segment during undulatory swimming, but no information is as yet available except for the fact that the same interneuronal building blocks are available as for mammals.

Jung et al. [3] have shown that the developmental building blocks, such as the LMC, needed for controlling the vertebrate limbs had already evolved when the elasmobranchs diverged, 420 million years ago, from the line leading to mammals. Up until now, it had generally been assumed that this circuitry evolved much later at the transition to terrestrial locomotion. Other main features of the vertebrate brain have recently been shown to be conserved including the detailed forebrain design with the basal ganglia, habenulae and pallium/cortex that emerged even earlier, around 560 million years ago [14–16]. It is striking that many aspects of the basic design of the vertebrate nervous system had already evolved at the dawn of vertebrate evolution — a fact not appreciated until recently. A design that works well, need not be modified!

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Social Behavior: Bonobos Are Nice but Prefer Mean Guys

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Human infants prefer to interact with prosocial individuals. Bonobos, our close relatives, however, prefer antisocial individuals, perhaps due to a preference for social dominance. Human prosocial behavior may be due to unique tendencies to positively evaluate prosocial others.

Humans are remarkably prosocial, routinely willing to take costs to benefit others. More so than any other species, humans cooperate with and help others they are not related to, they have never met before and they will never meet again. These prosocial tendencies are clearly beneficial: working together allows humans to achieve feats that no individual could achieve on her own, and these cooperative inclinations have allowed human cultures to bloom. But despite its utility, human prosociality also represents a profound evolutionary puzzle: why would unrelated strangers accept
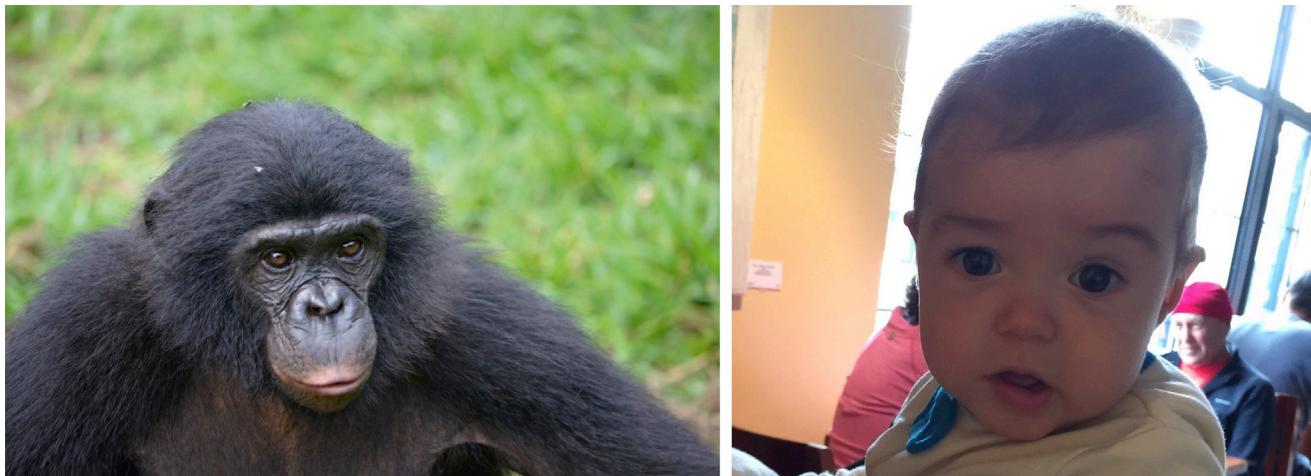
Figure 1. A tale of two apes.
An adult male bonobo (*Pan paniscus*), male bonobo named Chibombo who participated in some of the experiments, and a male infant human (*Homo sapiens*). Unlike infant humans who have been shown to prefer those who help others achieve their goals, Krupenye and Hare [5] report that adult bonobos prefer those who hinder others' goals. This species difference may reflect distinct evaluations of dominance. Photos: Chistopher Krupenye (left), Kiley Hamlin (right).

reduction of their own fitness to improve the fitness of others? It is unclear how such a system could evolve or be maintained, given that individuals can 'free-ride' on cooperative systems by reaping the benefits of others' cooperation while not cooperating themselves. One solution to this puzzle is that, in combination with other mechanisms, humans possess strong cognitive skills for social analysis and evaluation [1,2]. That is, humans are highly attuned to how others behave, and readily form preferences for those who are cooperative and helpful over those who are uncooperative and unhelpful [3]. These tendencies allow humans to selectively interact and cooperate with helpful individuals while avoiding harmful ones, thereby mitigating the risk of their own cooperative acts being exploited. Consistent with the possibility that social evaluations are part of an evolved system supporting human cooperation, recent work in developmental psychology suggests that human infants prefer prosocial to antisocial others within the first few months of life — arguably before socialization could be solely responsible for its emergence [4]. In a recent paper in *Current Biology* [5], Christoph Krupenye and Brian Hare explore the uniqueness of social evaluation and preferences for prosocial others in our close relatives, by extending methodologies developed for exploring

social evaluation in human infants to bonobos (*Pan paniscus*).

Bonobos (Figure 1) are a key species to study the evolutionary differences in preferences for prosocial others. Compared with the closely related chimpanzees (*Pan troglodytes*), bonobos are markedly less aggressive, both toward their own group members and toward members of other groups [6]. Unlike chimps, bonobos feed together and actively share food [7], and they are more successful at cooperating with each other to obtain and subsequently share food sources [8]. Compared to chimps, bonobos are highly socially tolerant, finding unrelated strangers appealing rather than threatening, and even sharing food with and incurring personal costs to help those who are not in their group [9,10]. Also unlike chimps, bonobos have been shown to help proactively even those who have not clearly signaled their need [9]. These social and prosocial tendencies may be grounded in bonobos' superior social attention and 'mentalizing' abilities relative to chimps': bonobos are relatively more attentive to others' eye regions than are chimps, and they outperform chimps on tasks requiring them to think about what others are thinking [11]. Thus, bonobos' social lives are — in some ways — more human-like than are chimps'.

Are bonobos' human-like tendencies for social tolerance and prosociality

mirrored by social evaluations and preferences for prosocial others? If so, bonobos who observe others help or hinder others should reliably prefer helpers, as do human infants [4]. However, results from previous work have been mixed. Bonobos have been shown to be socially selective in some circumstances; for example, they are more likely to accept food from someone who previously groomed or played with them than from someone who did not [12]. On the other hand, whereas chimps have been shown to selectively approach and to remain in the vicinity of someone who previously shared food with them or others, bonobos have not reliably shown these same tendencies [13,14]. Now, in a series of studies using multiple methods, Krupenye and Hare [5] provide compelling evidence suggesting that bonobos, like humans, do evaluate others based on their tendency to treat others prosocially versus antisocially. However, bonobos showed a surprising preference pattern: rather than selectively approaching those who helped someone to achieve his goals, bonobos preferred those who hindered someone's goals.

The preference of bonobos for hinderers was demonstrated in three experiments. In the first, bonobos watched an animated character trying but failing to reach the top of a steep hill [4]. On alternating events, a helper entered

the scene and pushed the needy character up the hill, facilitating his goal, and a hinderer entered the scene and pushed the needy character down to the bottom of the hill, blocking his goal. In a subsequent choice task, bonobos preferentially accepted food from the hinderer rather than the helper, suggesting they preferred the hinderer. Critically, this result was not due to bonobos simply responding to some low-level aspect of the displays such as downward versus upward movement: Bonobos in a control condition chose randomly between characters who pushed an inanimate object up versus down the hill. This preference for hinderers was then conceptually replicated in two more experiments, in which bonobos viewed a human helper who always tried to return a lost toy to its owner, and a human hinderer who always snatched the toy away. Once again, bonobos accepted food from the hinderer more often than from the helper, consistent with a preference for hinderers.

Why do bonobos prefer antisocial others? Krupenye and Hare [5] propose that, rather than actively preferring those who harm, bonobos may prefer those who are dominant, and in the current studies the hinderers appeared to be in charge of the hill and the toys. In a final experiment, they found direct support for the dominance hypothesis, by demonstrating that bonobos also prefer an individual who wins a competition for a certain location in a scene over a character who loses. This sensitivity to dominance is not necessarily surprising: hierarchies are ubiquitous in primate societies, and those who are dominant often retain preferential access to resources and mates and so may be worth befriending [15]. Even human infants are sensitive to dominance relationships; for example, recognizing that certain individuals are likely to dominate others [16,17]. Indeed, toddlers have also been shown to prefer dominant to subordinate characters [18]. However, the dominance preference of toddlers is critically distinct from that of bonobos. Whereas toddlers like those whom others appear to respect, they dislike bullies who dominate through force, as the hinderers did in the current studies [19]. These

results suggest that while humans and bonobos are both sensitive to dominance, each positively evaluating dominant individuals in some situations, humans' dominance concerns may be secondary to a relatively stronger aversion to antisociality. Interestingly, bonobos do not appear to share this aversion, preferring dominant others even if they acquired their status through force.

A host of questions remains. Given that bonobos are relatively prosocial but do not appear to positively evaluate prosocial others, what mechanisms do support bonobo prosociality? Perhaps bonobos would attend to proscociality in a situation in which dominance were less salient or antisociality were more salient. Are preferences for prosocial others unique to humans, or have other species that are also relatively socially tolerant and prosocial also developed them via convergent evolutionary processes? Some recent evidence suggests that capuchin monkeys (*Sapajus apella*) and domesticated dogs avoid non-helpers; however, there is little evidence that these species preferentially approach helpers [20]. In the end, although whether and how patterns of preference for prosocial and/or dominant others exist across primates and other highly social species remains to be seen, the work of Krupenye and Hare [5] suggests that exploring these questions is crucial to gaining a deeper understanding of the mechanisms supporting prosociality, both in humans and across the animal kingdom.

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