Insights into the biological foundation of human altruistic sentiments
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Abstract
The contributions of biology versus socialization practices to the emergence of human altruism have been the focus of a long-standing debate. New research on the development and evolution of helping behaviors provides important insight into the origins of our altruistic psychology. Current empirical evidence shows that both young children and chimpanzees instrumentally help others struggling with a problem — suggesting that basic forms of altruism are based upon a biological predisposition with shared evolutionary roots. In humans, the internalization of social norms and moral education can then build upon this early emerging predisposition.

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Introduction
What is the foundation of human altruistic behaviors? One critical factor is the social standards that members of a community espouse and enforce [1–3]. Given the importance of these social standards for adults, many theoretical views treat such socialization practices as central and even necessary for human altruism [4–8]. This socialization hypothesis therefore suggests that our altruistic inclinations stem from the internalization of learned standards of behavior for interacting with others. In this model, children are posited to be initially insensitive to the needs of others, and it is only due to a human-unique constellation of social norms and extensive child rearing that altruism is inculcated over development [9,10]. Here I propose an alternative hypothesis. I will advance the notion of a biological predisposition for human altruism. Although social norms clearly play a critical role for mature altruism and guide child development, they are not the condition sine qua non of our core altruistic tendencies. Rather, social norms build upon and refine preexisting sentiments that very young children — and even some other apes — already exhibit.

I further argue that addressing the origins of human altruism requires looking beyond mature altruistic behaviors in adults. In particular, developmental research is critical to adjudicate hypotheses about the origins of human altruism, as studies of young children can look at the initial state of altruism in human ontogeny before norm internalization has a major impact. However, it is not possible to answer questions about the nature of human altruism by only studying humans: comparative studies of nonhumans — who lack explicit social norms or moral instruction — provide a second critical line of evidence. By comparing the behaviors of human children with that of chimpanzees, we can discriminate which aspects are human-unique from aspects that have a shared evolutionary history, and thus predate human forms of socialization.

Helping emerges in early childhood
Helping behaviors are a good test case for the study of altruism in young children for three reasons. First, although children’s instrumental helping is far less complex than the altruism of adults, these behaviors nonetheless share core features (Figure 1): even simple acts of helping require a representation of the goal another person is trying to achieve, and a potentially altruistic motivation to facilitate the other person’s goal (as opposed to an immediate benefit for the self1). Second, infants do not yet know enough about the world to be good counselors, nor do they own many things they could sacrifice. However, they can already engage in manual tasks, enabling us to administer nonverbal, age-appropriate tests of altruistic behavior. Third, research on helping has flourished in recent years, providing a strong foundation for identifying the factors that are critical for altruism to emerge.

Studies of instrumental helping behaviors reveal that children start to help others at an early age, not long after their first birthday. When 14-month-olds see someone

1 I focus on psychological (i.e. proximate) processes, not ultimate function. ‘Altruistic’ is thus used in terms of the underlying motivation, i.e. a behavior that is aimed at resulting in a concrete benefit to another individual rather than oneself. This does not necessarily imply altruism in terms of fitness costs to the actor and fitness benefits to the agent as a different level of analysis.
reaching unsuccessfully for a dropped object, they will spontaneously pick it up and hand it over [11–13]. By at least 18 months, children help flexibly across a variety of problem situations (Videos S1–S4): retrieving out-of-reach objects, opening closed doors, assisting to stack objects, and even using a newly learned method to open a box for a klutz who uses the wrong approach [14*,15,16].

Children use fairly sophisticated social cognitive abilities to decide how to help in these situations. In particular, children specifically try to help other people with their intended goals, rather than just blindly join into the adult’s activity. For example, when an adult is ignorant about the true location of a desired object and struggles to open an empty box, 18-month-olds do not join in to this futile attempt. Rather, they retrieve the desired object from its actual location [17]. Similarly, when a person is not aware that the locations of a desirable and an unpleasant object have been switched, 18-month-olds will warn the person beforehand — correctly inferring that when holding a false belief, the adult is likely to take the wrong course of action [18,19*].

With increasing age, toddlers are able to make such inferences based upon more subtle cues. Children at 14–18 months typically help only in response to a salient cue of the other’s need, such as a person reaching for an object or directly asking for help [11,20]. However, 2-year-olds can help even when such behavioral cues are absent (Video S5). They assist an adult by returning cans to her if she had not noticed that they rolled off a table — and thus did not provide any cues that she needed help [21*] (significantly more often than in controls where cans dropping on the floor were not a problem for the adult). Thus, children can help even when concurrent cues to elicit helping are absent, demonstrating that they can use situational cues to infer what to do.

**What motivates children’s helping?**
Taken together, these results provide evidence for an early emergence of our basic altruistic tendencies: toddlers harness their social cognitive capacities to help others in need. But what exactly motivates their helping? One possibility is that the same social concerns that are important for adult social interactions — such as explicit norm learning or reputation-based assessments — also account for the emergence of these altruistic behaviors in children. However, the sum of the evidence suggests that this is not the case.

First, early helping does not seem to depend on reputation or other forms of social signaling to others. Helping occurs spontaneously in the parent’s absence, showing
that it is not due to parental cues, obedience, or the expectation of parental praise [21*,22]. Moreover, children do not seem to be concerned whether they are watched by others versus acting in private until around age 5, suggesting that early altruistic tendencies predate the emergence of reputational concerns [23–26]. It also seems unlikely that children are ‘showing off’ or want to demonstrate their mastery of a situation. For example, 2-year-olds show arousal when they witness a person failing to reach an object (as measured by their pupil dilation). They exhibit relief when they provide help — but also when some other bystander resolves the problem [27**].

Thus, what is critical for children is that the other person’s goal is fulfilled, not the child’s own participation in helping to fulfill the goal per se.

Second, concrete rewards do not drive children’s helping. In most studies, no concrete rewards are provided, yet children still help reliably [11,14*,15,16,18,19*,21,22,28–32]. Moreover, offering concrete rewards does not necessarily lead to more helping [28]. In fact, material rewards can have detrimental effects by undermining children’s intrinsic motivation and thus reducing future helping [29]. This set of findings contradicts the claim that children initially help only when promised concrete rewards [10], and then only in adolescence — after a long reward history — exhibit helping that is self-rewarding [9].

Finally, evidence for helping early in ontogeny indicates that it is implausible that helping requires an adult-like moral value system, as preverbal infants are unlikely to be motivated by normative principles. In fact, it is not until middle to late childhood that children begin to reason about social norms as obligatory. Only then do children begin to perceive failures to follow such norms as guilt-evoking [33], develop a moral self [34], and hold themselves and others to the same standards [35,36]. Hence, young children may have a predisposition for altruistic behavior that is not based upon socialization factors such as reputational concerns, a long history of rewarding, or a rich moral value system alone.

There is an important caveat to this claim, however. Although these particular socialization practices and social values are unlikely to be foundational to early helping, toddlers still could have been socialized into altruism through other means. Children grow up in a rich social environment where they witness and engage in various cooperative activities, and may be encouraged to help. In fact, experiments show that positive interactions and affiliative cues prime children to be more helpful later [12,13,37–41]. Moreover, children’s participation in household activities is correlated with helping in the lab, and parental discourse about other people’s needs and emotions is associated with more helping [42,43*,44]. However, the importance of these factors in the initial emergence of altruism, as opposed to its subsequent refinement, is difficult to assess from human data alone.

Helping in nonhuman apes

If data from humans alone cannot address these questions about the roots of human altruism, what can? I believe that comparative studies of nonhumans hold the key to making such issues scientifically tractable. If socialization practices such as parental modeling, talking about other people’s minds, or transmitting social standards are indispensable, then altruistic helping should not be observed in other species. Indeed, there is no indication that other apes transmit cultural norms about social behavior, actively reward others for helping, or model how they want their offspring to treat others. Thus, studies of our ape cousins provide valuable clues as to whether these types of socialization factors are actually necessary for helping behaviors to emerge.

Evidence is accumulating that apes share several of the basic capacities for helping. For example, chimpanzees help familiar and unfamiliar humans pick up dropped objects, without a direct request and without being rewarded [16,28] (Video S6). They also provide assistance to other chimpanzees, and do so in flexible ways [45,46*]. When chimpanzees view a conspecific trying to use an apparatus, they will select the appropriate tool from a set of potential options, assessing how exactly to be helpful [46*]. In another situation, they opened a door for a conspecific who was trying to access a piece of food in a neighboring room ([28,47], for bonobos: [48]) (Video S7). Moreover, when a conspecific struggled to pull in a bag with treats because the rope was attached to bars with a hook, chimpanzees unhooked the rope so that the other could pull it in [49]. Importantly, in these studies chimpanzees performed these acts significantly more often in experimental conditions where help was needed, than in matched controls where the same behavior would not be helpful. Hence, chimpanzees can make inferences about the other individual’s goal and help across various situations, not unlike human toddlers. Several of these situations were novel, ruling out that their helping was shaped by previous rewards or training.

What motivates the apes’ behavior in these contexts? In fact, chimpanzees are also motivated by the other’s problem, rather than an immediate benefit for themselves. Concrete rewards are neither necessary [16,45,46*,47,49–51], nor do they increase the rate of helping [28] — and chimpanzees help even if direct reciprocation is not possible [16,45,46*,47,49–51]. Taken together, the basic cognitive ability as well as the basic altruistic motivation to help others appears to be present in chimpanzees as well.

However, there are important differences between human and ape helping. While children help proactively — helping others who do not signal a need for help, by
inferring their goal from contextual cues [18,19*,21*,52] — 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, than when the recipient remains passive [49]. Similarly, chimpanzees virtually never offer a tool to a conspecific unless the recipient actively reaches for it [45,46*]. More generally, when recipients are not actively engaged in a task (such as trying to open or retrieve something), but are passively waiting, apes exhibit much lower rates of altruistic behavior [51]. It is an open question whether this difference between children and chimpanzees is best explained by a difference in the cognitive capacity to know when help is needed, or whether this reflects a difference in motivation such that chimpanzees require more active solicitation to be nudged into action.

Conclusion and future directions
While it is difficult to disentangle the socialization and biological disposition hypotheses by examining only adults, current developmental and comparative evidence has started to address long-standing questions about the emergence of human altruism. As both young children and other apes engage in helping behaviors, altruism would appear to have deep roots in ontogeny and phylogeny. This challenges the idea that human altruism necessitates human socialization practices in the form of parental instruction or the internalization of norms. While there is no doubt that socialization practices can profoundly influence the expression of altruistic (as well as selfish) tendencies, it appears that these practices shape and refine an altruistically oriented psychology that we share with our closest evolutionary relatives — rather than planting the first seeds of altruism in an initially selfish biological endowment.

To better understand this interplay of biological predispositions and social factors, two types of further research are particularly promising. The first are cross-cultural comparisons. Systematic cross-cultural studies are scarce, but the experiments conducted in different nations, as well as the few direct cultural comparisons [53*,54], suggest that helping consistently emerges in toddlerhood across societies. The basic capacity for helping may thus be universal. At the same time, the function and meaning of children’s helping differs across communities. For example, adults in one cultural context may view their children’s helping as a social obligation, whereas in another they may construe helping as an expression of individual preferences [54]. These different socialization goals and practices may shape the expression of children’s helping over development. Importantly, anthropological studies of traditional societies further provide some hints as to the evolutionary function of early helping: children can provide relevant assistance to adults and are an important factor in subsistence economies, so the early emergence of skillful altruism may be adaptive [55**].

A second approach is the study of individual differences. In particular, behavioral genetics studies can elucidate how individual variation in this basic capacity is accounted for by genetic and environmental factors. One powerful tool is the comparison of monozygotic and dizygotic twins. Such twin studies reveal a substantial heritability for prosocial behaviors, with genetic factors accounting for 30–50% of individual variance [56,57,58**], in addition to environmental effects that are usually of the non-shared kind (effects unique to the child, not the family environment). Moreover, these genetic effects are not necessarily additive, but can interact with environmental factors in predictable ways. For example, the dopamine receptor D4 7-repeat allele has been hypothesized to influence susceptibility to environmental input [59]. In fact, there is evidence that children who carry this allele show stronger associations between parenting and prosocial behavior than do non-carriers [56]. Therefore, it is important to consider individual differences, with a child’s degree of susceptibility to socialization itself being partly due to genotypic variation.

Overall, recent research on the development and evolution of helping has provided new insights into the origins of our altruistic tendencies. This research has highlighted the importance of our biological inheritance, as very young children and chimpanzees use a rich set of social cognitive capacities to help others achieve their goals, based upon an altruistic motivation. These initial tendencies can then be refined by socialization practices that teach explicit moral and social norms. Thus, a framework that accounts for both human ontogeny and human phylogeny is critical to understand the cultured nature of human altruism.

Conflict of interest
None declared.

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Appendix A. Supplementary data

References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

14. Dunfield KA, Kuhlmeier VA: Classifying prosocial behavior: children’s responses to instrumental need, emotional distress, and material desire. Child Dev 2013, 84:1766-1776. This study examines the early development of different types of prosocial behavior, indicating that helping, sharing, and comforting behaviors may undergo different developmental trajectories depending on the types of cues that elicit prosocial action.
19. Knudsen B, Liszkowski U: One-year-olds warn others about negative action outcomes. J Cogn Dev 2013, 14:424-436. The study showed that infants make inferences about another person’s false belief when deciding whether to helpfully intervene by warning the other of an imminent problem.
21. Warneken F: Young children proactively remedy unnoticed accidents. Cognition 2012, 126:101-108. This study demonstrates that 2-year-olds can infer from the situation when help is needed and do not require behavioral or communicative cues from the recipient. This provided important insight into the spontaneity of children’s instrumental helping and the cognitive inferences they are able to make.
27. Hepach R, Vaish A, Tomasello M: Young children are intrinsically motivated to see others helped. Psychol Sci 2012, 23:967-972. This study for the first time introduced a measure of pupil dilation to assess children’s level of sympathetic arousal in helping situations. Findings suggest that children are motivated by a concern for another person’s success rather than receiving credit for their own helping.
35. Smith CE, Blake PR, Harris PL: I should but I won’t: why young children endorse norms of fair sharing but do not follow them. PLOS ONE 2013, 8:e65910.
43. Brownell CA, Svetlova M, Anderson R, Nichols SR, Drummond J: Socialization of early prosocial behavior: parents’ talk about emotion is associated with sharing and helping in toddlers. Infancy 2013, 18:91-119. This study investigated the relationship of parents talking with their children about other people’s emotion and how it relates to different forms of helping behaviors.


This is the first study to show that chimpanzees help conspecifics with an understanding of the other individual’s need. They helped by selectively giving the one tool from a whole set of tools that the conspecific needed to complete a task.


48. Tan J, Hare B: Bonobos share with strangers. PLOS ONE 2013, 8:e51922.


The first cross-cultural investigation of the early development of instrumental helping behaviors with children in Canada, India, and Peru.


This opinion piece discusses different hypotheses about the potential evolutionary function of altruistic helping behaviors to emerge in early ontogeny, using a life history framework.


A recent review of genetically informed studies that assess the relative contributions of genes and environment on individual differences in the development of prosocial behaviors.