners as social tools rather than forming joint goals with them and developing joint intentions and commitments to pursue those goals.

Taken together, chimpanzees are able to engage in quite sophisticated mutualistic cooperative activities, including an understanding when a partner is needed and which partner might best be suited to solve a mutualistic task. Nevertheless, more research is needed to assess how chimpanzees represent their own and the partner’s contribution to the task. Specifically, the current empirical evidence can be interpreted by the social-tool hypothesis, according to which chimpanzees view the other individual as a social tool that is needed to produce self-serving outcomes, rather than a collaborative partner with whom they interact based upon a joint plan toward a joint goal. This feature and their lack of communication during cooperative interactions are two aspects in which mutualistic cooperation in chimpanzees and humans appear to differ fundamentally.

Future Directions
- When, during human ontogeny, do factors such as reciprocity, reputation formation, and group membership begin to play a role in children’s cooperative behaviors?
- What mechanisms sustain altruistic and other cooperative behaviors in nonhuman apes?
- What are similarities and differences in the cooperative behaviors of chimpanzees and bonobos as our two closest living primate relatives?
- Are there cross-cultural differences in the cooperative behaviors of young children?

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