The Psychology of Cooperation: Insights from Chimpanzees and Children

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Introduction

Across all cultures, humans engage in cooperative activities that can be as simple as preparing a meal or sharing food with others and as complex as playing in an orchestra or donating to charity. Although intraspecific cooperation exists in many other animal species, only humans engage in such a wide array of cooperative interaction and participate in large-scale cooperation that extends beyond kin and even includes strangers.

Humans' wide breadth of cooperative behaviours rely on a complex set of cognitive abilities and motivations. However, there is much controversy about which of these psychological mechanisms (if any) are derived from our evolutionary relatives, and which aspects are unique to humans. Furthermore, there is much debate about whether our cooperative abilities are mainly the result of cultural influences, in particular socialization practices and social learning that shape children over ontogeny. In the last decade, a growing number of experiments have started to address these questions, providing new evidence on the cooperative abilities in great apes, and comparing them to the behaviour of humans. Therefore, we review here the most recent experimental studies from comparative and developmental psychology that investigate the phylogeny as well as the early ontogeny of human cooperation. By studying human children, we can examine the developmental trajectory of cooperative behaviours, and thus evaluate hypotheses about the prerequisites for cooperation, in particular how biological predispositions and social experience may interact over development. By also testing chimpanzees and bonobos, our two most closely related ape cousins, we can determine whether certain psychological and social characteristics are necessary for certain types of cooperation (such as abstract cognitive abilities or the internalization of social norms), and make inferences about the cooperative abilities that the common ancestor of humans and other apes possessed.

Traditionally, the puzzle of cooperation was phrased in terms of its ultimate function -- explaining how natural selection could favour behaviours associated with fitness costs for the actor and benefits for the recipient. We now know that, based on inclusive fitness theory, actors must increase their average inclusive fitness, either directly (increasing their own fitness) or indirectly (behaving cooperatively towards kin that share genetic similarity) for a certain trait to be under positive selection.[1,2] In addition to explanations that address the evolutionary pathway that lead to an increase in inclusive fitness, we need explanations about the proximate processes that support this behaviour. For example, reciprocally altruistic behaviour can be based on sympathy and true concern for the welfare of others or be the result of a calculated strategy motivated by the prospect of future selfish benefits. So what are the psychological – cognitive, emotional, and motivational – mechanisms that support cooperative interactions? A better understanding of the proximate mechanisms that support cooperation will provide important insights into the variety and complexity of the problems that individuals are adapted to solve, as well as the limitations to cooperate that they face.

We look at two classes of cooperative behaviour: Collaboration and prosocial behaviours. We define collaboration as social acts in which two or more individuals coordinate their actions to produce outcomes that neither one could obtain alone. Prototypically, this would yield benefits for the collaborating individuals, such as obtaining a common resource.[3] In this case, we would speak of mutualistic collaboration. We define prosocial as behaviours in which an individual performs an act that benefits another individual rather than oneself, perhaps even at their own cost. The benefit may be the success at an action-problem or the sharing of a valuable resource. We mainly focus on chimpanzees for the simple reason that most studies have been conducted with this species. Where possible, we include evidence from bonobos as well.

Collaboration

Mutualistic collaboration appears easy to explain in terms of payoffs and the motivation for individuals to participate therein. After all, it is in every individual's self-interest to collaborate if that enables him to acquire resources that are otherwise inaccessible. However, the challenge of collaboration is also a cognitive one, especially when the collaborative problem is complex. In its simplest form, individuals act in parallel but independently from each other, without any consideration of each other's actions and how success is dependent on their joint efforts. A simple mechanism such as social facilitation is sufficient to explain how individuals increase their chances of success by acting simultaneously towards the same goal. However, humans also collaborate in much more complex ways by forming joint intentions to pursue the shared goal, recognizing how their different roles are interrelated, and employing different social and communicative means to coordinate actions between partners. This set of abilities makes human collaboration highly effective and flexible. Although these are the two extremes of the spectrum, intermediate but still highly effective mechanisms are also possible.

In the following, we review a series of studies designed to investigate the psychological mechanisms that underlie chimpanzees' and children's collaborative interactions. We first focus on those aspects and skills which chimpanzees master in a way similar to humans, and then describe the differences between the two species.

Similarities between chimpanzees' and children's collaborative skills

When individuals of any animal species act simultaneously towards the same goal (e.g. hunting episodes), it is difficult to know from observations alone whether their actions

are intentionally coordinated and how they represent each other's actions. The question is whether success is the by-product result of independent but simultaneous actions or the result of intentionally coordinated actions that take into account the partner's actions in relation to their own actions and the common goal.

In order to tease apart these different possibilities, several studies presented pairs of chimpanzees with a collaborative food-retrieval task in which individuals had to coordinate actions to obtain otherwise inaccessible food. Since it is possible for individuals to learn to act simultaneously with a partner without grasping the interdependence of their actions, the dependent measure in these studies was not merely whether individuals acted simultaneously, something which chimpanzees and several other species have shown to be capable of learning.[4-6] Instead, the dependent measure was whether individuals recruited the partner and helped her perform her role, making a clear choice between allowing the partner to collaborate or not. Melis, Hare, and Tomasello [7] investigated chimpanzees' ability and willingness to recruit a conspecific (by opening a door) when subjects could not pull an out-of-reach baited tray on their own. The results showed that subjects spontaneously initiated opening a door to recruit the partner, and that they recruited the partner significantly more often when collaboration was necessary than when they could succeed on their own. Furthermore, when given the choice between two potential partners, they preferentially recruited the most skilled one, showing that they are capable of tracking good and bad collaboration partners. In another study, [8] pairs of chimpanzees cooperated by performing complementary and sequential roles. In this task, each individual needed a specific tool to perform her role (one individual needed to rake and the other needed to push), and one individual alone could not perform both roles because of the spatial set-up. Focal subjects were given the two tools and we measured whether they would help their partner by transferring the tool she needed to perform her role. Overall, subjects spontaneously initiated

transferring the tool the partner needed to perform her role, independent of which action/role they had to perform.

These studies suggest that chimpanzees can not only learn to inhibit their own behaviour and wait for the partner, but they also solve additional obstacles (opening a door or transferring a tool) to allow and help their partner perform her role. This shows that they understand the role that the partner plays in mutualistic joint activities, relating how their actions and those of the partner are needed for success.

From 14 to 18 months of age, children are capable of coordinating simple actions with adults[9,10]. However, in all of these early instances of collaboration, successful coordination is limited and largely dependent on adults' scaffolding.[11] In collaborative problem-solving tasks among peers (which are the best comparison to the collaboration studies with chimpanzees reviewed above), children are not capable of coordinating parallel and complementary actions until their third year of life (24 to 36 months). [12] Between 23 and 36 months children show increasing skill at coordinating actions, actively monitoring the partner, and adjusting their goal-directed actions in relation to the peer. At younger ages, success among peers is the result of fortuitous but independent actions that suggest little awareness about the role of the partner.

Although further studies are necessary to fully understand how chimpanzees represent collaborative activities with others, we can conclude, given that they are capable of adjusting their goal-directed actions to their partner (e.g. recruiting her, or transferring to the partner the tool she needs), that in experimental tasks they perform similar to children between 24 and 36 months of age. However, from three years of age, there seems to be an important qualitative change in how children conceive and represent joint collaborative activities. While 2.5-year-olds and chimpanzees stopped performing their role in a collaborative task when

they had obtained their own reward (suggesting that they could be conceiving the partner as a social tool to reach their *individual* goal), 3.5-year-olds were mutually committed to help each other until both have obtained their goal.[13-15]

Differences between chimpanzees' and children's collaborative skills

Several studies have revealed that one main difference between chimpanzees' and children's ability to work together with others is chimpanzees' low levels of inter-individual tolerance when it comes to acquiring resources. Whereas young children will easily work together with familiar (and unfamiliar) peers to reach otherwise inaccessible rewards,[16] chimpanzees only cooperate with partners with whom they are very tolerant.[17] The same individual chimpanzee who is capable of spontaneously cooperating with a tolerant partner, will not approach the cooperation task when paired with a less tolerant partner. This is the case even when rewards have been pre-divided and separated to avoid competition between them. Furthermore, even when chimpanzees are paired with tolerant partners, cooperation tends to break down when resources are clumped and are easily monopolizable.[17,18] In these situations, subordinate partners lose interest because they anticipate or directly experience that their more dominant partners monopolize the totality of the rewards. Both children and bonobos share food more easily than chimpanzees[16,18], and are therefore capable of maintaining cooperation even when resources are clumped and could be easily monopolized.[19]

Sharing the resources of collaborative work is crucial for the long-term stability of cooperation. If two (or more) partners put in effort to acquire resources but one of them rips the partner off by not sharing the spoils, partners will lose motivation, and cooperation will break down. Young children not only share clumped resources more easily than chimpanzees,

but they even share equally after collaborative work. When pairs of 3-year-olds work together to obtain the resources, they share equally or restore equality much more frequently than when they obtain the resources independently and the partner does not contribute to the collaborative enterprise.[20,21] This shows that from a fairly young age, children recognize partners' contribution to a collaborative task and reward them accordingly. This demonstrates that humans are, from a young age, well adapted to maintain collaboration over time.

On the other side, collaboration does not encourage equality among chimpanzees. In two different studies, chimpanzees did not restore equality after collaboration [20] or share more after collaborative than individual work.[22] Melis et al. [22] presented pairs of chimpanzees with big pieces of fruit which one of the subjects could grab and keep in her possession while eating it. The study manipulated whether subjects cooperated or obtained the resources individually. The results showed that since the reward was large and it took some time to feed on it, partners were generally capable of obtaining some scraps (as in the case of meat sharing in the wild). However, whether or not subjects cooperated played no role in individuals' sharing patterns. The results of this study and the study by Hamann et al. [20] suggest that chimpanzees do not seem to take into consideration whether others have contributed to the acquisition of the resources, and do not share the resources of collaborative work more fairly, whereas children from three years of age do.

This line of studies shows that chimpanzee collaboration (at least to acquire edible resources) is mainly constrained by competition between partners and the difficulty of sharing afterwards. Under the right circumstances, high inter-individual tolerance levels and low possibilities to monopolize the resources, collaboration can emerge and stabilize over time, since individuals quickly grasp the need for collaboration and are capable of employing different means to guarantee coordination with the partner. However, in comparison, children

are, from a fairly young age, less constrained and better equipped to maintain collaboration over time due to their higher levels of inter-individual tolerance and higher sharing skills.

Chimpanzees' motivation to collaborate is pragmatic and purely goal-oriented. This is demonstrated by another study that shows that chimpanzees avoid collaboration unless it is the only option to access higher payoffs.[23] When presented with a choice between working alone or with a tolerant partner to obtain the exact same payoff (the partner would also obtain the same payoff), chimpanzees chose to work alone. However, when the collaborative option offered higher payoffs, all subjects were willing and able to collaborate.[23] In a similar study, children prefer collaboration over working alone,[24] suggesting that for children collaboration it is not just a means to obtain otherwise inaccessible goals, but also a gratifying activity in itself.

In summary, chimpanzees and children show important differences in their levels of inter-individual tolerance, their willingness to share the obtained resources, and their motivation to collaborate. Furthermore, from three years of age, children conceive collaboration as a collective enterprise that entails a commitment to mutually support each other.

Prosocial behaviour: Helping and Sharing

Beyond cases in which individuals cooperate for mutualistic benefits, sometimes individuals act to benefit others rather than themselves. Prototypical cases are helping behaviours in which an agent assists another individual with an action-goal, and sharing behaviours in which someone gives up a valuable resource to benefit someone in need. One contentious issue is the extent to which a behaviour that benefits others is actually based upon an altruistic motivation. It is possible that some apparent prosocial acts are just side-effects of habitual behaviours, triggered by stimuli that have nothing to do with the beneficiaries' goal

or need, or the agent acts only because they expect to be rewarded, praised, or want a favour in return. For these reasons, recent experiments have systematically varied the social context to determine which factors actually lead to prosocial behaviour. This research on the proximate mechanisms for helping and sharing also provide insight into the perennial question about the origins of human altruism. Therefore, comparative and developmental studies can add important insights because they enable us to determine what prosocial inclinations, if any, human children possess before relevant socialization practices impact their development and, in addition, address whether these inclinations are human-unique or shared with our closest evolutionary relatives.

Helping: Similarities between chimpanzees and children

One important test case for prosociality are helping behaviours. It requires that helpers cognitively represent the goal another individual is trying, but failing to achieve and have the motivation to act on behalf of that goal. If the helper acts with this goal in mind, rather than a benefit to the self, this helping behaviour qualifies as altruistically motivated. There are several anecdotal reports that suggest that occasionally chimpanzees may be willing and able to help others altruistically. For example, de Waal[25] reports the case of a young female chimpanzee helping an older one who suffered from arthritis to climb up a structure in their enclosure. He also reports the case of a younge male who helped an older female, reaching and bringing to her, the rubber tire that she had been unsuccessfully trying to obtain.[26] Sometimes, chimpanzees have also been observed to intervene and assist in more dramatic and potentially dangerous situations, rescuing companions from drowning in the moat of their enclosure.[25,27,28] Chimpanzees and human infants show striking similarities in the basic helping behaviours. For example, a series of studies tested whether chimpanzees and children would help an individual obtain an out-of-reach object. Infants saw an experimenter sitting down at a desk to write a letter, who then dropped the pen on the floor

and was unsuccessfully reaching for it.[10,29] Already 14-month-olds readily help these clumsy adults by picking up the dropped pen and handing it to the adult, even without any requests or solicitation from a parent. Importantly, children perform these acts when help is actually needed, not in matched control conditions where the adult had discarded the object on purpose. When human-reared chimpanzees were tested in similar situations, they too helped a human caregiver by picking up dropped objects, without a direct request and in the absence of rewards, differentiating between situations in which help was needed or not.[29] Chimpanzees display these helping behaviours also towards conspecifics. In one such test, chimpanzees passed a tool to a neighbouring room when a conspecific in need of the tool to retrieve food was unsuccessfully reaching into the subject's room.[30]

As another example, when 18-month-old infants witnessed how an adult helplessly bumped into the doors of a cabinet with a stack of magazines in hand, they readily opened the door so that he could put them away.[29] Similarly, when a chimpanzee failed to open a door to access food, chimpanzee subjects opened the door for the conspecific.[31] In another situation, chimpanzees were willing to unhook a rope attached to a bag so that the recipient could access the rewards in the bag.[22] In all of these studies, subjects performed these acts selectively in experimental conditions where help was needed over control conditions in which these acts would not have been helpful. Very few studies have tested bonobos, but evidence suggests that they will help when a conspecific struggles to open a door to obtain food.[32] Therefore, these studies show that not unlike human toddlers, chimpanzees and bonobos make inferences about the goal other individuals are trying to achieve and lend a helpful hand.

What motivates these helping behaviours? One obvious candidate is that they expect to be rewarded. However, experiments show that chimpanzees and children help over and over even if no reward is forthcoming and help at the same rate whether they receive a

reward or not. [33] In children, material rewards can even undermine their intrinsic motivation and lead to a reduction in future helping. [34] Another potential motivator for helping is that individuals act strategically to receive return benefits through reciprocation. However, studies with children and chimpanzees show that helping occurs in the absence of any subsequent opportunity for reciprocation. Moreover, young children help irregardless of whether their parent is watching[35] and it is not before three to five years of age that children begin to be affected by opportunities of direct reciprocation and indirect, reputation-based reciprocation across various types of prosocial behaviour, showing that before this age they do not take into consideration the potential future impact of their behaviour.[36-39] In chimpanzees, there is evidence suggesting that they may be capable of past-driven or attitudinal reciprocity,[40] establishing emotional proximity and behaving prosocially towards previously helpful or generous partners more than towards unhelpful ones.[41-43] The chimpanzees of our studies have shown to remember and base some of their decisions to interact and cooperate with others on previous interactions.[7,42] However, this does not mean that they help others anticipating reciprocation and future selfish benefits. In fact, in studies in which they could have benefited themselves by strategically helping others, they do not perform well. [44,45] In this last study chimpanzees were confronted with a collaboration task, in which two chimpanzees had to work together but only one of them could obtain the resources on a given trial. The only long-term solution was to alternate across trials who got the reward. The results showed that individuals were unable to find an alternating strategy, so that with increasing number of trials collaboration levels started to decrease. This suggests that such future-oriented and calculated behaviour is probably beyond their cognitive abilities, making future reciprocation an unlikely explanation for their observed prosocial behaviours.

Helping: Differences between chimpanzees and children

Despite these similarities, young children and chimpanzees differ in several aspects of their helping behaviours. One difference appears in the versatility of helping. While both chimpanzees and human infants hand over out-of-reach objects or remove physical obstacles, children help in more intricate ways. They can correct a person's path of action by handing over a functional object when the person asks for a non-functional object, [46] help when they never see the adult succeed and thus have to infer the intended goal, [29] point to the location of an object that an adult has misplaced [47] and take into account whether a person is knowledgeable or ignorant about the actual location of a desired object. [48] Thus, human children use sophisticated social cognition to determine when and how to help.

Another difference appears to be in the cues that elicit helping. While children help more readily when a person gives verbal and nonverbal cues, [49] they are able to help when these cues are absent altogether. For example, 2-year-olds helped proactively when a person was not even aware that she needed help: Children picked up cans that had rolled off a table without the adult noticing the accident and thus not providing any cues. [50] Children can even help in anticipation of a problem by warning an adult who is about to reach into a bucket that holds an aversive object. [51] Thus, children had to rely on situational cues and their representation of another person's goal to decide when and how to help.

While children help proactively, chimpanzees only help reactively. Specifically, Melis et al. [22] found that chimpanzees were far more likely to help when the recipient was actively trying to pull in a bag with rewards or communicated towards the subject than when the recipient was passive. Similarly, Yamamoto et al. [30,52] found that chimpanzees virtually never offered a tool unless the recipient was actively reaching for it. More generally, when recipients are not actively engaged in a task (such as trying to open or retrieve something), but are passively waiting, experiments find much lower rates of prosocial behaviour. This evidence comes from targeted helping tasks, where actors' choice is between action or

inaction. However, in prosocial choice tasks, in which actors choose between a prosocial (1/1) and a selfish (1/0) option, the evidence is less clear-cut. For example, Horner et al. (2011) found that actors chose the prosocial choice more often when partners remained neutral or communicated their desire using attention-getters. In this study, more directed and harassing requests (e.g. begging with open hand, displaying with pilo-erection or hooting) did not have a positive effect on helping. Other studies using the prosocial choice paradigm have not found that recipients' requests increase actors' prosocial choices.[53,54] However, as pointed out by several researchers, including Cronin,[55] Horner et al.,[56] and Tan & Hare,[57] several methodological factors, such as physical separation and low possibilities for communication between actors and recipients, or poor understanding of the contingencies of the task, may have contributed to these negative results. 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 a difference in motivation, with chimpanzees requiring more active solicitation to be nudged into action.

In summary, the basic helping capacities are similar in young children and chimpanzees. Moreover, children display these behaviours very early in ontogeny. These two pieces of evidence together suggest that basic prosociality in the form of helping is not due to the internalization of cultural norms alone, but may be based in biological predispositions that humans share with chimpanzees. However, the sophisticated social cognition that emerges over human ontogeny, perhaps combined with human-unique socialization and social experience, quickly leads to forms of helping that are beyond the abilities of chimpanzees.

Sharing: Similarities between chimpanzees and children

Sharing behaviours are an important topic for studies on cooperation because they, by definition, incur a cost to the actor and create a benefit to the recipient. Therefore, research

has documented how much individuals share (if at all), looking at sharing events from a cost-benefit perspective. In addition, research has tried to address the question about the motivation for resource sharing. When we compare resource sharing of chimpanzees and children, the dissimilarities are more apparent than the similarities. If anything, what chimpanzees and at least very young children have in common is that giving up a resource is not their default response. As reviewed in our section on collaboration, chimpanzees have a strong tendency to monopolize resources. The best examples of chimpanzees sharing occur after a hunt, when males allow others to take pieces from the carcass. However, this is a context characterized by a lot of begging and harassing from other group members. This suggests that giving up part of the carcass is perhaps less costly than trying to monopolize the totality of it. [58] More generally, chimpanzee sharing is more passive in nature, where a possessor allows others to take some of the food rather than actively offering it. [59,60] Interestingly, two studies have shown that bonobos are more tolerant around food than chimpanzees. [18,19,although see 61] Moreover, experiments in which chimpanzees could deliver food to others at no additional cost to themselves indicate that active food donations are rare to nonexistent. Specifically, Silk et al. [53] and Jensen, Hare, Call, and Tomasello [62] sat chimpanzees in front of an apparatus where they could pull on one side so that it would deliver a piece of food to themselves and one to the other (1/1 option) or pull on the other side so that food would go to themselves, but not the other (1/0 option). In most studies, chimpanzees were indifferent between these options. One exception is Horner et al. (2011),[56] where chimpanzees chose a 1/1 option more frequently when tested in a token trading paradigm. The authors suggest that chimpanzees may have revealed this preference here, but not prior studies because individuals had been more familiar with token-exchange than other chimpanzees with the novel apparatuses that often resulted in side-biases. On the other hand,

Amici et al. (2014)[63] used the same paradigm and did not find reliable prosocial behaviors in neither pulling tasks nor token-exchange tasks.

Studies with bonobos show that they too are unlikely to actively deliver food to others in prosocial choice paradigms. When given a choice between a 1/1 and a 1/0 payoff, they appeared to be indifferent.[57] Moreover, they were not willing to sacrifice food resources they could obtain for themselves,[32] in contrast to situations in which food sharing was accompanied with socio-sexual play.[19,32] Hence, if sharing only serves the purpose of benefiting a conspecific, also bonobos show no strong tendency to present others with food resources.

In summary, the majority of the evidence suggests that neither chimpanzees nor bonobos reliably choose to act prosocially when given different payoff options. Features of the experimental methodology may have contributed to the lack of apes' prosocial behavior and explain why some studies show inconsistent results. It remains for future research to assess whether this reflects apes' lack of prosocial sharing, lack of adequate methods, or the possibility that apes' prosocial sharing is inherently fragile.

Similarly, young children have a strong tendency to keep most or all resources to themselves. Studies using variations of the "dictator game" adapted for children found a strong self-serving bias that gradually gives way to more generosity over middle childhood.[64] Moreover, 18-month-old children tested in a similar setup as Silk and Jensen did with chimpanzees were indifferent between a 1/0 and a 1/1 option. [65] Thus, at least in situations with a recipient who remains passive (or is absent altogether in tasks with anonymous others), young children are not inclined to give up resources, not unlike what is found in chimpanzees.

Sharing: Differences between chimpanzees and children

While active sharing is rare in chimpanzees overall, young children share resources in several contexts. As described above, children share the spoils of their joint labour. In addition, they are willing to share windfall gains -- at least in situations in which the need is made salient. When, in the study by Brownell, Svetlova, and Nichols, [65] an adult recipient verbalized her desire and reached for the resource, 24-month-olds were more likely to choose the 1/1 option over the 1/0 option. Moreover, when adult recipients make their need salient (by showing that they lack a resource or actively gesture towards the desired object) children as young as 14 to 18 months are willing to give up some of their resources. [66,67] Thus, while younger children share their toys or food usually only after an explicit request from the recipient, 2-year-olds help spontaneously without a request, sometimes immediately when they see that a recipient is deprived of a resource.

Over development, children become more likely to share resources even if these overt cues are absent. Children become increasingly more generous by sharing larger amounts with peers in variations on the "dictator game" where they simply decide how much of a resource to give away. [68-70] Interestingly, equality appears to emerge as the dominant norm over development. This sense of equality comes in two forms: Starting at four years of age, children are averse to disadvantageous inequality, rejecting an unequal allocation that benefits a peer more than them (e.g. one candy for self, four for other). They are willing to sacrifice their own reward so that no one gets anything, [71] a behaviour driven by spite. [72] By around eight years of age, children display another sense of equality as well: They show an aversion to advantageous inequality, rejecting unequal allocations that favour themselves, [71,73] e.g. four candies for self, one for other. Therefore, older children are willing to make sacrifices to uphold equality, even if it they are acting against their own benefit and against their own relative advantage. This is perhaps the strongest case for the idea that children share resources based upon a sense of fairness.

Studies on inequality aversion with chimpanzees and other great apes have produced conflicting findings. Some studies have concluded that chimpanzees (and other primates) reject low-quality food when partners are obtaining better rewards for similar work, [74] whereas others have not replicated these findings with slightly improved methodologies. [75] However, even if we accept the possibility that chimpanzees may occasionally react negatively towards disadvantageous unequal distribution of resources, there is no evidence for advantageous inequality aversion, like children show from age eight onwards.

Conclusions

The similarities and differences between chimpanzees' and young children' cooperative abilities allow us to draw some inferences about what components of human cooperation are evolutionary ancient and what components are human-unique.

Chimpanzees, similar to children between ages two and three, possess socio-cognitive skills that enable the emergence of mutually beneficial collaboration. Their success in these tasks is not the accidental by-product of independent actions towards the same goal. It is the result of intentional coordination and individuals realizing how their actions and those of the partner complement each other to achieve the desired outcome. In the chimpanzees' experiments, individuals were knowledgeable of the different actions required to reach their goal. In addition, they must have had some expectations about the goals and goal-directed actions of their partners, which allowed them to create the favourable circumstances (by recruiting the partner and giving her the tool she needed) to guarantee successful coordination. Young children develop these social-coordinative abilities as well, with one important addition: By around three years of age, humans express the additional mindset to treat these interactions as collective mini-enterprises that entail the mutual commitment to subsume one's own actions and interests under a collective goal and ensure each other's

success. Borrowing the concepts from Butterfill, [76] this suggests that chimpanzees and young children engage in a more basic form of collaboration that involves sharing goals in terms of representing how actions can result in common effects. Slightly older children then develop a notion of collaboration as involving joint action-plans that fit the criteria for joint intentionality as defined by Tomasello et al. [77] Thus, similar to young children, our primate cousins are capable of successful and functional coordinated behaviour in order to achieve goals that they could not achieve individually, even if they lack the capacity for joint intentionality and do not understand commitment or the normative dimension of collaborative activity. The main limitation in chimpanzees, and the most important difference to even very young humans, is therefore not cognitive but related to their different temperament, lower level of inter-individual tolerance, or higher competitive disposition around food. This means that given the right circumstances of strong dependence on collaborative efforts to obtain resources and high tolerance between individuals, chimpanzees share with us the basic psychological mechanisms necessary for collaboration.

In the area of prosocial behaviours aimed at benefiting others, chimpanzees and children appear to share the basic capacities for instrumental helping, although children help more flexibly and more spontaneously. This difference becomes even more apparent when we look at the developmental trajectory of children who expand their skills to help in a variety of ways. When it comes to resource sharing, the differences are more apparent than the similarities. Toddlers share actively at least when the recipient is signalling need, while chimpanzees rarely share actively, and sometimes only when they are being harassed by others. Perhaps the tendency to monopolize resources constrains both their mutualistic collaboration as well as their prosocial sharing, a constraint that is removed when helping others with action-goals. Therefore, chimpanzees and children display important similarities in the basic tendencies to act prosocially for others, while chimpanzee prosociality is more

fragile, especially when competing selfish demands surrounding food are salient. It has been proposed that increased social tolerance is an important contributor to the increased cooperativeness in humans. [78] In addition, social norms likely lead to levels of human cooperation that are not found in other apes. The role of social norms increases over human ontogeny, with children developing a sense of fairness that regulates how to share resources and how to interact with others.

Table 1. Similarities and differences between chimpanzees' and children's cooperative behaviour.

Collaboration	**Chimpanzees**	**Children**
Behaviour	Successful temporal and spatial coordination	
Representing roles	Understanding of complementary actions	

Social tolerance	Low	High
Resource division	Monopolization	Equal sharing*
Commitment	One-sided: helping other to help self	Mutual*: partners expect to help each other
Motivation	Pragmatic, goal-oriented only	Pragmatic & intrinsic value of collaboration

Prosocial behaviour	**Chimpanzees**	**Children**
Instrumental helping	Helping with action-goals	
Sharing	Monopolization, passive sharing	Costly and active sharing of resources*[#]
Reactive prosociality	Yes	
Proactive prosociality	No	Yes[#]

From 2 years of age

* From 3 years of age

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