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# How Children Solve the Two Challenges of Cooperation

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## Abstract

In this review, I propose a new framework for the psychological origins of human cooperation that harnesses evolutionary theories about the two major problems posed by cooperation: generating and distributing benefits. Children develop skills foundational for identifying and creating opportunities for cooperation with others early: Infants and toddlers already possess basic skills to help others and share resources. Yet mechanisms that solve the free-rider problem—critical for sustaining cooperation as a viable strategy—emerge later in development and are more sensitive to the influence of social norms. I review empirical studies with children showing a dissociation in the origins of and developmental change seen in these two sets of processes. In addition, comparative studies of nonhuman apes also highlight important differences between these skills: The ability to generate benefits has evolutionary roots that are shared between humans and nonhuman apes, whereas there is little evidence that other apes exhibit comparable capacities for distributing benefits. I conclude by proposing ways in which this framework can motivate new developmental, comparative, and cross-cultural research about human cooperation.

## Contents



## INTRODUCTION

Cooperation is a defining feature of human social life. Humans share valuable resources, assist others who need help, and pool their efforts to yield outcomes beyond the capabilities of any one individual. Our species depends on cooperation more than any other primate, exhibiting levels of sophistication and flexibility in cooperation that are not seen elsewhere in the animal kingdom. How do these cooperative abilities emerge, especially given the fact that selfish motivations can often prevail over our cooperative tendencies? Developmental studies with children are a powerful tool to study the human condition, providing insight into the early origins of our social abilities, as well as how these abilities change over the lifespan. In addition, comparative studies with our closest primate relatives can determine which aspects of our cooperative capacities are unique to humans and which are shared with other apes and, thus, potentially evolutionarily ancient. Thus, integrating developmental and comparative approaches can shed light on the biological origins and social forces that shape human cooperation.

This article reviews the recent surge in research on the cooperative abilities of children and our ape cousins—as well as the limitations in these abilities. I propose a new framework that connects evolutionary models concerning the fitness benefits of cooperation with the proximate psychological mechanisms that implement these behaviors in the mind. I argue that, for individuals to become proficient cooperators, they must have two different sets of psychological skills to address two different challenges. The first set of abilities deals with the challenge of generating benefits through cooperation, whereas the second deals with distributing those benefits and stabilizing cooperation once it emerges. To date, little work has taken a synthetic view of both of these sets of skills (Calcott 2008). For example, there has been much empirical work on human abilities to

create benefits—aiming to explain how human cooperation (including aspects such as our ability to feel empathy or to collaborate in teams) differs from that of other animals—without directly addressing the second challenge of how benefits will be distributed to make cooperation a viable option over the long term (Batson 2011, Hoffman 2000, Tomasello et al. 2005). Conversely, evolutionary models tend to target the second challenge and show how cooperation can be sustained when people reciprocate or punish selfishness to support cooperation, but these theories do not give much regard to the issue of how these benefits could be generated through cooperation in the first place (Nowak 2006).

## The Two Challenges of Cooperation: Creating and Distributing Benefit

I propose that the two challenges of generating and distributing benefits are supported by two different sets of psychological capacities that can be dissociated in both ontogeny and phylogeny. Ontogenetically, the skills to generate benefit through cooperation arise early in development, whereas mechanisms to distribute benefit in a way that safeguards cooperation against defection are acquired later—and sometimes strongly depend on children's understanding of social norms that prescribe how cooperative benefits should be distributed. These norms increasingly guide children's own cooperation as they grow older and also shape their expectations about how others should interact with them. That is, children start out as cooperators who are focused on creating benefits and only begin to safeguard their cooperative tendencies against the exploitation of free-riders later on (see **Figure 1**). This distinction is also apparent phylogenetically, as humans and chimpanzees share the basic abilities to generate benefit, but humans have species-unique processes to distribute benefit that enable cooperative behaviors at a scale not found in our closest evolutionary relatives. It is, of course, important to emphasize the fact that several other factors

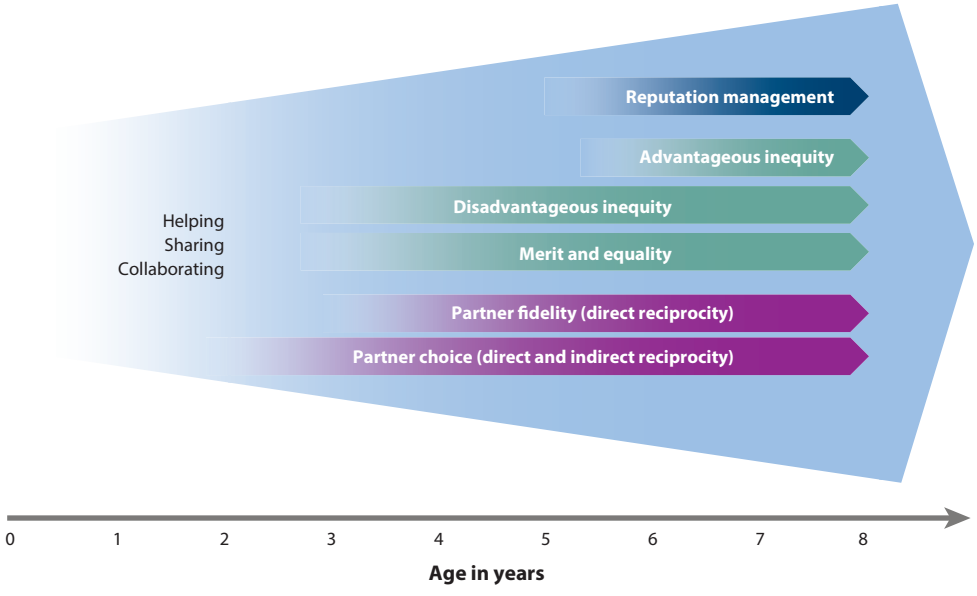


**Figure 1**

Developmental onset of abilities to generate benefits (*written in black*) and to distribute benefits (*written in white*).

may influence rates of cooperative behaviors in humans and other species. Like many other social behaviors, children's cooperation may fluctuate depending on their mood, whether they are interacting with a familiar or unfamiliar person, or whether they are tested in a friendly environment (Barragan & Dweck 2014, Carpenter et al. 2013). However, although context can play an important role, this proposal concerns the developmental onset of psychological capacities that can solve the challenge of distributing benefit and stabilize cooperation.

An alternative to the view I propose in this review is that both of these sets of skills are integrated from the beginning, emerging in the same timeframe. This view conjectures that children safeguard their cooperation against free-riding from the time they can first generate benefit, with decisions to cooperate already motivated by concerns about how the generated benefit can be recouped in some form, such as by benefiting kin, promoting reciprocity, or improving one's own reputation (Nowak 2006). This view is often assumed in evolutionary theories: Cooperative behaviors that are vulnerable to free-riding cannot be sustained, so the capacities to generate and distribute benefits must evolve in tandem (Calcott 2008). A similar view is often applied to the ontogenetic emergence of these skills. For example, young infants already possess several concepts that are critical for distributing benefits, such as identifying cooperative individuals, preferring them to uncooperative individuals (Hamlin et al. 2007, Kuhlmeier et al. 2003), and expecting to see equal resource divisions (Sloane et al. 2012). This work is often viewed as evidence that young children can solve the free-rider problem to some degree. However, I would argue that, just as hearing is not the same as talking, representing and evaluating the social world in this way does not mean that children already regulate their own actions based upon these principles. I show that, in terms of their actual cooperative behaviors, children exhibit a clear developmental lag between the two skill sets, and it is only during middle childhood that children integrate the two set of skills and become able to cooperate in ways that are sustainable in the long term. Children are thus initially rather naive and become more vigilant against free-riding and more proficient at negotiating the balance between their own and a partner's interests over the course of development.

To evaluate these hypotheses, I review the current empirical evidence concerning the development of the critical social-cognitive skills that underpin different forms of cooperation in children. I focus in particular on the age of emergence of different forms of altruistically and mutualistically motivated cooperation to assess whether the different mechanisms of generating benefit emerge earlier than the skills to distribute benefit, such as reciprocity and expectations about fairness. Finally, I examine what biological and social factors may influence this sequence of emergence. In particular, I argue that comparative evidence shows that basic skills for generating benefits have biological roots shared with great apes, whereas skills for distributing benefits are more sensitive to local cultural norms of behavior.

## Integrating Psychological Mechanism and Ultimate Function

The question of the causes of cooperation (or any behavior) can be broken down into proximate questions about psychological mechanisms and ultimate questions about evolutionary function (Mayr 1961, Tinbergen 1963). Ultimate questions focus on the fitness consequences and evolutionary history of behaviors—why the behaviors exist—whereas proximate questions concern the implementation and development of these behaviors in the mind and brain—how the behaviors work. Cooperative behaviors, especially altruistically motivated behaviors, have long been puzzling because they appear to reduce an individual's evolutionary fitness. However, modern evolutionary theory has developed several accounts of how different forms of cooperation can evolve through natural selection (Nowak 2006, West et al. 2007). These models show how cooperative behaviors can, in fact, lead to fitness benefits, although sometimes in indirect and intricate ways; for instance,

altruistically motivated behavior can be explained through the genetic relatedness with recipients or reciprocal relationships where current costs are outweighed by future benefits.

However, models focused on the ultimate function of cooperative behaviors do not tell us what psychological capacities individuals need to perform these behaviors. While there are multiple ways in which cooperation could evolve, proximate mechanisms put a constraint on what can actually emerge. For example, reciprocity may seem to be a straightforward solution to the problem of cooperation, but it is not viable if individuals cannot individuate others or do not know who did what to whom. Similarly, reputation and punishment may, in principle, be able to weed out uncooperative individuals, but not if individuals cannot represent third-party relations, cannot communicate to others what they saw, or lack the motivation to stand up for others. Thus, although it is critical to distinguish these different levels of analysis, it is equally important to understand their interrelationship—how proximate mechanisms can constrain or enable behaviors with different ultimate consequences. Following Calcott (2008), I propose that there are two distinct classes of proximate mechanisms that instantiate human cooperation: those for generating benefit and those for distributing benefit.

## HOW CHILDREN LEARN TO GENERATE BENEFIT THROUGH COOPERATION

The first challenge for cooperation is creating benefits. How can individuals produce benefits that would be absent without cooperative action? Acts of mutualistic collaboration provide a good example. When individuals collaborate, they create benefits for the participating cooperators that they would not obtain if they had acted alone. From a mere payoff perspective, it is easy to explain why individuals would choose to engage in a collective act (such as hunting together rather than alone) that creates these mutualistic benefits. However, this presupposes that individuals have the ability to identify the added value that may result from this collective act. Furthermore, even if individuals recognize these added benefits, they have to find a way to actually accomplish the task by socially coordinating their behaviors with others. Thus, even though the emergence of mutualism appears fairly straightforward from an ultimate perspective, identifying such opportunities and executing the cooperative act successfully can be quite challenging in terms of the proximate mechanisms needed.

Other examples include altruistically motivated acts that are aimed at benefiting another individual rather than the self. These may come in various forms depending on the type of need an altruist has to detect and whether emotional support, practical help, or sharing of resources would be most appropriate. A lack of altruistic intervention could be due to limitations in detecting the need or to a lack of motivation. Such acts can be altruistically motivated (in that they are intended to help another individual) but not necessarily altruistic from an evolutionary perspective (in terms of fitness costs and benefits). Rather, they are best thought of as building blocks for behaviors, such as kin-directed helping or reciprocity, that depend on an initial act of altruism that (in real life if not in experiments) can later be recouped through indirect fitness benefits or additional interactions with that partner.

### Helping and Comforting

Helping is one of the earliest manifestations of altruistic behaviors. In the second year of life, children begin to comfort others who are in distress or pain, lend a helping hand to someone who is struggling with a practical problem such as reaching for an object that is too far away, and offer helpful information with the simple act of pointing to an object a person is searching

for. What is striking about children's helping is not only its early emergence but also the fact that children are able to help with a diverse set of problems, often in flexible ways. For example, when encountering someone in pain or distress, children can employ many different responses, including directly comforting the victim, helping to repair a broken toy, handing over their own toy, or seeking help from others (Eisenberg et al. 2015). Similarly, 18-month-olds are able to infer various types of action goals and flexibly offer the appropriate instrumental help by picking up objects that someone has dropped on the ground, helping put away objects by holding doors open, or applying a newly acquired technique for accessing the contents of a novel box when a clumsy adult fails to do so (Warneken 2016). In these situations, children know both when to help—differentiating between intentional and accidental outcomes—and how to help—by handing over and pointing to objects a person needs rather than those that are irrelevant (Hepach et al. 2016, Liszkowski et al. 2006). Control conditions rule out the possibility that children do this for unrelated reasons, such as stimulus enhancement, social interaction, or simple reestablishment of the original physical state (Hepach et al. 2017a, Warneken 2013, Warneken & Tomasello 2006). Taken together, these results show that children intelligently adapt their helping to facilitate the fulfillment of another person's action goal.

As children develop into sophisticated helpers, they require fewer cues to know when and how to act. One example of this development is children's response to other's emotions. Babies can already respond to an overt expression of distress, such as a face that is in pain or drenched in tears. By 18–24 months, children begin to take the situational context into account. They react appropriately when the situation calls for it, showing concern and helping when a victim loses her belongings to a destructive bully, even when the victim remains stoic and shows no overt facial expression to cue the child to their emotional distress (Vaish et al. 2009). Conversely, when 18-month-olds see an adult be upset over an event that could not actually have hurt the person, they show little sympathy for this "cry baby" (Chiarella & Poulin-Dubois 2013, Hepach et al. 2013).

Children make inferences based upon fairly minimal cues in instrumental helping and informing contexts, as well. Although verbal and nonverbal communication increase the likelihood that children will help, especially in cases where the problem is more opaque, they are often not necessary (Pettygrove et al. 2013, Svetlova et al. 2010). Indeed, by 2 years of age, children are able to help proactively in the absence of any eliciting cues—such as when a person does not realize that the objects she wanted to clean up had rolled off a table while she was turned away (Warneken 2013). This suggests that children are able to draw on situational cues to infer when help is needed. Young children can also help in anticipation of a problem. When a person is mistaken about the actual location of an object she is searching for, 18-month-olds direct her to the correct location before she looks in the wrong spot (Knudsen & Liszkowski 2012b). Similarly, they warn a person who is unaware that two buckets had been swapped and would thus likely reach into the wrong bucket, which holds an aversive object (Knudsen & Liszkowski 2012a). Thus, children can predict the person's action in light of her state of knowledge and intervene proactively. Finally, children can even correct a person's course of action and do what is actually helpful. That is, children do not blindly assist in completing any concrete action that another person pursues, but rather use their understanding of the person's ultimate action goal (e.g., ignoring a request for a cup with a hole and instead handing an intact cup; Martin & Olson 2013) or even their ignorance about the true state of the world (Buttelmann et al. 2009) to help appropriately.

Importantly, there is strong evidence that children's early helping behaviors are altruistically motivated, i.e., aimed at creating a benefit for others rather than a benefit for the self. Children often help spontaneously without solicitation from the recipient or a third party (Warneken 2016). They care about the needs of their peers as well as those of younger children, not just potential authority figures (Hamann et al. 2012, Hepach et al. 2017b, Kaneko & Hamazaki 1987). They

help when their parents are not watching (Warneken 2013, Warneken & Tomasello 2013b) and even when the beneficiary is away (Hepach et al. 2017a). Moreover, in studies on instrumental and emotional helping, children still help even when they are neither rewarded nor praised. The offering of rewards does not elicit more helping in the immediate situation (Warneken et al. 2007) and can even undermine children's intrinsic motivation and reduce future helping (Warneken & Tomasello 2008). Last but not least, children seem to genuinely care about the other person's need as a goal in itself. One striking example comes from helping situations in which 2-year-olds show arousal (as measured by changes in pupil dilation) when they witness a person's goal remain unresolved because an object is out of reach or the person receives the wrong object. However, they are relieved when the person receives the appropriate help and attains the goal, regardless of whether they themselves or some other bystander provided the help (Hepach et al. 2012, 2016). Thus, children appear motivated to help another person achieve their goal for other reasons besides demonstrating their mastery of the situation or obtaining a reputation for goodwill.

## Sharing Resources

Like children's tendency to help with practical and emotional problems, children's resource sharing emerges in the second year of life. When someone else is in need, 18-month-olds are willing to give up their own resources. For example, toddlers are willing to share food snacks when they have a bowl of crackers and the experimenter's bowl is empty (Brownell et al. 2013, Dunfield & Kuhlmeier 2013, Dunfield et al. 2011, Pettygrove et al. 2013), sacrifice some of their own toys so that a deprived experimenter can play as well (Warneken & Tomasello 2013a), and give up one of their own balloons when an experimenter has lost hers (Vaish et al. 2009). Importantly, these are instances of sharing in which children give up a resource, thus paying a real cost for sharing, rather than instances of sharing for mutual play or to initiate a social interaction.

For children to give up a valuable resource, cues of the recipient's needs are important, as they are with early helping. For example, children are more likely to share when the recipient provides more explicit behavioral and communicative cues about her desire for a resource. This is particularly true at younger ages. For example, 18-month-olds share toys and food only after the recipient makes her need explicit or even directly asks the child to share, including by palm-up gestures or stating, "I don't have any crackers." For 24-month-olds, much more subtle cues are sufficient. They typically share before a recipient makes a request and often immediately upon realizing that the other person ended up empty handed (Brownell et al. 2013, Dunfield & Kuhlmeier 2013, Dunfield et al. 2011, Pettygrove et al. 2013, Warneken & Tomasello 2013a). In these studies, the vast majority of toddlers share something, and the age differences are the spontaneity and speed, rather than the overall rate, of sharing. In sum, these studies show that children are willing to intervene even at their own cost, at least when the need for intervention is salient. Very young children appear to need more explicit cues about another's need of a resource, but, upon realizing the need, they are willing to share.

These studies with toddlers may also explain why sharing rates are initially low in studies using the dictator game. In this game, children are given a choice in how to divide up a resource between themselves and a passive recipient (who is often not present or known). In such dictator games, young children are mainly self-serving and give away little, if anything (see Ibbotson 2014 for an overview). By contrast, adults give, on average, 30% of their resources away (Engel 2011). However, in these cases, neither the circumstances nor the absent recipients evoke any signs of need, hunger, or urgency. This is often done deliberately to eliminate opportunities for reciprocity or reputational effects, a methodology that is appropriate for older children and adults but that limits the validity for young children. In other developmental studies, the situation is

slightly more interactive, with two children sitting across from each other and the participant (the dictator) choosing between two predetermined options, e.g., one reward for the self and none for the other versus one reward for each (Graves & Graves 1978, Thompson et al. 1997). Although this task is more concrete than regular dictator games, several researchers have raised concerns about the task demands, as young children often fail comprehension checks, and small variations in task administration result in wide age variation, perhaps due to attentional demands (Burkart & Rueth 2013, House et al. 2012, Tomasello & Warneken 2008). These kinds of tasks are better suited for older children, especially to test for children's developing sense of fairness, but are not suitable to determine whether sharing is present in toddlers. These tasks elicit little sharing in young children, not necessarily because children lack altruistic sentiments, but rather because the tasks lack the core features that elicit it.

## Mutualistic Collaboration

Young children not only act for others to achieve individual goals, they also act with others collaboratively. This collaboration encompasses social games and problem-solving tasks in which two individuals have to join forces because one person cannot retrieve a reward alone. For example, one person has to activate a mechanism on one side of an apparatus while the partner simultaneously manipulates the other side of the apparatus to retrieve a reward (Brownell & Carriger 1990). Other examples involve objects that are too large for one person to handle, such as when a wooden block bounces on a large trampoline that two people have to hold up (Warneken & Tomasello 2007, Warneken et al. 2006). From approximately 14 to 18 months of age, children begin to coordinate their actions successfully in such situations.

Children are not just responding to the other person's action and rigidly performing one role (like a dog playing fetch), but rather appear able to represent both roles as interconnected parts of a social activity. Children quickly learn how to interact in novel situations after very little experience and often only a single demonstration (Warneken et al. 2006). They also engage in role reversal, flexibly switching between two complementary actions, performing whatever role is necessary to successfully engage in the activity (Carpenter et al. 2005; Warneken et al. 2006, 2007). This indicates that they are able to represent the respective actions as part of an overarching action plan, rather than just executing their own individual act. This is also apparent from studies in which 14-month-olds are onlookers of an act between two collaborators: The infants form a representation of each individual's act not as an isolated means–end relationship but as an act that complements the partner's action (Henderson & Woodward 2011). With active experience, even 10-month-olds seem to form such an expectation (Henderson et al. 2013).

In addition, children do not just follow the partner's lead but actively participate; when an adult partner interrupts the joint activity, children often try to reengage the partner by communicating, offering the toy, or trying to help the partner with their role (Gräfenhain et al. 2009, Ross & Lollis 1987, Warneken et al. 2006). Children treat the other person not just as a social tool that they need to accomplish their own goal, but as an agent with intentions to either collaborate or not. For example, 21-month-olds try to reengage a collaborator who is unable to continue (by helping and informing) over someone who is unwilling to continue (Warneken et al. 2012). Thus, children respond not only to the behavioral outcome, but also to the partner's intention that leads to it.

Toddlers collaborate not only with adults, but also with peers. This result 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. In contrast, children are left to their own devices during peer interactions, enabling researchers to assess their skill level independent of adult scaffolding. Second, this result 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 should be distributed in mutualistic tasks in which two individuals work toward an otherwise unobtainable resource.

Peers begin to successfully coordinate their actions with each other during the second half of the second year of life (Brownell 2011, Eckerman & Peterman 2001). This includes coordinated attempts to initiate social interactions with peers, such as taking turns to act on an object (Eckerman et al. 1989), as well as synchronizing one's own action with that of a peer, as in the case of two children simultaneously pulling two handles protruding from a music box to make a puppet sing (Brownell et al. 2006). In tasks that require the temporal and spatial coordination of two actions, children younger than 2 years old often struggle, but during the third year of life, they become proficient at tasks such as pulling handles simultaneously or performing complementary roles, as when one child manipulates a lever so that another child can retrieve an object (Ashley & Tomasello 1998, Brownell & Carriger 1990, Brownell et al. 2006). Thus, children are capable of collaborating with each other without adult scaffolding but become successful in this collaboration slightly later than they are in collaboration with an adult partner.

## HOW CHILDREN LEARN TO DISTRIBUTE BENEFIT

The previous section showed that children develop the basic skills to generate benefit early, in the second year of life. But the second challenge for cooperators is to find a way to distribute benefit that can sustain cooperation. This challenge is particularly apparent for cooperation among genetically unrelated individuals, where cooperation is threatened by free-riders who reap the benefits while paying fewer or no costs. For example, when individuals collaborate to create a collective good, free-riders are better off if they obtain the same benefit without contributing. Similarly, when two individuals interact repeatedly, a defector who receives more often than she gives to the other will be better off in the long term than a cooperator who always gives. Therefore, abilities to create benefit through cooperation must be complemented by mechanisms to guard against free-riders. When do children first begin to exhibit these behaviors in cooperative contexts?

### Direct Reciprocity

How cooperation evolves in the face of free-riding is at the core of many game-theoretic and evolutionary models. Such models show that reciprocity is a powerful way to stabilize cooperation. Specifically, in direct reciprocity, two individuals exchange favors by acting in a manner that is contingent on how a partner has treated them and can be better off in the long term than if they had not cooperated at all. An important distinction for mechanisms of reciprocity is that between partner fidelity and partner choice (Baumard et al. 2013, Hammerstein 2003, Kuhlmeier et al. 2014). Partner fidelity concerns situations where two social partners interact repeatedly and make decisions about how to interact. Partner choice concerns situations in which individuals can, in addition, make choices about with whom to interact. Therefore, partner fidelity and partner choice likely tap into different psychological abilities.

**Partner fidelity.** At what age do children begin to cooperate differently depending on how a social partner has treated them in the past? The earliest instances of reciprocity in terms of partner fidelity have been found in 3.5-year-olds. Children shared more resources with a partner who had previously shared with them than with a defector who had never shared with them (Warneken & Tomasello 2013a). By contrast, 2.5-year-olds cooperated at the same level with both cooperators and defectors. Similar results were found in forced choice tasks, where 2.5-year-olds generally

chose a prosocial option that provided a payoff to both actors rather than a selfish option that provided a reward only to themselves, regardless of whether an adult partner had acted prosocially or selfishly toward them before (Sebastian-Enesco et al. 2013). Studies with peers found that it was not until around 5.5 years of age (House et al. 2013a) that children began acting in a manner that is contingent on the choices of a peer partner; in some contexts, this development occurred even later, at 6–8 years of age (Dahlman et al. 2007). Therefore, the earliest age for which there is evidence that children look back on how their partner has treated them and adjust their cooperation accordingly is approximately 3.5 years and, in many cases, even older.

Another important aspect of reciprocity is the ability to look ahead, i.e., being able to anticipate whether a partner will likely reciprocate later—the so-called shadow of the future. Whereas 5-year-olds share more when they know the interaction will be iterated compared to a one-shot interaction, 3-year-olds share the same amount regardless (Kenward et al. 2015, Sebastian-Enesco & Warneken 2015). Similarly, when one of two children can obtain a valuable resource every other time, 5-year-olds spontaneously develop a strategy of turn taking so the beneficiary alternates across trials (Melis et al. 2016), whereas 3-year-olds do not. Thus, current evidence shows that contingent reciprocity in terms of partner fidelity does not emerge before middle childhood. Although young children already possess the skills to generate benefit through cooperation, they are not yet using contingent reciprocity to adjust how cooperative they should be toward a given individual.

**Partner choice.** Although young children do not yet adjust their level of cooperation contingent on an agent's cooperation, studies suggest that partner choice could emerge earlier in development: When children are forced to choose between two potential partners, they prefer to interact with cooperative over uncooperative individuals. In one study, 21-month-olds interacted with a clumsy adult who tried and failed to hand them objects and with an unwilling adult who had teased them with the toy. When both adults then simultaneously reached for the same object, children gave it to the nice rather than the mean adult (Dunfield & Kuhlmeier 2010). Similarly, 3.5-year-olds helped someone who had previously told them where to find a toy over someone who had withheld helpful information (Dunfield et al. 2013). Therefore, children direct their helping preferentially toward those with good intentions over those who prove to be downright mean.

These two studies provide some initial information about children's developing preferences in partner choice situations, but many open questions remain. So far, only helping behaviors have been studied, and nothing is known about partner choice when children have to sacrifice resources—unlike much of the work on partner fidelity, which has also focused on more costly sharing decisions. Moreover, there has been no work examining whether children are more likely to engage in a mutualistic collaboration with nice over mean individuals.

## Indirect Reciprocity

In indirect reciprocity, cooperation can emerge in triads or larger groups where cooperators gain a good reputation and are treated more favorably by third parties. One important component of this development is attending to the third-party behaviors of others and preferentially choosing to interact with partners who cooperated with others. A second component is managing one's own reputation: taking into account how one's behavior will look in the eye of the beholder. These two components of indirect reciprocity both emerge later in development, with reputation management not coming online until middle or even late childhood.

**Partner choice.** There is clear evidence that young infants can evaluate how agents treat others, detecting and preferring cooperative agents who help others over those who are antisocial (Hamlin et al. 2007, Kuhlmeier et al. 2003). One important question is at what age children actually start to apply these social evaluations to choose with whom to cooperate. Several studies have combined social evaluation and cooperative partner choice by first introducing children to a nice and a mean adult and then having both adults reach for the same object to solicit help. In fact, these evaluations do not seem to drive cooperative choices until later in development, much later than the first emergence of helping, at 14–18 months. One study found that 17- and 22-month-olds helped indiscriminately, but 26-month-olds helped the nice over the mean adult, at least in the first trial (Dahl et al. 2013). Similarly, Vaish et al. (2010) found that 3-year-olds preferentially helped by giving a marble to a cooperative or a neutral adult over an antisocial adult (who had destroyed another person's belongings). This was apparent even when the antisocial person tried but failed to harm an individual, indicating that children assess the person's intentions, not just the outcome of their actions. Interestingly, when children then distributed a second marble, they mostly gave it to the antisocial agent. Thus, although children have a bias toward helping nice over mean individuals, they do not completely withhold help from uncooperative individuals and appear to countervail their initial choices.

Other studies have used resource distributions as a dependent measure. Kenward & Dahl (2011) found that, when 4.5-year-olds were asked to distribute three cookies between a mean and a nice puppet (who had previously helped or hindered a third puppet), they tended to give more to the nice puppet. However, these children also had a strong tendency to try to make things equal: They gave the same amount to both the mean and the nice puppet when there were even numbers of cookies to distribute (see Olson & Spelke 2008 for similar conclusions). Therefore, 4.5-year-olds bias their sharing to cooperative over uncooperative individuals only when forced to do so. In contrast, 3-year-olds share indiscriminately in the same situation. Taken together, these studies show that, over the course of development, children become more discriminating in their helping and sharing with cooperative over uncooperative individuals. Infants and toddlers up to 2 years old seem mostly indiscriminate in their cooperation; starting in the third year of life, children begin to bias their helping in forced choice situations and, between 3 and 4 years old, also begin to favor a cooperative over an uncooperative individual when allocating unequal resources.

**Reputation management.** The previous section examined how children evaluate others based on their behavior with third parties and whether they use those evaluations when choosing how to interact in cooperative contexts. But what about children's own cooperativeness when others observe them? At what age do children begin to care about their own reputation? To assess such observer effects, studies have manipulated several features of the situational context: the presence of peer recipients (who are affected by the cooperation), peer or adult observers (who are just watching), and subtle cues of being observed (such as pictures of eyes).

The earliest instances of reputation-based effects have been found in 5-year-olds in the presence of peer recipients who were affected by the child's decision. Specifically, Leimgruber et al. (2012) found that children exhibited more generosity when they were observed by the recipient sitting across from them than when visual access was blocked. Buhrmester et al. (1992) found that children between 5 and 13 years old shared more when deciding face-to-face than when deciding in private, at least with an acquaintance or disliked peers—when the recipient was a friend, privacy did not reduce sharing.

Other studies looked at the effect of uninvolved third-party observers who are not directly affected by the decision. In this case, 5-year-olds were significantly less likely to steal a sticker from an absent child when a peer was watching, but showed only a trend toward more helping

(Engelmann et al. 2012). When an observing peer could later give resources to the participant, 5-year-olds shared more with another child than they did when there was no observer (Engelmann et al. 2013). Other studies put an adult into the observer role. Findings varied quite dramatically in terms of the age of onset, finding observer effects at 5 (Fujii et al. 2015), 6–8 (Shaw et al. 2014), 7–8 (Froming et al. 1985), or 10 years old (Zarbatany et al. 1985). Indeed, there is no evidence that children younger than 5 years of age are influenced by such adult surveillance.

More indirect audience effects on children appear to emerge much later, if at all. For example, children are insensitive to whether others will later find out about their cooperative decisions, for example, because their decision will be publically written on a blackboard for everyone to see (Blake et al. 2015b, Zarbatany et al. 1985). When participants decided in a classroom setting with peers nearby, rather than being monitored directly, evidence indicated that these effects occur at 9–10 years of age at the earliest (Houser et al. 2012, Takagishi et al. 2015). Moreover, there is no evidence that subtle observational cues, such as pictures of eyes, influence children (Fujii et al. 2015, Vogt et al. 2014); in contrast, this effect may influence cooperation in adults, although to a limited degree (Northover et al. 2016). Thus, subtle cues of being observed do not appear to affect sharing in children at an age when the presence of an actual adult observer directly monitoring them influences their costly sharing.

Furthermore, it is important to note that many studies that do detect evidence that children manage their reputation actually involve an observer who, in principle, could directly respond to the child's concrete action in the moment (by scolding, being upset, etc.). Consequently, it is not necessarily required that children represent to themselves how other individuals will form an opinion of the child as a cooperative or uncooperative person, let alone share those insights with other group members. Cases where effects in terms of forming a public image could occur through reputation have rarely been tested, and current studies suggest that these effects emerge at approximately 7–10 years of age. This development seems to involve more complex processes, with children having to consider what image the public may form of them, coinciding with their explicit understanding of impression management (Aloise-Young 1993, Banerjee 2002, Hill & Pillow 2006). Together, this evidence shows that potential threats to reputation are not part of children's early repertoires, and reputational effects are based upon late-developing processes that require higher-level social-cognitive reasoning and, probably, much experience.

## Principles of Fairness

A final critical mechanism in sustaining cooperation is fairness. A large body of work shows that adults use principles such as equality and equity (or merit) to decide how to distribute resources. Moreover, adults police others who violate these principles, judging unfair individuals negatively and even punishing them for being selfish to others. Although there is debate over the specific function of these principles, especially over whether they serve to uphold group standards or resolve conflicting interests between individuals, there is consensus that they play an important role in stabilizing cooperation. Therefore, it is essential to understand at what age these different mechanisms begin to influence children's cooperation.

**Collaboration as the basis of equality and merit.** The principles of equality and merit are first used when children actively collaborate with others. This can be seen in 3-year-old children. When they collaborate to obtain a common resource, such as by jointly pulling in a board with rewards, they usually split resources equally (Ulber et al. 2015, Warneken et al. 2011). Moreover, when a lucky child ends up with more resources than an unlucky partner, they correct the situation so that both end up with similar amounts (Hamann et al. 2011). Importantly, children

equalize the outcome more often after collaboration than after either individual work or windfall gains, indicating that collaboration evokes a stronger sense of equality. Children appear to be intrinsically motivated to share in this way, as children who were offered a reward if they share after collaboration are subsequently less likely to continue sharing in an equal manner (Ulber et al. 2016). These behaviors occur spontaneously, even in the complete absence of any prompting from authority figures such as experimenters or parents.

The connection between collaboration and more equal outcome distributions has been consistently found in 3-year-olds (Hamann et al. 2011; Melis et al. 2013; Ulber et al. 2015, 2016; Warneken et al. 2011). By contrast, 2-year-olds tend to accept unequal outcomes even if they work together to acquire the rewards, as well as to share pooled resources in a more haphazard manner irrespective of how they have been obtained (Hamann et al. 2011, Ulber et al. 2015). Thus, although younger children already coordinate to retrieve resources, children's strategies for distribution of the resources based upon equality emerge only by approximately 3 years of age.

At the same age, children also share resources based upon merit. When one child has to work more than the other, 3-year-olds are more likely to give more rewards to the one who worked more (Hamann et al. 2014, Kanngiesser & Warneken 2012, Schäfer et al. 2015). An even starker contrast occurs when the partner does not contribute anything at all. Whereas 3-year-olds will share with a collaborator, they share very little with a free-rider who dares to request some of the spoils without participating in the work task (Baumard et al. 2011, Melis et al. 2013). This can be seen as evidence for an appreciation of a basic sense of merit in terms of ordinal equity, where someone who works more or more successfully receives relatively more. This is likely a precursor of proportional equity, where rewards are exactly proportional to the work input, a concept that obviously requires much more sophisticated quantitative reasoning. In fact, merit (or equity) may be the overarching principle, with equality being the outcome of merit-based decisions: Equal work deserves equal pay. It is thus possible that mutualistic collaboration may lay the foundation for children's fairness-based sharing.

**Children's emerging sense of equality: inequity aversion.** Over the course of childhood, equality-based sharing becomes more prominent, including in situations of windfall gains. Three types of phenomena highlight this pattern: children's sharing in dictator games, their responses to advantageous inequality, and their willingness to engage in third-party punishment. First, in dictator games, children become more likely with age to distribute resources equally when dividing them up and to opt for equal over unequal allocations in binary choice tasks (for overviews, see Gummerum et al. 2008, Ibbotson 2014, McAuliffe et al. 2017). Although children's increasing tendency to give more could be explained by a developing sense of generosity, it is striking that children often appear to give exactly half, which might indicate that they are aiming for equality.

The second line of work, testing children's advantageous inequity aversion, presents a similar developmental pattern. When children are confronted with an allocation that favors them over a peer, such as four candies for themselves and only one candy for a peer, and are then given a choice to either accept this allocation or reject it, younger children accept it without hesitation. However, by 7–8 years of age, children frequently reject these allocations, opting that no one should get anything if the alternative is that they themselves receive more than the peer (Blake & McAuliffe 2011). This suggests a strong sense of equality, where children are willing to sacrifice both their own and the partner's resources to avoid inequality—a behavior that cannot be explained by self-interest or generosity.

The third line of evidence comes from third-party punishment. In this case, research shows that school-aged children not only care about sharing in dyadic situations where resources are distributed between themselves and peers, but also care about how resources are being distributed

between others when they have no direct stake in the outcomes. Starting at 6 years of age, children will pay a cost to intervene against a selfish peer who wants to keep all the resources rather than splitting them equally with another peer (Jordan et al. 2014, McAuliffe et al. 2015). This is another piece of evidence for the notion that children care about equality, enforcing it in others even when they themselves are not directly affected, and actually sacrifice their own resources to prevent inequality. Yet this more adult-like sense of equality emerges much later than children's earliest forms of helping, sharing, and collaboration.

## HOW NONHUMAN APES GENERATE AND DISTRIBUTE BENEFIT

Children provide insights into the developmental origins of human cooperation, and nonhuman apes can provide further insights into the biological origins. First, nonhuman apes present a strong test of whether certain abilities and social practices are necessary for cooperative behaviors to emerge. There is no indication that nonhuman apes reward their offspring for good behavior or teach them social norms, and they would obviously not be able to give explanations even if they wanted to. They thus provide a natural experiment for how cooperation works in a cognitively sophisticated species that nonetheless lacks human socialization practices. Second, chimpanzees and bonobos are our two closest living relatives, so they can reveal which aspects of human cooperation rely on late-evolving human-unique traits and which aspects may have deeper evolutionary roots.

### Helping and Sharing in Nonhuman Apes

There is clear evidence that chimpanzees engage in instrumental helping, use fairly sophisticated social-cognitive skills to identify when help is needed, and help flexibly in different kinds of situations. For example, chimpanzees help when a human or a conspecific fails to retrieve an object that is out of reach (Warneken et al. 2007, Warneken & Tomasello 2006). They even select the correct tool from a set of options, demonstrating that they know when to help and in what way (Yamamoto et al. 2012). Moreover, when a conspecific fails to pull in a rope that has a bag of food attached to it, they unhook the rope so the partner can pull it in (Melis et al. 2011), and they also unlock doors for conspecifics who try to access a neighboring room (Melis et al. 2008, Warneken et al. 2007; for similar results with bonobos, see Tan & Hare 2013). In these studies, subjects perform these acts selectively in experimental conditions where help is needed compared to matched control conditions in which these acts would not be helpful. Therefore, chimpanzees make inferences about the goal another individual is trying to achieve and try to help in a variety of ways. Importantly, chimpanzees also succeed in novel situations, ruling out the hypothesis that their helping is simply the outcome of previous rewards or training.

Chimpanzees also seem motivated by the other individual's problem, rather than obtaining a benefit for themselves. Concrete rewards such as being offered a piece of food are not necessary to elicit helping (Greenberg et al. 2010; House et al. 2014; Melis et al. 2008, 2011; Warneken & Tomasello 2006; Yamamoto et al. 2009, Yamamoto et al. 2012), nor do they increase the rate of helping (Warneken et al. 2007). Moreover, chimpanzees help even if direct reciprocation from a conspecific is not possible (Greenberg et al. 2010; House et al. 2014; Melis et al. 2008, 2011; Warneken & Tomasello 2006; Yamamoto et al. 2009, 2012). Chimpanzees are even willing to pay some opportunity and effort costs in order to help, as they will climb to a farther location to retrieve something for the recipient (Warneken et al. 2007, experiment 2) or leave an attractive activity behind to offer help (Melis et al. 2011, Warneken et al. 2007). Taken together, these studies show that the basic cognitive ability and motivation to help are present in other apes as well as in young children.

Apes create benefits not only through helping, but also through sharing, although to a more limited degree. Experiments and naturalistic observations converge on the finding that, although chimpanzees occasionally give up food that they have in their possession, they mostly do so in the form of passive rather than active food transfers, and often only after harassment (Boesch & Boesch 1989, Gilby 2006, Hockings et al. 2007, Tanaka & Yamamoto 2009, Ueno & Matsuzawa 2004). Therefore, chimpanzee sharing is rarely self-initiated and requires strong cues from the recipient. Studies with bonobos paint a slightly different picture. Although they are equally closely related to humans as are chimpanzees, they are more likely to share food with others than are chimpanzees. Bonobos are generally more socially tolerant and are willing to cofeed side by side rather than monopolizing the resource (Wobber et al. 2010). They even actively open a door so a conspecific can join them, especially if it is an unfamiliar individual (Hare & Kwetuenda 2010). However, this behavior occurs primarily in cases where they gain direct physical access to the partner, showing that a desire for unobstructed social and sexual play trumps their desire for food (Tan & Hare 2013). Thus, food sharing is not only a human attribute: It is also present in our closest evolutionary relatives, although to different degrees in chimpanzees and more tolerant bonobos.

Despite these commonalities between chimpanzees and young children, there are also important differences. One such difference concerns the cues that elicit helping and sharing behaviors across species. Whereas children help proactively—helping others who do not signal a need for help—chimpanzees only seem to help reactively in response to explicit goal cues. For example, they are far more likely to help when the recipient actively tries to pull in a bag or communicates toward the subject, rather than when the recipient remains passive (Melis et al. 2011). Similarly, chimpanzees virtually never offer a tool to a conspecific unless the recipient actively reaches for it (Yamamoto et al. 2009, 2012) and exhibit much lower rates of helping when recipients are not actively engaged in a task (such as trying to open or retrieve something) but are rather passively waiting (House et al. 2014). Along the same lines, sharing is rare in experiments in which chimpanzees passively wait for another chimpanzee subject to deliver food to them, even when it comes at no additional cost to the provider (Hamann et al. 2011, House et al. 2014, Jensen et al. 2006, Melis et al. 2011, Silk et al. 2005, Vonk et al. 2008, Yamamoto & Tanaka 2010). Thus, these studies on food sharing corroborate the notion that actively signaling need is a critical component for chimpanzee altruism. It is an open question whether the difference in proactive and reactive cooperation is best explained by a difference in the cognitive capacity to detect when help is needed or by a difference in motivation such that chimpanzees require more active solicitation to be nudged into action.

## Mutualistic Collaboration in Nonhuman Apes

Chimpanzees and bonobos are able to coordinate efforts in mutualistic tasks, as well. Several studies have shown that chimpanzees succeed in collaborative tasks that one individual cannot solve alone. This has been demonstrated in variations of a simple but ingenious apparatus where a board with food is placed out of reach and two chimpanzees have to each pull one end of a long rope threaded around the board to move it closer and access the food. If one chimpanzee acts alone, they end up with a rope but no food (Hirata & Fuwa 2007).

Studies show that chimpanzees will wait for a partner to arrive so they can pull together (Hirata & Fuwa 2007; Hirata et al. 2010; Melis et al. 2006a,b), actively solicit help from a partner (Hirata & Fuwa 2007; but see Warneken et al. 2006), and open a door to let a chimpanzee enter from a waiting room (Melis et al. 2006a). They even remember their prior success with different collaborators and selectively open the door for skillful over unskillful partners (Melis et al. 2006a). Chimpanzees succeed in situations where they and their partner have to perform the same action

at the same time, such as pulling ropes, but also when they have to perform two complementary actions in sequence, such as using two different tools on an apparatus (Melis & Tomasello 2013). Chimpanzees can even engage in a basic form of division of labor, keeping the tool they need and handing another tool to the partner (Melis & Tomasello 2013), and reversing roles when necessary (Fletcher et al. 2012).

Taken together, these results show that chimpanzees perceive their own and the partner's action as interconnected. They not only understand what they have to do but also what the other chimpanzee has to do. They can adjust their own actions to the actions of the partner and facilitate the partner's action in addition to their own. Chimpanzees are able to represent more than their own means–action sequence and integrate, at least on some level, the action that the partner has to perform and the ways in which each individual's actions are interrelated. Therefore, chimpanzees possess abilities that are critical to generating mutualistic benefit through collaboration.

## Mechanisms for Distributing Benefits in Nonhuman Apes

Given these findings, one may expect that helping and collaboration should be widespread in chimpanzees. However, apes are actually quite limited in their ability to solve the other cooperation problem: how to distribute benefits. First, helping behaviors occur mainly in situations that are low cost, where any distribution of a concrete benefit (such as food) is not necessary. By contrast, when chimpanzees can obtain or keep a valuable resource, such as food, for themselves, selfishness trumps their altruistic tendencies. Second, sharing tasks that directly measure how they distribute benefit show that dominance and self-interest usually prevail. Bonobos appear more tolerant in this regard, although food sharing simply for the other individual's sake is rare. Third, chimpanzees succeed at collaboration tasks only when paired with a tolerant partner and often do not even bother to start working with a dominant individual who monopolizes the apparatus and the food. Moreover, even when working with a tolerant partner, chimpanzees succeed only when the food-distribution problem has already been solved for them: When they are in separate rooms or the food is spread apart on a long board, they collaborate. When they would have to haggle over a pile of food in the center, they fail (Melis et al. 2006b). Interestingly, this is less of an issue for the generally more tolerant bonobos, who collaborate even when food is clumped (Hare et al. 2007). This highlights that, in cases of potential mutualism, finding ways to distribute benefits is essential for cooperation to ensue.

There are many other striking differences in how humans and other apes distribute benefits from cooperation. There is evidence that chimpanzees form reciprocal relationships with others in their natural behaviors, preferentially cooperating with individuals with whom they uphold a long-term friendship (Gomes et al. 2009). However, these patterns can be regarded as forms of partner choice that operate over longer timescales and are supported by positive feelings toward the other [also called attitudinal reciprocity (Schino & Aureli 2010)] rather than as contingent reciprocity, as seen in human children. Whether chimpanzees can engage in contingent reciprocity based on a conspecific's prior behavior is less clear. Although some studies find that chimpanzees return a favor (Engelmann et al. 2015, Melis et al. 2008), chimpanzees do not seem to initiate future-directed reciprocity when they could choose to take turns at receiving a reward (Melis et al. 2016). These differences between humans and nonhuman apes are likely due to increased psychological demands, with contingent reciprocity requiring individuals to keep track of favors given and received, delay gratification, and anticipate future return benefits, all of which are psychological processes that are more taxing than partner choice. Even more taxing are cases of indirect reciprocity based on reputation. In fact, chimpanzees do not take into account how their own behavior is viewed in the eye of the beholder: They share or steal food from another

chimpanzee whether a third party is watching or not (Engelmann et al. 2012) and do not intervene against uncooperative behavior when they are in the role of a third party (Riedl et al. 2012).

Lastly, apes do not appear to respond to or enforce fairness norms. Chimpanzees do not correct an unequal outcome after collaboration (Hamann et al. 2011), nor do they share more with a collaborator over a laggard (Melis et al. 2013), in contrast to 3-year-old children, who treat joint benefits differently from windfall gains and individual work. One issue under debate is whether chimpanzees show inequity aversion in instances when they refuse to engage in a token exchange with an experimenter who offers a conspecific a better deal (Bräuer et al. 2006, Brosnan & de Waal 2003). However, these instances would, at best, reflect disadvantageous inequity aversion. In contrast, there is no evidence that chimpanzees show advantageous inequity aversion, a more stringent criterion for a sense of fairness that emerges much later in humans (McAuliffe et al. 2017). This lack of concern for fairness principles is also apparent in their punishment decisions: Chimpanzees seek revenge against others who stole from them (Jensen et al. 2007), but not when they are an uninvolved third party witnessing one chimpanzee steal from another (Riedl et al. 2012). By contrast, at 3 years of age, children intervene against theft and other antisocial behaviors (Riedl et al. 2015, Vaish et al. 2011) and, at approximately 6 years of age, enact fairness norms against selfish individuals (McAuliffe et al. 2017). Therefore, a striking difference between the species appears in the adoption and enforcement of fairness norms—a way of regulating cooperative behaviors that is only found in humans.

## CONCLUSION AND FUTURE DIRECTIONS

Overall, current developmental and comparative evidence suggests a major distinction between skills for generating benefits and skills for distributing benefits from cooperation. From early in life, children are able to generate benefits through acts of helping, sharing, and collaboration. Although these abilities become more sophisticated over the course of development, the core abilities to engage in altruistic and mutualistic cooperation emerge early and are already in place in the second year of life. Yet there is a different developmental trajectory for the complementary abilities to distribute benefits. These skills—such as contingent reciprocity, managing one's own reputation, and sharing based upon fairness norms—only emerge later in development, after children have gained some practice in cooperating with others (see **Figure 1**). This is apparent for both altruistically and mutualistically motivated behavior, supporting the hypothesis of a developmental lag between these two different sets of abilities. Comparative studies also support this dissociation. Children's abilities to generate benefits find many parallels in chimpanzees and bonobos, suggesting deep evolutionary roots that date back to at least the last common ancestor of humans and our primate cousins. By contrast, humans and other apes differ qualitatively in the mechanisms of distributing benefits, with future-directed reciprocity, fairness norms, and reputation building as likely candidates for human-unique ways of stabilizing and expanding cooperative behaviors. This distinction provides a new framework for current empirical evidence on children's developing cognition. Moreover, it points to outstanding questions about the origins of cooperation in development, the specificity versus universality of these processes across diverse cultural groups, and the ways in which human cooperation differs from that of other apes.

### Developmental Origins

What explains the developmental emergence and dissociation of the different sets of abilities? Children develop the basic skills to generate benefit early. In the second year of life, children begin to help others in a variety of ways, based on their emerging ability to detect other's emotional

needs, action goals, and knowledge states. They quickly develop more sophistication in knowing when and how to intervene, requiring less overt cues about when others are in trouble and when they should take action. Similarly, children also begin to successfully coordinate their actions 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. This experimental work is corroborated by observational studies of children in their naturalistic interactions, which have identified the second year of life as the age window during which children begin to help, share, and cooperate with parents, siblings, and peers (Brownell 2011, Dahl 2015, Dunn & Munn 1986, Eckerman & Peterman 2001, Hay et al. 1999, Howes & Farver 1987, Zahn-Waxler et al. 1992).

Even fairly young children can, therefore, solve the first challenge of cooperation with a behavioral repertoire that is flexible and intelligent, harnessing their increasingly sophisticated social-cognitive capacities and using them for cooperative ends. This evidence from children is complemented by evidence that nonhuman apes share many of the same skills. Overall, this suggests that these abilities may be based upon a biological predisposition and do not intrinsically require human-unique socialization practices to emerge. Socialization practices can, of course, build upon this foundation, but young children are neither purely selfish individuals nor motivational blank slates that have to be (re)programmed to cooperate with others (Melis & Warneken 2016, Warneken 2016). For example, as children gain more experience with cooperation and learn relevant social norms about such behavior, they expand the circle of individuals they cooperate with and learn new ways to respond in such contexts. Nonetheless, the groundwork for these behaviors is laid in early ontogeny.

Regarding the mechanisms of distributing benefits, this framework proposes that the first step for developmental research is to identify those strategies that support cooperation from an ultimate perspective (such as direct and indirect reciprocity), and the second step is to then elucidate the psychological mechanisms necessary for children to actually use such strategies in their cooperative behavior. One prediction from this framework is that mechanisms that serve important foundational functions across many diverse social behaviors—such as a preference for kin or familiar individuals over unfamiliar individuals—will likely apply earlier to cooperative contexts. That is, such mechanisms can be coopted for cooperative interactions or operate in this way simply by virtue of cooperation being a subclass of social behaviors. By contrast, strategies that are more specific and narrowly tailored to cooperative behaviors—even if they are deceptively simple rules, such as tit-for-tat—may emerge later. For example, instantiating reciprocal interactions may be nontrivial from a psychological perspective, as this requires the ability to delay gratification and, perhaps, the ability to represent future events, which children do not master before middle childhood (Atance 2008). Reputation-based reciprocity may emerge even later, after children develop the perspective-taking skills necessary to understand how others represent their behavior and how they may spread the word in a social group. Therefore, this framework can motivate specific predictions about the age of emergence of different strategies to distribute benefit, based upon the required psychological capacities.

Current empirical evidence supports this view (**Figure 1**). Infants and toddlers appear to be initially fairly indiscriminate in their cooperation, but then to gradually add more ways to safeguard their cooperation. This starts with the emergence of selective partner choice at approximately 2 to 3 years of age and then develops into contingent reciprocity between 3 and 4 years of age, such that children look back at how a given partner has cooperated with them and adjust their cooperation accordingly. However, it is not until 5 years of age that they look ahead and cooperate more when the partner can reciprocate in the future. Early cooperative behaviors are also not yet mediated by concerns of audience effects. The earliest age for which there is evidence of observer effects is

5 years, although this is only in very restricted contexts where the observer is literally in their face, and more prototypical audience and reputation effects do not occur until 7–8 years of age. Finally, the earliest forms of fairness concerns emerge in collaborative contexts at approximately 3 years of age, with responses to advantageous inequity aversion and costly third-party punishment being signs of a strong, impartial sense of fairness that develops later in childhood, at around school age.

## Cultural Similarities and Differences

This distinction between early-emerging, biologically based abilities to generate benefits and later-emerging, socially shaped abilities to distribute benefits also provides new predictions about where we should observe cultural variation in developmental patterns. In particular, early-emerging skills to generate benefits through cooperation should be more universally present across cultural groups. Although local customs and parental practices may influence the specific expression and prevalence of cooperative behaviors (e.g., household chores, farming, caring for siblings), the basic capacity for flexible cooperation should be found in young children across populations. Existing studies support this prediction, showing that the basic cooperative capacities expressed in, e.g., helping and collaboration emerge in toddlerhood across diverse cultural groups (Callaghan et al. 2011, Drummond et al. 2015, Kärtner et al. 2010, Köster et al. 2016).

Conversely, the framework suggests that there should be greater variation in the abilities to distribute benefits across cultures. The ways in which children solve the second cooperation problem may be tied to their specific social ecology and cultural traditions, so some (but not all) of these skills will be more sensitive to such cultural inputs. For example, individuals across all populations generally have close ties to relatives, but also interact with nonrelatives on a regular basis, so strategies supporting kin selection and direct reciprocity should be more widely observed. However, other mechanisms—such as giving either egalitarian or merit-based norms greater weight—depend on social expectations, and norms may differ depending on the values of the social group. Similarly, moral norms vary widely in terms of obligations to favor an in-group versus those to be impartial, factors that could radically sway a child's decision of how to treat others and divide resources. In fact, research shows strikingly different developmental trajectories of fairness-based behaviors in egalitarian sharing (House et al. 2013b), ordinal versus proportional equity (Schäfer et al. 2015), and advantageous inequity aversion (Blake et al. 2015a) across different populations. Echoing the call for more research in diverse cultural groups, this framework specifically proposes that the extent of cross-cultural variation will differ for the two sets of skills for cooperation and why such variation would occur.

## Evolution and Human Uniqueness

Finally, this proposal suggests a new path for comparative research about the evolution of the human mind. By studying cooperative behaviors in terms of the means to generate and distribute benefits, we can gain a deeper understanding about the presence or absence of cooperative behaviors in different species. Empirical research should specify what psychological mechanisms are required for a given cooperative activity with the goal of identifying which cognitive, motivational, or behavioral capacities may explain why a given species performs or fails to perform certain acts of cooperation.

An analysis of solutions to the free-rider problem that focuses on ultimate function may miss a critical proximate factor that explains differences between species. Certain animal species may lack a certain cooperative behavior not because of problems with distributing benefits and mitigating the free-rider problem, but rather because they are not sophisticated enough to perform

benefit-creating acts that require them to assess when and how to cooperate. On the flip side, individuals from a certain species may possess the required abilities to generate benefits through cooperation (such as identifying need or coordinating joint efforts) but may not use them reliably across contexts because they have not found a general solution to the problem of how to distribute benefits and stabilize cooperation as a viable strategy. In experimental studies, it is possible to remove these constraints (such as by predividing the spoils of a collaborative activity). As such, experiments can sometimes reveal cooperative abilities that were previously thought to be absent based on naturalistic behaviors. This could explain why chimpanzees engage in cooperative behaviors such as helping and collaboration in controlled experiments even though these behaviors remain fragile and are not expressed at a similar scale as in humans. Over the course of human evolution, these same kinds of constraints needed to be lifted in order to generate robust cooperative tendencies in our species.

The framework developed in this review provides a new look at the question of how human cooperation may have evolved, putting the interrelationship between abilities to generate and to distribute benefits at the center of theoretical explanations and empirical inquiry. It suggests that, as new ways of distributing benefits emerged in human evolution, cooperative behaviors were strengthened and expanded, creating a positive feedback loop between mechanisms to generate and distribute benefits. Humans found novel ways to address the two challenges of cooperation, with more sophisticated psychological abilities and new social practices expanding the scope of cooperation and taking it to a level that is unparalleled in the animal kingdom.

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