The Evolutionary Roots of Prosociality: The case of Instrumental helping

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Abstract

Comparative studies with closely related primate species are crucial to understand the origins of human prosociality. One type of prosocial behaviour that probably relies on evolutionary ancient skills and motivations is instrumental helping. Recent experimental studies have shown that bonobos and chimpanzees will help others achieve their action goals. Chimpanzees have shown to help others picking up and giving objects to a recipient, opening locked doors for conspecifics struggling to open them, and releasing stuck rewards that recipients were trying to reach. Recent studies have now replicated some of these results with bonobos. However, whereas chimpanzee's helping emerges mainly in response to recipients' signals of need, bonobos also help proactively. This difference could rely on bonobos' enhanced socio-cognitive skills.

Introduction

Are humans inherently good or bad? The question of whether prosociality is the result of moral education and cultural influences, or whether humans have a natural predisposition to behave prosocially, has been repeatedly debated throughout history. In recent years, evidence from comparative and developmental psychology has accumulated, suggesting that humans may have a biological predisposition for prosociality [1]. Here, I argue that comparative studies with other species, in particular closely related primate species, are crucial to understand the origins of human prosociality. I continue by reviewing what recent studies with other great apes species suggest about the evolutionary foundations of human prosociality.

I define prosocial behaviour as behaviour in which an individual performs an act that benefits another individual rather than oneself, perhaps even at her own cost and where the actors' motivation is to intervene towards the other individual's goal, problem, need, or emotion [1]. Warneken and Tomasello [2] argued that prosociality should not be considered a homogeneous trait since individuals may behave differently depending on the context and costs of the prosocial act. They proposed different domains of prosociality: sharing resources, helping others reach their goals, providing information and providing emotional support to others [2].

Why Comparative Psychology?

A particular case of prosocial behaviour that emerges very early in human ontogeny is instrumental helping, when individuals intervene to help others achieve their goals [3-5]. Developmental studies with young children suggest that helping behaviour, together with informing, emerges at around one year of age, long before socialization has played a large role and children could have internalized the moral norms of their societies [6-8]. However, even studies with very young children cannot completely rule out that children have not been influenced by cooperative practices at home or specific parenting styles that encourage caring about and helping others [9,10]. Therefore, a second important line of research about the origins of human prosociality is the study of closely related primate species.

Studies with closely related primate species, such as chimpanzees and bonobos, can provide insight into the biological roots of human prosociality because our primate cousins

do not have cultural or social norms about cooperative behaviour like humans do. There is no evidence outside of humans for cultural variation with respect to norms of social conduct, in the same way that there is no evidence that chimpanzees teach or model prosocial behaviour or punish individuals who fail to act prosocially. Therefore, nonhuman primates offer a unique opportunity to investigate the biological predisposition for prosociality in humans, because they lack precisely those cultural factors that are important but nearly impossible to rule out in humans. Furthermore, since they are our closest living primate relatives (the human and great ape lineages split off only 6 to 7 million years ago), we share many biological, behavioural and cognitive similarities due to common descent [11]. Therefore, similar prosocial behaviours in great apes and humans are more likely to be based upon shared psychological mechanisms due to common descent, than when distantly related species exhibit similar behaviours[1].

The two ape species, chimpanzees and bonobos, are particularly interesting model species to study prosocial behaviour, since they have been observed to behave prosocially in several different contexts. There are several examples of naturally occurring behaviours in which both *Pan* species act to benefit others, sometimes even at a cost for themselves [13]. Prototypical cases are cases of consolation behaviour [14,15], instrumental helping or intervening to help others that are struggling with an action goal [16,17], and sharing of valuable resources, such as meat or fruits [18-20]. However, apparently prosocial acts could be selfishly motivated, for example if individuals act prosocially expecting an immediate or future reward, or in order to avoid harassment by the potential helpee [21,22]. Therefore, in recent years, a variety of experimental approaches have investigated primates' prosocial behaviour in controlled situations, where underlying motivations can be singled out.

Prosociality in chimpanzees and bonobos

[1] Comparative studies with other animal species also offer important insights regarding the necessary preconditions for certain skills to emerge (e.g. if animals other than humans have theory of mind skills, then language cannot be a necessary prerequisite for ToM), and insights about potential selection pressures that may have pushed forward the convergent evolution of certain traits. For example, with regard to prosociality, one hypothesis suggests that callitricid monkeys could have evolved prosocial motivations as a result of selection pressures associated with cooperative breeding [12. Burkart JM, Hrdy SB, Van Schaik CP: **Cooperative breeding and human cognitive evolution**. *Evolutionary Anthropology: Issues, News, and Reviews* 2009, **18**:175-186. However, in this case, similarities to humans would not be the result of shared mechanisms due to common descent, but due to convergent evolution.

In recent years there have been three main experimental approaches to study primate prosociality. Two of them have investigated forms of prosocial behaviour that are not associated with high costs or any costs for the actor, whereas the third approach has investigated at a more costly form of prosocial behaviour: sharing valuable resources that the actor could keep for herself (2,23). The results from these studies provide converging evidence that under certain circumstances (reviewed below) chimpanzees and bonobos, like human children, are willing and able to help others achieve their goals. However, the sharing psychology has proven to be very different for the two *Pan* species. Whereas chimpanzees are highly competitive over food, bonobos exhibit a much more relaxed nature around food, and even the willingness to share food in exchange for physical proximity to others, especially strangers. I will focus in this review on the findings from instrumental helping tasks and prosocial choice tasks, the two main experimental paradigms investigating non-costly prosociality (but see [23] also).

Helping acts are an interesting case of prosocial behaviour because, despite being relatively low-cost, they require helpers inferring the goals that others are trying to achieve and are based upon a prosocial disposition to act on other's behalf. Studies with human infants have shown that from 14 months of age, children engage in instrumental helping [24].

Similar to human infants, chimpanzees and bonobos have been observed to intervene in various ways helping others achieve their goals. For example, chimpanzees help picking up objects and giving them to a human partner that is struggling to reach them [3,25]. They do this in the absence of direct requests and rewards. One could possibly argue that chimpanzees have been reinforced in the past for bringing objects to humans and that this has become habitual behaviour. However, chimpanzees also help conspecifics that are struggling to reach a tool by giving it to them (and there is also some evidence for orang-utans [26]). More importantly, they do this flexibly, and do not just give them any tool, but they choose the correct tool based on the problem that their partner is trying to solve [27,28]. Interestingly, bonobos do not to help transferring objects. What is even most puzzling is that they seem to be more willing to help transferring food than non-food items [23].

Chimpanzees also help by removing obstacles that prevent their partners from reaching their goals. For example, in one study chimpanzees helped a conspecific partner entering a room with food [25]. The partner' door was locked with a chain that only the helper could remove (without the helper herself being able to access the room with food), and subjects released the chain. In another study they also helped releasing a hanging reward that

a conspecific partner wanted to reach [29]. In both of these studies subjects showed that they had a good understanding about the helping apparatuses and the consequences of releasing the chain or the reward. In addition, control conditions showed that the target actions were not intrinsically rewarding, the result of boredom or habitual behaviour acquired in the familiarization phase with the apparatus, since helpers did not perform the target behaviours when neither themselves nor the recipients could benefit. Two recent studies with bonobos have found similar results [23,30]. In these studies bonobos also helped social partners access a room with food and obtain an out-of-reach fruit hanging from the ceiling. Interestingly, they helped both familiar and unfamiliar partners. They also showed full understanding of the consequences of their actions, and the capacity to inhibit the target actions in control conditions in which nobody would profit.

There is an interesting difference between the two *Pan* species regarding their helping behaviour. Chimpanzees engage in what has been called *reactive* prosociality [31], where the recipients signal, intentionally or unintentionally, their need for help [1,27,29] (although see [32] and [33]). However, in the two helping tasks conducted with bonobos, subjects also helped *proactively, i.e.* in the absence of recipients' signals of need [23]. Bonobos have been found to outperform chimpanzees in two theory-of-mind related tasks, gaze following and understanding of intentions, and they also have a natural tendency to fixate and look at other's faces and eyes much more than chimpanzees [23,34,35]. This suggests that cognitive or attentional factors could underlie the differences found between bonobos' proactive and chimpanzees' reactive prosociality. Bonobos' enhanced interest in other's faces and eyes may make them more similar to humans, who from 2 years of age are also capable of helping proactively [36]. It has been argued that reactive helping is less prosocially motivated than unsolicited helping [12], but this is not necessarily the case if helpers are not being coerced into action. For example, if humans donate money for natural disasters in response to a fundraising campaign, does this mean that there is no real motivation to help? If chimpanzees are less likely to pay attention to others and reason about their intentions, the recipients' signals may help drawing their attention to the problem and the partner's need.

Recently, it has been suggested that chimpanzees help, not to benefit others, but because they are attracted to the apparatus where recipients signal what they want, i.e. due to stimulus enhancement [37]. However, in several studies the target objects could not be manipulated at all by the recipient since they were out of her reach [3,25,27,28]. This stimulus-enhancement hypothesis can also not explain why chimpanzees would help those

individuals, who have helped them previously, more [38,39,40]. And lastly, the bonobo results also pose a problem for this explanation, since they help proactively, so either one believes in that a different alternative explanation would be needed for them.

The conclusion that chimpanzees and bonobos share with human infants a basic natural predisposition to help others altruistically achieve their goals has been challenged by the results from the prosocial choice task [41], which presents individuals with the opportunity of delivering food to a partner at no cost. In this task subjects are presented with a choice between a mutualistic or prosocial option that delivers food to her and to the partner (1/1), and a selfish option that only delivers food to her (1/0 option). In this task chimpanzees and bonobos typically do not choose the prosocial option more in the test than the non-social control condition, which has been interpreted as evidence for their indifference to the welfare of others ([42-46] see [32] the only exception in which they choose prosocially in a token-exchange paradigm). However, evidence is accumulating that different problems of this task could be limiting subjects' capacity to exhibit prosocial behaviour. Tan and colleagues [47] have reviewed in detail the difficulties of the prosocial choice task and concluded that in most studies either subjects had not demonstrated an understanding of the apparatus [43,44], or the negative results were due to a bias for the prosocial option that subjects carried over to the control condition [42,46,47]. Furthermore, they argued that the task may be cognitively too demanding since subjects need to pay attention to four dishes. This conclusion seems to be supported by a study with children that found that even 2-5 year-old human children do not choose the prosocial (1/1) over the selfish (1/0) option, whereas they choose a purely altruistic option (0/1) over an empty option (0/0) [48,49]. More caution is needed when drawing conclusions from experimental paradigms that lack strict controls of the animals' understanding of the task, or when the negative results are due to potential problems of the task itself.

Conclusions and Future Directions

Studying our closest primate relatives can help us elucidate the roots of human behaviour. Furthermore, methodologically, nonverbal tasks developed for nonhuman apes can be adapted and employed with young children. Both chimpanzees and bonobos exhibit prosocial motivations mainly in the form of instrumental helping, when individuals intervene to help others reach their goals. It is often argued that individuals could be acting prosocially

in expectation of a future favour by the recipient but there is no evidence suggesting that any nonhuman animal is capable of future-oriented reciprocal behaviour. In humans, future-oriented reciprocity, or the capacity to understand the long-term self-beneficial consequences of exchanging favours, emerges rather late in ontogeny [50-52]. The differences found between bonobos' proactive and chimpanzees' reactive prosociality offer an exciting avenue to investigate further the relationship between socio-cognitive skills and prosocial behaviour. The early age at which human infants engage in instrumental helping, together with the findings from our two nearest related species, suggests that the skills and motivations that underlie this type of prosocial behaviour, probably date back to the last common ancestor of humans and *Pan*. In humans, however, helping behaviour becomes potentiated over human ontogeny as the result of increasingly complex social cognition combined with socialization and human-unique cultural influences.

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