20 Altruistic Behaviors from a Developmental and Comparative Perspective

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Humans are not oblivious to the needs of others. Indeed, people will act on the behalf of others, even in situations that are of no obvious immediate benefit to the actor and may involve some kind of cost to him or her. Philosophers and scientists have debated the origins of these altruistic tendencies for centuries. More recently, empirical methods in the behavioral sciences and insights from evolutionary theory have provided some answers and added new questions to this perennial debate about human altruism. Importantly, some of the most illuminating research has broadened the scope beyond the altruistic behaviors exhibited by adult humans, and put it into context by determining their origins, both in terms of the phylogenetic roots and concerning the development of altruistic behaviors in human ontogeny. A powerful method to accomplish this goal is to study human children and compare their behavior to our closest living evolutionary relatives, chimpanzees (Pan troglodytes) and bonobos (Pan paniscus). By studying young children, scientists can assess the psychological capacities with which humans are equipped early in life that prepare them to develop altruistic behaviors, and by examining their development, scientists elucidate the interplay between these biological predispositions and social learning. Furthermore, studies of chimpanzees and bonobos allow inferences concerning which aspects of human altruism may have already been present in the last common ancestor of apes and humans, versus those components of the human mind that are species-unique and emerged only in the human lineage. In this chapter, I will therefore explore some of the major new insights that have emerged from the behavioral sciences about the origins of human altruism in ontogeny and phylogeny.

Specifically, I will focus on the proximate mechanisms for altruism that underpin behaviors where an individual does something beneficial for another. In contrast to perspectives from evolutionary theory that focus on the fitness consequences of altruistic behaviors, the current framework examines the psychology of altruism: What motivational factors make individuals want to help others, and what cognitive capacities are required to do so effectively? In this formulation, behaviors that I here consider as "psychologically altruistic" may not necessarily result in lifetime fitness costs at the
ultimate level. On the other hand, altruism defined at the ultimate level—in terms of fitness costs and benefits—does not necessarily depend on complex psychological mechanisms, as “a mindless organism can be an evolutionary altruist” (Sober, 2002, p. 17). However, the behaviors of such a “mindless altruist” may be confined to a very restricted set of situations and cannot be modified when confronted with novel exigencies. Thus, I here want to emphasize that one reason to pay special attention to the proximate mechanisms is that humans engage in a variety of altruistically motivated behaviors that are likely unparalleled anywhere else in the animal kingdom—even if the fitness consequences of these behaviors do not fundamentally differ from those in other species. That is, humans appear to possess psychological processes to perform flexible, situation-specific acts of helping, sharing, and other types of altruistically motivated behaviors that make humans special—perhaps unique—at the proximate level. By studying these, we can learn more about the factors that enable and constrain certain types of altruistically motivated behaviors and explain to what extent different forms are human-unique or mirror behaviors that are found in other animals as well.

Consequently, here I propose that human altruistic behaviors are not based on a unitary psychological trait, but that humans engage in a variety of altruistic behaviors that likely recruit diverse psychological mechanisms. Specifically, recent research indicates that humans and other apes may display greater or lesser altruistic tendencies in different domains of activity. Warneken and Tomasello (2009a,b) proposed the following typology to classify different altruistic behaviors in the commodity provided to the recipient: comforting others by providing emotional support, sharing valuable goods such as food, informing others by providing useful information, and helping others to achieve goals by acting for them. Traditionally, developmental psychology has focused on comforting (or empathic intervention), but in recent years, several new empirical insights have emerged concerning the latter three categories, often complemented by comparative studies with chimpanzees. Therefore, in the current chapter, I will focus on recent findings on sharing, informing, and helping, starting with developmental studies with children and moving on to comparative studies with chimpanzees. I will use these studies to develop the argument that human altruism is not due to socialization alone. Specifically, it has been proposed in many places that a long period of socialization practices such as external rewards by adults, explicit teaching, or the internalization of moral norms through imitation are the main or only factor inculcating altruistic motivations into otherwise self-focused and selfish children (Bar-Tal, 1982; Dovido & et al., 2006; Henrich et al., 2005). In contrast to this view, I will argue that humans have a biological predisposition to develop altruistic behaviors, and that socialization practices can build on this predisposition, which is apparent early in human ontogeny and is also expressed in certain forms of altruistic behaviors in chimpanzees. I will conclude this chapter with a proposal to investigate how factors of reciprocity influence behavior in sharing.

Sharing

Sharing of valued goods or food only as a productive exchange, on the other hand, may be an evolutionary strategy that enables one to lack a resource that benefits itself. One of the best known examples is that of the chimpanzees at the Svetlova, offering a snack to a child with a 18-month-old option, they did so by bringing the food to the child's mate. In some cases, the child's mate then asked to elicit sharing, which is not always the case. I will briefly discuss these experiments and some others.
how factors that are important mediators of altruistic behaviors in adults, such as reciprocity and cultural norms, begin to play a role during the emergence of altruistic behavior in childhood.

Sharing

Sharing of resources can be regarded as perhaps the prototypical form of altruistic behavior. By definition, it involves an immediate cost, as one person is giving up a valuable resource that benefits another individual. Obviously, the effects on biological fitness are difficult to establish in most cases, and concrete resources can serve only as a proxy at best. Nevertheless, it can provide insight into the mechanisms involved, that is, the motivation to sacrifice a concrete resource for the benefit of another individual. Correspondingly, sharing of resources is the most studied form of altruism among anthropologists investigating food-sharing in hunter-gatherers, behavioral economists using the dictator or the ultimatum game, or biologists observing food-sharing among animals. Despite the importance of this behavior, surprisingly few systematic studies have been conducted with young children, which invites the question: To what extent are young children able to detect that other individuals lack a resource and are willing to share with them—even if doing so involves a cost to themselves?

One of the few studies investigating this question is an experiment by Brownell and colleagues, which indicates that 2-year-old children begin to take into account another person’s needs when they have the opportunity to share with others (Brownell, Svetlova & Nichols, 2009). Specifically, toddlers were confronted with an apparatus offering the choice to either pull one rope that would deliver a snack to themselves and a snack to an adult bystander (1/1 option) or to pull another rope that would bring a snack to themselves, but no snack to the bystander (1/0 option) (task adapted from Silk et al., 2005). Thus, the children could provide food to the bystander at no cost to themselves (in terms of either resources or effort). Interestingly, whereas 18-month-old children chose randomly, 25-month-old children more often chose the 1/1 option, benefiting both themselves and the bystander simultaneously. Notably, they did so only in a condition in which the bystander had verbalized her desire for the food, indicating that young children require explicit cues to note the other person’s need in this context. This shows the importance of cues provided by the recipient to elicit sharing. This is also the conclusion from a study by Dunfield and colleagues, in which 18- and 24-month-old children performed costly sharing acts by giving some of their own food to an adult who expressed a desire by making a sad face and requesting sharing with a palm-up gesture (Dunfield et al., 2011). Taken together, these experiments show that young children are willing to share in some circumstances and that the absence of sharing might not always be due to a reluctance to give up
a resource, but rather to the lack of social cognitive understanding about the other person's need.

Later on during development, children begin to engage in sharing with absent individuals (for an overview see Gummenrum, Hanoch & Keller, 2008). For example, Moore (2009) shows that, even though the recipient was not present during the test, 4- to 5-year-old children more often chose equal rewards for both themselves and another child over a selfish option with a higher payoff for the themselves only—at least when the recipient was a friend. Toward school-age, costly sharing becomes more common, and also occurs in situations in which children have the choice to share with anonymous others. Blake and Rand (2010) point out that their own experiment and other studies using the dictator game (in which the subject divides up a resource between oneself and another individual) indicate that children's tendency to give at least something increases continuously over development between 3 and 9 years of age. Moreover, these 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). Thus, from early on in ontogeny, children begin to share resources with others. Initially, it appears crucial that the recipient is copresent and expresses her desire. It seems that later during development, children begin to share with absent individuals, adhering to equality norms even if this requires self-sacrifice on the part of the actor.

This finding stands in contrast to several studies with chimpanzees, who in similar sharing situations do not seem to act on behalf of others even if the costs to themselves are minimal or nonexistent. Specifically, in Silk et al. (2005), chimpanzees chose randomly when confronted with the 1/1 and 1/0 option, and in Jensen et al. (2006), chimpanzees did not act altruistically even when doing so would only have required pulling a rope that moved an otherwise unobtainable board with a piece of food toward another conspecific (see Vonk et al., 2008, for variations on this food-provision paradigm leading to similar results). Thus, these studies indicate that chimpanzees are not particularly inclined to actively share resources with others even if this would come at no cost to themselves.

Chimpanzees appear to be quite limited in their tendency to share resources, even in mutualistic situations in which both individuals could potentially benefit. For example, studies by Melis and colleagues showed that in problem-solving tasks in which chimpanzees can only succeed if they together simultaneously pull in a board with food on it, they mostly failed when the food was clumped in the middle of the board, making it easy for the more dominant individual to monopolize. They only succeeded when the rewards were spread apart so that each individual was able to access their portion without potential interference from the other chimpanzee. More-
over, success was highly dependent on the degree of social tolerance between the partners. The only dyads who cooperated successfully on this mutualistic task were those who had in pretests co-fed peacefully over a food resource rather than trying to monopolize it (Melis, Hare & Tomasello, 2006a). Thus, social tolerance appears to be an important constraining factor for chimpanzee cooperation.

The importance of social tolerance over food is also highlighted by cross-species comparisons. Specifically, bonobos are known to be generally more socially tolerant over food, as indexed by their tendency to co-feed without individuals trying to monopolize a resource. As a consequence, when they were tested in the same board-pulling task as the chimpanzees, the location of the food as either clumped in the middle or spread apart did not matter. In contrast to chimpanzees, who mainly succeeded when the rewards were spread apart, bonobos were equally likely to succeed in the clumped and the dispersed version (Hare et al., 2007). Thus, probably because there was no expectation of competition over the spoils at the end, it was of less importance whether the rewards were monopolizable or not. These experiments demonstrate that chimpanzees are highly competitive over monopolizable resources and are thus less inclined to actively provision food for others or cooperative mutualistically with others.

Naturalistic observations have also shown that when sharing occurs in chimpanzees, it predominately consists in passive sharing, in which one individual lets the other individual take a resource, rather than transferring it to the other proactively (Boesch & Boesch, 1989). In particular, meat-sharing after cooperative hunts occur mainly in response to harassment (Gilby, 2006) in which the possessor lets another individual have part of the bait. This is probably not due to generosity, but because sharing parts of the carcass is less costly than trying to defend it, that is, risking getting in a fight or potentially losing the carcass altogether. Also, in mother-infant pairs, infant-initiated food transfers in which the infant attempts to take food and the mother tolerates it are more common than mother-initiated food transfers (Ueno & Matsuzawa, 2004). Moreover, the latter occurred exclusively with less desirable parts of the fruits such as seeds and husks.

Thus, striking differences between humans and chimpanzees emerge when it comes to resource sharing. Chimpanzees appear to be less inclined to actively provide food, especially when it involves giving up a valuable resource. They appear to have a strong tendency to monopolize valuable resources, which often precludes cooperative behaviors, including those that would result in mutualistic outcomes. Interestingly, this constraint appears to be mitigated in bonobos, who are better able to deal with situations that involve monopolizable resources. Human children are willing to share resources, even if it involves a cost, but at least early in development, sharing occurs mainly in situations in which recipients actively express their need; older children demonstrate proactive sharing behaviors, indicating that sharing not only requires the willingness
to give up a resource, but also the social-cognitive capacity to understand other people’s needs and desires.

Informing

Another important form of altruistically motivated behavior becomes apparent in the gestural communication of young children: Infants will point to things other people are searching for. These kinds of behaviors are obviously of low immediate cost (requiring neither great effort nor sacrifice of material resources), but they provide another example for an altruistic motivation to act on behalf of another person’s goal or need. Specifically, a series of studies demonstrates that from the time that infants begin to point (at around one year of age), they already use this simple but efficient communicative means for altruistic purposes by providing helpful information to others. In one such study, a protagonist sat at a desk and used an object such as a hole-puncher on a stack of papers (Liszowski et al., 2006). After she had left, a second “evil” experimenter took the hole-puncher as well as an irrelevant object and placed them on different platforms behind the desk out of the protagonist’s view. Upon returning to the desk to punch more papers, the protagonist looked around in bewilderment, unable to locate the hole-puncher. Infants pointed more often to the hole-puncher than the distracter object, indicating that they were trying to help her in her search and were able to differentiate between the relevant and the irrelevant object. A follow-up study demonstrated that 1-year-old children can also differentiate between an object that disappeared unknown to the protagonist and an object that she saw disappear (Liszowski, Carpenter & Tomasello, 2008). Thus, prelinguistic infants use pointing not only imperatively to make other people do things for themselves, but also to provide information that other people need. This form of altruism is interesting because it requires the cognitive capacity, on some level, to differentiate between one’s own state of knowledge about the world and that of another person’s, and to provide the lacking piece of information to the ignorant other. Thus, in contrast to comforting (based on a determination and intervention toward the emotional states of others), and in contrast to sharing (based on the provision of a concrete resource), altruistic acts of informing others critically depend on a cognitive capacity to take into account and act on epistemic states.

This rather sophisticated cognitive capacity required for acts of informing might explain why, despite the low costs of the act itself, this form of altruistic behavior is not ubiquitous across the animal kingdom. More specifically, chimpanzees do not appear to have developed a communicative system that would allow for such acts. Chimpanzees do not point for each other (Leavens, 2004; Tomasello, 2006). Captive chimpanzees do point in interactions with humans, but it seems like they do so only imperatively, to entice them to do things for them such as bringing an object; there is no conclusion by another (see et al. 2011) extract a rat an experiment condition.

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is no conclusive evidence that they point in order to provide information needed by another individual (Tomasello, 2008). More concretely, in a study by Bullinger et al. (2011), chimpanzees reliably pointed to a misplaced tool that they needed to extract a reward for themselves (a selfish "for-me" condition), but rarely did so when an experimenter needed the tool to retrieve a reward for herself (an altruistic "for-you" condition). In an experiment closely matching this scenario, 2-year-old children pointed equally often in both conditions, demonstrating that they use pointing gestures for selfish and altruistic purposes. The interpretation by Bullinger and colleagues is that in contrast to human children, chimpanzees do not engage in informative pointing with an altruistic motivation to help the other, and in fact do not even use pointing as a means to convey a piece of information the ignorant experimenter is lacking (letting the experimenter know where the tool was), but rather point in order to direct her behaviorally to the tool. Thus, they do not aim to change the epistemic states of others, but try to directly influence the other's behavior for their own purposes.

As a matter of fact, chimpanzees do not even seem to be able to comprehend pointing gestures when they would be useful to them. A large number of experiments demonstrates that chimpanzees fail to use gestural cues in object-choice paradigms in which an experimenter is using a pointing gesture, or, in a variation of this, placing a marker to indicate the location of food under one of two opaque containers (see Call & Tomasello, 2005, for an overview). One-year-old human children have no problem with this (Behne, Carpenter & Tomasello, 2005), but chimpanzees appear to be unable to interpret the helpful communicative gestures of others. Interestingly, when the same situation (in which a piece of food is in one of two opaque containers) is framed as a competitive one, chimpanzees are suddenly successful. Hare and Tomasello (2004) directly compared a competitive and a cooperative version of this object-choice task: When chimpanzees saw a competitor (human or chimpanzee) unsuccessfully reaching for one of two containers with a hand gesture very similar to pointing, they were able to infer that this one was the container with food in it, and chose accordingly when it was their turn. However, when a cooperative experimenter pointed to the correct container, they chose at random. Thus, chimpanzees were able to infer the location of the food based on the other's attempt to snatch the food but did not understand the communicative intention to inform them of the correct location.

Why can't chimpanzees comprehend communicative cues produced by a helpful experimenter? One possible explanation for why chimpanzees fail is that they do not seem to grasp the helpful communicative intent of others. Specifically, these gestures become meaningful only under the premise that the receiver views the pointing gesture as part of a joint collaborative activity, with the receiver being able to understand that the sender has the helpful communicative intention to guide their
searching—that you are producing this gesture for me to help me find the object (for details, see Tomasello, 2006, 2008). 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) or imperative giving (like handing a container so that the human opens it [Tomasello, 2008]). Taken together, although the reasons are rather unclear, the experimental evidence suggests 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 and in that of the receiver.

**Instrumental Helping**

Human altruistic behavior is expressed not only in the tendency to, on occasion, share material resources or information, but also in such mundane acts as picking up a dropped object, holding open a door for someone, or trying to fix something for others if they fail to succeed. To engage in these behaviors in a competent way, the helper has to be able to represent the other person’s goal and to have the motivation to act on behalf of the other’s goal. These behaviors—for which I use the term “instrumental helping”—differ from sharing and informing, as different commodities are involved: Rather than giving up a resource or providing a piece of information, the helper assists instrumentally by contributing to the other’s goal fulfillment through his own action. These behaviors also differ from empathic intervention (such as comforting a person who is in distress) because, rather than being affected by the emotional state of others and acting in response to this state, acts of instrumental helping require a cognitive understanding of goal-directed action.

Do young children engage in acts of instrumental helping? With regard to the social-cognitive component of helping, it is a well-established finding that infants from around 12 to 18 months of age understand other people’s behaviors in terms of their intentions. For instance, infants can differentiate accidental from purposeful actions (for an overview, see Tomasello et al., 2005). They can determine whether a similar environmental outcome was either the result of a purposeful act (when the outcome matches the goal) or an accident (when goal and outcome do not match). Similarly, they can infer the goals that another person was trying to achieve without actually witnessing the intended outcome (Meltzoff, 1995). Thus, infants already appear to possess the crucial social-cognitive component necessary for instrumental help.

With regard to the motivational component of helping, children as young as 12 months begin to show concern for others in distress and sometimes intervene by comforting them (for an overview, see Eisenberg, Fabes & Spinrad, 2006). However, these instances are all based on the infant’s empathic responses to the emotional needs of another person. In contrast to these instances of empathic intervention (or what
one could also call “emotional helping”), little was known about whether infants would also perform acts of instrumental helping: helping another person achieve an unfulfilled goal.

To explore this issue, Warneken and Tomasello (2006) presented 18-month-old infants with ten different situations in which an adult was having trouble achieving a goal. This range of tasks presented the children with a variety of difficulties in discerning the adult’s goal. For instance, in one task, while using clothespins to hang towels on a clothesline, an experimenter accidentally dropped a clothespin on the floor and unsuccessfully reached for it. In this case, the child had the opportunity to help by picking up the clothespin and handing it to the experimenter. In another task, the experimenter was trying to put a stack of magazines into a cabinet but could not open the doors because his hands were full; the child could thus potentially help by opening the doors for him. The finding of this experiment was that children displayed spontaneous, unrewarded helping behaviors when another person is unable to achieve his goal (and performed these behaviors significantly less often in control conditions where no help is necessary). This helping was observed across a range of situations: Infants handed the experimenter out-of-reach objects; completed an action after his failed attempt at stacking books; opened the door of a cabinet for him; and brought about the experimenter’s goal by different means: Rather than using the experimenter’s wrong approach to try to squeeze his hand through a tiny hole in order to retrieve an object from a box, children lifted a flap on the side of the box and gave the object to him. In another study, even 14-month-old children acted helpfully, although only with cognitively less demanding tasks (such as a person reaching for an object), but failed to do so in situations with presumably more complex goals and more complex types of intervention (like the cabinet task, [Warneken & Tomasello, 2007]). This is also exemplified in a study by Svetlova and colleagues, in which children from 1.5 to 2.5 years were more likely to help with concrete goals (such as reaching for a dropped object) than with tasks that involved at least one more inferential step in how to help (such as bringing a blanket to a person who is shivering) (Svetlova, Nichols & Brownell, in press). In order to help appropriately, younger children in particular more often needed explicit communicative cues from the helper in the latter kind of situation than in tasks with concrete action-goals. Taken together, these studies show that shortly after their first birthdays, human children begin to spontaneously help others, becoming more flexible in their ability to intervene in various types of situations over the second year of life, and requiring fewer direct communicative cues also in contexts in which the type of intervention does not follow straightforwardly from situational cues alone.

During the second year of life, children even become able to infer another’s goal based on what the person does or does not know. Specifically, in one helping situation (Buttelmann, Carpenter & Tomasello, 2009), a protagonist put his toy into box A,
which was then moved to box B either while the protagonist was absent (ignorant condition) or present (knowledge condition). In the ignorant condition, when the protagonist tried but failed to open box A, children did not help him to open box A (the previous location of the toy) but instead opened box B (where the toy actually was), indicating that they did not just blindly join into the erroneous action to open box A, but inferred that the protagonist was actually trying to get at the toy (which was now in a new place). Children in the knowledge condition, however, were more likely to open box A that the protagonist was trying to open, presumably reasoning that he was not trying to get at his toy (which he witnessed having moved to box B) but must have another goal in mind. Therefore, this study indicates that young children actually help other people with their goals (and not just complete a concrete action such as the failure to open something) and are able to infer goals from representations about the other person’s state of knowledge or ignorance.

These young children help even when the costs of helping are slightly raised. As an example, when children are having fun playing with a novel toy (a box with buttons that light up and produce sounds), they continue to help even if it means they have to disengage from this activity (Warneken & Tomasello, 2008). As another example, children do not stop helping over repeated trials even if they have to surmount an array of obstacles, something that can be quite challenging for a toddler who just learned to walk (Warneken et al., 2007). Children are thus motivated to help another person even if it involves opportunity costs or effort to do so.

Children are thus willing to put some effort in helping—but do they expect to be rewarded in return? One experiment directly addressed this question of whether 18-month-old children are motivated by the other person’s goal or by an immediate benefit for themselves by varying whether the helpee would offer a reward in return for their helping effort (Warneken et al., 2007). The results could not be clearer: Children helped by picking up objects for which the experimenter was unsuccessfully reaching, irrespective of whether they received a rewarded for their help. Rewarding was not necessary to elicit helping, nor did it increase the rate of helping. Thus, what determined children’s helping was the other’s unfulfilled goal, not an immediate benefit for themselves. Using a crucial distinction from motivational psychology, we may thus ask whether such acts of helping are intrinsically or extrinsically motivated: Do children help one another because the helpful act itself is inherently rewarding, or only because the helpful act is instrumental in bringing about separate outcomes such as material rewards? To investigate the effects of rewards on young children’s helping more closely, Warneken and Tomasello (2008) took advantage of a curious feature of intrinsic motivation: It is a well-established phenomenon that intrinsic rewards can be undermined by salient extrinsic rewards (what has also been called the “overjustification effect”) (Deci, 1971; Lepper, Greene & Nisbett, 1973). Warneken and Tomasello found that children who had received a material reward for helping during
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An initial test phase were subsequently less likely to engage in further helping than those children who had not received such a reward (see also Fabes et al., 1989, for school-aged children). This rather surprising finding provides even further evidence for the hypothesis that children's helping is driven by an intrinsic rather than an extrinsic motivation. Rewards are often not only superfluous, but can even have detrimental effects as they may undermine children's intrinsic altruistic motivation.

In sum, this series of studies demonstrates 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 flexible in their ability to read others' 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 by an immediate benefit for themselves, as external rewards are not necessary to elicit helping nor do they increase the rate of helping. On the contrary, children appear to have an initial inclination to help that maybe be diminished by extrinsic rewards.

Would chimpanzees perform such acts of instrumental helping? A series of experiments shows that under certain circumstances, chimpanzees do in fact act on behalf of others. In an initial study, Warneken and Tomasello (2006) adapted the helping scenarios 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 for which she was unsuccessfully reaching (and they did not do so in the control condition, in which she was not reaching for them). These chimpanzees were thus able to determine the experimenter's goal and had the motivation to help her with the goal in the absence of a reward. However, in contrast to the out-of-reach tasks, these chimpanzees 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.). Perhaps importantly, this discrepancy in chimpanzees' willingness to help in different types of tasks parallels a finding with 14-month-old human infants, whose helping was also limited to tasks involving out-of-reach objects (Warneken & Tomasello, 2007). These findings suggest that the occurrence of helping may be influenced by the complexity of the goal structure and the type of intervention necessary. This once again shows the importance of taking into account the social-cognitive demands of certain tests of altruism. These human-raised chimpanzees were in principle willing to help, but showed this behavior only in contexts in which the other's goal was easy to identify.

It should be noted, though, that the subjects were human-raised chimpanzees who helped a caregiver with whom they maintained a close relationship. Chimpanzees
with such a rearing history often possess superior social-cognitive skills and develop behaviors not found in individuals with less human contact (Bering, 2004; Call & Tomasello, 1996; Tomasello & Call, 2004; Tomasello & Carpenter, 2005). However, in a follow-up study, chimpanzees with a different rearing history also helped. Specifically, Warneken et al. (2007) tested a sample of semi-free ranging chimpanzees who were born in the wild and now live in a sanctuary in Uganda. These chimpanzees spend the day in the forest of an island where they come to a human shelter for feeding and sleeping. They thus have regular contact with humans, but have not been exposed to rearing practices comparable to those of human-raised chimpanzees in zoos (as the chimpanzees from the initial helping study had been). Most importantly, they were tested by a human who had not interacted with them before the experiment.

One major finding of this study was that, just like human infants tested in a similar situation, chimpanzees helped over consecutive trials by handing the out-of-reach object when the experimenter indicated that he was trying to get the object, and they did so irrespective of being rewarded. This indicates that the chimpanzees were motivated to help the experimenter with his unachieved goal, and not by the possibility of retrieving a material reward for themselves. Moreover, chimpanzees continued to help even when doing so involved not only picking up the object, but also required that they first climb into a raceway to retrieve the object for the other (Warneken et al., 2007, Experiment 2). Taken together, these two experiments show that also semi-free ranging chimpanzees perform acts of helping toward a human stranger, even when helping is made effortful and they receive no immediate benefit for themselves.

However, all of these instances of chimpanzee helping involved humans as recipients. The question remains: Will chimpanzees help other chimpanzees? As mentioned before, studies on sharing of resources among conspecifics came to a negative conclusion (Jensen et al., 2006; Silk et al., 2005). However, experiments with negative results all involved the active provision of food, which, owing to the tendency of chimpanzees to compete over monopolizable resources, might preclude altruistic behaviors. Moreover, in these experiments, the need for help might not have been obvious to the subjects, as the recipients often remained passive during the trials, and did not have an opportunity to actively try to access the desired object. To this end, Warneken et al. (2007) created a situation in which the need for help would potentially be more salient, by having a chimpanzee actively struggle with a problem. Namely, one chimpanzee (the recipient) was faced with the problem that a door leading to a room containing a piece of food was fixed with a chain that he could not unlock. Only if the other chimpanzee (the subject) released this chain from another room could the recipient enter. Results showed that chimpanzees helped in the majority of cases by releasing the chain. They did so significantly more often than in control conditions, in which releasing the chain would either not help the recipient or no recipient was present. This likely to relet that door. Th chimpanzees are critical in to another in situations in which the tool (i.e., a hammer) is also found in a bag containing chimpanzees performing to access the tool from bag or container. Mice or a token (that the presence of) offers a reward (as co the activity of this finding).

These findings suggest that human infants express these tendencies of helping, if imposed by the adults. Infants yet have had a value system that these infants have. And even perception, the achievements explain the advantage for children's reflection, in turn, c

These behaviors represent evidence for the presence of a biological basis for helping in chimpanzees.
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and develop (2004; Call & de Waal). However, chimpanzees have also demonstrated positive consequences for feeding as a result of being in zoos (as opposed to being in the wild). Quantitative experiments have shown that chimpanzees can successfully open the door to a food reward when given the opportunity, and that they are more likely to do so if the reward is placed out of reach. However, this experiment suggests that the chimpanzees were more likely to release the door if the recipient was successfully trying to enter through the door. Thus, this experiment suggests that when the door is made more salient, chimpanzees use a novel skill to help conspecifics gain access to food in a novel situation. In a related study, Yamamoto and colleagues showed that cues by the recipient are critical in eliciting altruistic behaviors. In their study, chimpanzees passed a tool to another individual who needed it to retrieve food, but did so almost exclusively in situations in which they previously observed the conspecific attempting to reach for the tool (Yamamoto, Humle & Tanaka, 2009). Chimpanzees virtually never handed over the tool to another individual who did not appear to need it, even when they were rewarded for doing so. The importance of cues was also found in a study by Melis and colleagues (2010), in which the subject could release a tool to allow it to slide down a chute toward a recipient chimpanzee. chimpanzees performed this behavior more often when the recipient was actively trying to access the reward (by pulling a rope, which was attached to the bag) or communicate with the subject, than when the recipient remained passive. In addition, Melis and colleagues manipulated whether the reward was a piece of food or a token (that the recipient could later exchange for food), testing the hypothesis that the presence and necessity to actively provision food might impede helping. However, this study revealed that the tendency to help was not diminished with food rewards (as compared to tokens). Thus, the main factor predicting helping was again the activity of the recipient.

These findings elucidate both the ontogenetic and phylogenetic origins of human altruism. Human children possess social-cognitive capacities that enable them to express these tendencies in a variety of ways, as highlighted by the early emergence of helping, informing, and sharing. These results challenge the view that altruism is imposed by the social environment (Bar-Tal, 1982; Dovidio et al., 2006; Henrich et al., 2005). Infants show altruistic tendencies at an age when socialization could not yet have had a major impact on their development. Also, the internalization of norms or value systems is inapplicable to 1-year-old children. Moreover, we can assume that these infants had had few opportunities to help and receive reinforcement for helping. And even if it is the case that they have had some exposure to helping and reinforcement, they also help in novel situations with unfamiliar adults. Thus, these early achievements are unlikely to be due to socialization practices alone. A more plausible explanation for the various results from these studies is that altruistic acts in young children reflect a natural predisposition to develop these altruistic behaviors. Socialization, in turn, can then build on these early, preexisting tendencies.

These behaviors are not completely absent in chimpanzees, providing further evidence for the notion that the ontogenetic emergence of these behaviors is based on a biological predisposition. Moreover, it indicates that the altruistic tendencies seen
in humans have deep phylogenetic roots, potentially dating back at least to the last common ancestor of humans and chimpanzees. Specifically, chimpanzees also on occasion act on behalf of others, specifically in instrumental helping situations. Moreover, the fact that they show some flexibility in helping (toward different recipients who pursued different goals) indicates that chimpanzees can utilize their social-cognitive skills in reading others’ goals for altruistic purposes. However, chimpanzee altruism appears to be much more restricted and more fragile than what we see already in young humans. This appears to be due in part to limitations on their social cognition, as they do not seem to engage in the communicative acts that characterize human intentional communication and neither comprehend nor produce gestures aimed at helping other individuals. Moreover, chimpanzees appear to have a strong tendency to monopolize food, which often predominates and in particular precludes instances of sharing. Thus, rather than asking whether altruistic tendencies are present or absent in chimpanzees, research should move forward and explore the specific circumstances under which chimpanzees do or do not act altruistically.

**Mechanisms to Sustain and Facilitate Altruism**

The studies reported above highlight that young children, and, to some extent, non-human apes, possess the necessary cognitive and motivational capacities to engage in some forms of altruistically motivated behavior. But what are the biological consequences of these types of psychological processes? Evolutionary theory suggests that this type of unconstrained altruism is not an evolutionary stable strategy, because individuals that provide help unconditionally will accrue high fitness costs. Thus, biology suggests that individuals must also be selective, biasing their altruistic efforts only toward certain social partners under certain circumstances. That is, altruistic psychological mechanisms that detect the needs of others and act on them must be complemented by other mechanisms that prevent the altruist from being exploited by others (e.g., Cosmides & Tooby, 1992). Thus, a mature altruist has to possess both the psychological mechanisms to engage in acts of altruism and the psychological mechanisms to decide whom to help and when, in order to be viable at the ultimate level. Multiple theories have proposed how altruistic motivations can be biologically beneficial at the level of lifetime reproductive success. For example, individuals might direct altruistic acts toward kin (Hamilton, 1964) or toward those who reciprocate over those who reap the benefits without reciprocating in the future (Trivers, 1971). In this section, I thus explore the development of these altruistic “safeguards.”

Importantly, these safety measures need not be in place ontogenetically at the same time when children begin to engage in altruistic behavior. For instance, the ability to detect cheaters who profit from helpful acts but do not reciprocate in the future is potentially of less relevance early in ontogeny when children are mainly surrounded by family altruists, with strangers standing at the periphery. Therefore, the selective development of economic mechanisms, which can complement these strategies, is likely a more efficient strategy (Trivers, 2006). As children mature, the existence of such mechanisms allows the use of reciprocity to reward others who cooperate with them.

Even the most basic altruistic motivations are unlikely to be the only mechanisms in children's helping behavior. Moreover, the apparent costs of helping to children may be relatively low in the sense that their caregivers and peers will also be divide
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mainly surrounded
by family members and protected by their parents. The ability to distinguish between
altruists and cheaters probably becomes important only later in life, as interaction
with strangers increases. Thus, some proposals suggest that children start out as rather
indiscriminate altruists who become more selective as they grow older (Hay, 1994;
Warneken & Tomasello, 2009a). Specifically, children’s emerging social-cognitive under-
standing and new experiences should lead to more selective helping, informing, and
sharing. Here I will therefore address whether (or at what point in development) such
selectivity characterizes the social behaviors of human children—and to what extent
this selectivity characterizes the social behaviors of chimpanzees. Many models from
evolutionary theory and empirical findings from social psychology and behavioral
ecology with adults have focused on direct and indirect reciprocity as important
mechanisms that support cooperative behaviors. Direct reciprocity refers to cases in
which commodities are exchanged between two individuals over repeated encounters
(by, for example, taking turns in helping each other over time). In cases of indirect
reciprocity, two individuals might not directly interact again, but the interaction is
registered by third parties, and thus altruistic acts (or lack thereof) can affect one’s
reputation and thus future opportunities to interact positively with others (Nowak,
2006). As such, I will here focus on when during ontogeny these factors begin to
influence altruistically motivated behaviors in children.

Even though direct reciprocity as originally proposed by Trivers (1971) was con-
ceived as a simple way to sustain cooperation in a way that was mutually beneficial
in the long term, more recent examinations of reciprocal strategies such as Tit-for-Tat
have suggested that they may actually be quite cognitively demanding. For example,
as the temporal delay between paying a cost to help others and ultimately recouping
it in terms of benefits received, psychological capacities including delay of gratification
(in which individuals forgo an immediate benefit in favor of a higher future benefit),
identifying those individuals with whom one will interact again in the future, and the
ability to detect cheaters become increasingly important (Stevens & Hauser, 2004).
Moreover, reciprocal behaviors can have diverse psychological bases, ranging from
symmetrical relations where two individuals associate at high rates and thus show
apparent reciprocity, to more contingent reciprocity where individuals account for
the costs and benefits accrued in their relationship (Brosnan & de Waal, 2002). When
do children show these capacities and start to engage in broadly reciprocal behaviors?
To what extent are these behaviors based on mental accounting of others’ actions and
their consequences?

In developmental psychology, reciprocity has been mainly studied in the domain
of sharing and distributive justice. When asked about their explicit judgments, pre-
schoolers at 4 to 5 years of age show no understanding of reciprocity (Berndt, 1979)
and do not refer to reciprocity in their justifications about how a resource should
be divided before 6 to 7 years of age (Damon, 1975; De Cooke, 1992). Using a simpler
paradigm, Olson and Spelke (2008) demonstrated that when 3.5-year-olds are asked how a puppet character should divide up a resource between two other characters, they advise giving more to the character who had shared with the puppet previously versus to the one who hadn’t shared. Thus, at this age children appear to possess some basic notion of reciprocity in the sense of two individuals treating each other alike. However, it is unclear how these judgments of others’ actions translate into young children’s own altruistic behaviors, such as sharing their own resources or putting effort into helping. In fact, there is only one correlational study on sharing in 3-year-olds indicating that they perhaps engage in reciprocal altruism. Specifically, when one child had lots of toys and the other one was toy deprived, only those “rich” children who shared with a “poor” child after prompts from their mother in the initial phase of the experiment received toys back when roles of “rich” and “poor” subject were switched in the second phase (Levitt et al., 1985). Concerning instrumental helping, one experimental study shows that 21-month-old infants will selectively help a person who was willing but unable to share a toy with them over a person who was unwilling to do so (Dunfield & Kuhlmeier, 2010). Specifically, even though during the exposure phase, the outcome of either person’s action was the same (the child didn’t receive the toy), children were attentive to the “nice” person’s intention who was trying but failing to give them a toy (which accidentally rolled away) in contrast to the “mean” person’s intention (who offered the toy, but then withdrew it in a teasing fashion). During the subsequent test phase, both persons reached for a single object, and results showed that children preferentially gave it to the previously “nice” unable person over the “mean” unwilling person. Thus, children kept track of how each person had behaved toward them before and adjusted their helping accordingly, thus demonstrating that they possess a critical capacity required for contingent reciprocal altruism by keeping track of who had had helpful intentions in the past. Nevertheless, it is still unclear whether children engage in calculated reciprocity by performing an altruistic act in the present in anticipation of reciprocation in the future (Brosnan & de Waal, 2002; de Waal & Luttrell, 1988).

Regarding indirect reciprocity, recent research has examined how infants and children encode third-party interactions, as well as observing how dyadic interaction influences how the children direct their subsequent altruistic behaviors. For example, infants in the first year of life differentiate between “helpers” and “hinderers,” namely agents displayed as geometric shapes who either assist another agent to climb up an incline or push it down (Kuhlmeier, Wynn & Bloom, 2003), and show a preference for the helper by touching the helper over the hinderer in a forced-choice paradigm (Hamlin, Wynn & Bloom, 2007). At least by 3 years of age, children use such discriminatory abilities in their own altruistic behaviors by avoiding the provision of help to mean people: After they have observed how one “mean” adult harmed another individual, they are less likely to subsequently help the mean adult over a helpful or
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10-year-olds are asked to choose characters, one of whom previously possessed some object and another who did not. They are then asked to give the toy to a child who was a stranger. The results showed that older children were more likely to choose the stranger who had been given the toy, even if they themselves had never interacted with the child. This suggests that children are sensitive to the intentions of others and are motivated to help those who have been treated unfairly.

Older children also tend to show more empathy towards others who have been wrongdoing. For example, they are more likely to feel sorry for a child who has been treated badly than for a child who has been treated fairly. This suggests that children are able to attribute mental states to others and to respond to these mental states in a way that is consistent with their own desires.

Finally, it is important to note that altruistic behavior is not limited to humans. Chimpanzees, for example, are known to engage in reciprocal altruism, where they give help to others in the hope of receiving help in return. This is evident in their cooperation in foraging for food and in their willingness to share food with others. Thus, altruistic behavior is a universal characteristic of social animals.
that contingency-based reciprocation within a short time-interval can slightly alter the basic tendency to help conspecifics, but it accounts for only a small proportion of the variance (as in correlational studies, de Waal, 1997; Koyama, Caws & Aureli, 2006). However, again in a food-provision context without active solicitation from a recipient similar to those used by Silk et al. (2005) and Jensen et al. (2007), chimpanzees do not appear to take advantage of the opportunity to engage in contingent reciprocity (Vonk et al., 2008; Brosnan et al., 2009; Yamamoto & Tanaka, 2010). It is not clear why contingent reciprocity does not appear to emerge as a consistent strategy in chimpanzees (at least when tested in short-term interactions in the laboratory). Chimpanzees possess the critical components necessary for contingent reciprocity, including the ability to delay gratification (Rosati et al., 2007), detect whether someone was unwilling or unable to give food to them (Call et al., 2004), help others (see above), retaliate against uncooperative individuals (Jensen, Call & Tomasello, 2007) and select partners for mutualistic cooperation (Muller & Mitani, 2005, for observational studies in the wild; Melis, Hare & Tomasello, 2006b, for experimental evidence). It is possible that contingent reciprocity operates over longer time frames than those employed in experiments (Melis, Hare & Tomasello, 2006b; Schino & Aureli, 2009). It is also possible that in most situations that could initiate bouts of reciprocal exchange, immediate selfish interests predominate: The myopic tendency to accrue resources that interferes with sharing more generally also jeopardizes the long-term benefits that could be gained from reciprocity. Thus, although there is evidence that altruistic and other cooperative interactions are characterized by reciprocity, it remains unclear what mechanisms account for these patterns. In particular, there is no strong experimental evidence that chimpanzees engage in bouts of contingency-based reciprocation.

Beyond the issue of direct reciprocity, do chimpanzees cooperate with others based on their reputation? Do they take into account how their (un)cooperative behavior affects their own reputation in the eye of the beholder? To the best of my knowledge, there is currently no published experiment that speaks to these issues. However, some experimental evidence indicates that chimpanzees learn about the cooperative behaviors of others (broadly construed) through third-party observation. Specifically, in Subiaul et al. (2008), after being trained over several sessions to differentiate between a “nice” and a “mean” experimenter who either gave them food or refused to do so in a direct interaction, chimpanzees observed how a novel pair of “mean” and “nice” experimenters treated another chimpanzee in a feeding situation. When the subject now had the opportunity to beg from these two new individuals, they showed a preference for the previously “nice” person, indicating that they had learned from observing other people’s behaviors. Russell, Call, and Dunbar (2008) came to a similar conclusion based on an experiment in which chimpanzees first monitored an interaction among three humans, in which a “nice” person gave food to a human beggar and a “mean” person slapped the beggar’s hand when he reached for the food. This was obse...
can slightly alter small proportion i, Caws & Aureli, solicitation from a (2007), chimpanzees contingent reciprocity, whether someone others (see above), , 2007 and select experimental studies). It is possible those employed , 2009. It is also exchange, immesources that interact ants of task that could altruistic and other ins unclear what ong experimental reciprocation.

with others based perative behavior best of my knowe issues. However, the cooperative ation. Specifically, ferentiate between r refused to do so mean” and “nice” When the subject s, they showed a had learned from i came to a similar tutor an interact a human beggar the food. This was observed in four incidents. Results showed that chimpanzees then approached the previously “nice” over the “mean” experimenter when both had food in front of them, presumably because they thought that they would have more luck with him. Taken together, these experiments suggest that chimpanzees learn from observing third-party interactions, and that they apply this information to feeding situations in which they are in the position of the recipient. However, it is not totally clear from these results that the chimpanzees learn that the experimenter is a social agent with “nice” or “mean” intentions or just a more or less reliable food dispenser. Last but not least, even if one grants chimpanzees the ability to attribute these social qualities to the two agents and use it for their own choice with whom to interact, these results do not address the question of whether chimpanzees will alter their own cooperative behavior after observing others’ cooperation, let alone whether they are influenced by the knowledge that others are watching them. Insight into the relationship between reputation formation and cooperative behaviors remains an important focus for future studies.

Conclusion

I have attempted to provide a comprehensive overview of the variety of human altruistic behaviors as they emerge in human ontogeny and phylogeny, focusing on the development of young children and comparative studies with chimpanzees and bonobos. Recent studies indicate that humans and other apes share some of the core capacities required for altruistic behaviors, especially in the form of instrumental helping. The expression of altruism depends to some extent on the domain of activity, such as helping others, sharing resources or sharing information, which suggests that different proximate mechanisms might be at play and that such mechanisms are not necessarily all present in humans and other apes. The basic motivations and cognitive capacities for altruistic behavior emerge early in human ontogeny, perhaps reflecting a biological predisposition that we share with our closest evolutionary relatives. Future research should investigate the transformation of these early forms of human altruism into the mature form seen in adults, while paying special attention to the critical proximate mechanisms that serve to maintain altruistic behaviors evolutionarily. Humans may have created unique social mechanisms to preserve and foster the basic altruistic tendencies found in young children and other apes, resulting in altruistic behaviors not found outside the human species.

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