

Review

On the psychology of cooperation in humans and other primates: combining the natural history and experimental evidence of prosociality

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In any given species, cooperation involves prosocial acts that usually return a fitness benefit to the actor. These acts are produced by a set of psychological rules, which will be similar in related species if they have a similar natural history of cooperation. Prosocial acts can be (i) *reactive*, i.e. in response to specific stimuli, or (ii) *proactive*, i.e. occur in the absence of such stimuli. We propose that reactive prosocial acts reflect sensitivity to (i) signals or signs of need and (ii) the presence and size of an audience, as modified by (iii) social distance to the partner or partners. We examine the evidence for these elements in humans and other animals, especially non-human primates, based on the natural history of cooperation, quantified in the context of food sharing, and various experimental paradigms. The comparison suggests that humans share with their closest living relatives reactive responses to signals of need, but differ in sensitivity to signs of need and cues of being watched, as well as in the presence of proactive prosociality. We discuss ultimate explanations for these derived features, in particular the adoption of cooperative breeding as well as concern for reputation and costly signalling during human evolution.

Keywords: cooperative breeding; costly signalling; food sharing; other-regarding preferences; reciprocal altruism; reputation

1. INTRODUCTION

Cooperative and altruistic behaviours can be favoured by natural selection if they increase the inclusive fitness of the actor (see Brosnan & Bshary 2010; Lehmann & Rousset 2010). The conditions under which this is the case are now well known (see Brosnan & Bshary 2010; Lehmann & Rousset 2010). However, which proximate mechanisms make an actor engage in such behaviours are less well understood. Here we focus on the *prosocial acts*, i.e. acts of help or assistance to others (Silk 2007), which together constitute cooperative and altruistic behaviour as defined by Brosnan & Bshary (2010). We propose that these acts are regulated by a set of psychological rules (henceforth: *rules*) that on average produce fitness-increasing behaviour. For instance, the rule to adjust prosocial acts to the recipient's need and preferentially directing them towards partners that reciprocated in the past is generally adaptive, because it maximizes the

return benefits through reciprocity (Trivers 1971), whatever exact cognitive or emotional mechanisms underlie it.

The idea that behaviour is produced by a set of rules follows the tradition of classical ethologists, who attempted to identify the corresponding intrinsic motivations and responses to extrinsic stimuli (Tinbergen 1951). In figure 1, the intrinsic motivation is indicated by the intercept (*b*), whereas the tendency to respond to extrinsic stimuli is indicated by the slope of the response (*a*). Because natural selection works by modifying these rules over time, it is parsimonious to assume that they are similar in closely related species owing to homology (de Waal 1991). Specifically, this view implies that humans and great apes are likely to have a similar psychology underlying prosocial acts. However, the psychology may change when one taxon evolves a different style of cooperation from that of its sister group, as we will argue for humans and great apes, which could lead to convergent evolution with other taxa that evolved similar patterns of cooperation. Thus, the goal of this paper is to examine the psychological rules underlying prosocial behaviour in humans, based on natural history and experimental evidence, and to compare them with those of other primates, and in particular our closest living relatives,

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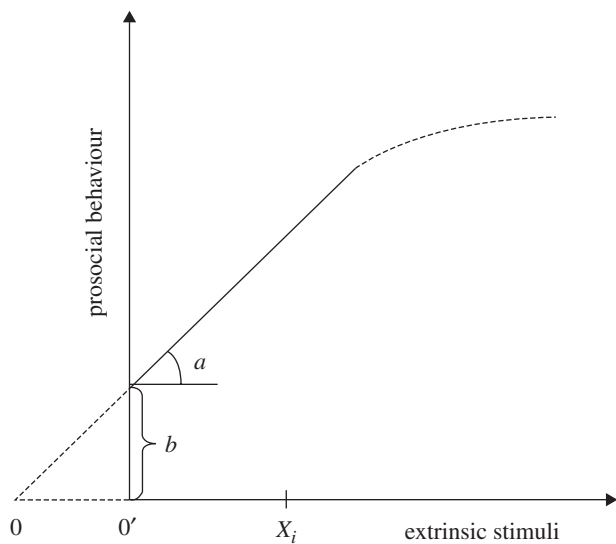


Figure 1. Prosocial behaviour as a function of extrinsic stimulus strength and intrinsic prosocial motivation. In humans, these stimuli can be perceived need of the recipient and/or the perceived presence and size of an audience. Social distance to the partner further modifies the prosocial response, i.e. at a given point X_i , kin, reciprocating partners or in-group members will generally elicit a higher prosocial response. Thus, prosocial behaviour in response to these stimuli may be called reactive. Eventually, the response will reach ceiling levels, as indicated by the dashed curve. If the intrinsic motivation b is greater than zero, prosocial behaviour may occur even in the absence of such stimuli and can thus be called proactive. However, since in practice it may be impossible to exclude all extrinsic stimuli, experiments trying to do so may measure prosociality at $0'$ rather than 0 , and proactive thus refers to either a high intrinsic motivation or a high sensitivity to the remaining stimuli, as indicated by the dashed lines leading to 0 . Ultimately, natural selection can work by changing the sensitivity to stimuli, a and/or the intrinsic motivation, b , depending on the average certainty of return benefits to the actor. Humans have probably acquired a greater intrinsic prosocial motivation, as well as a higher response to extrinsic stimuli since their divergence from great apes.

the great apes. The potential endocrinological correlates of these rules are discussed elsewhere (Soares *et al.* 2010). We identify features in which humans generally differ from other animals and discuss hypotheses explaining the evolution of these features. (For the purpose of this chapter, we ignore the large intraspecific variation documented in humans with respect to cooperative and antisocial behaviour; Gächter *et al.* 2010.)

2. THE NATURAL HISTORY OF COOPERATION

Human foragers, whose ecology and social organization are probably closest to the conditions under which our psychology evolved (Tooby & Cosmides 2005), systematically and frequently engage in various forms of cooperation. Thus, common prosocial acts include voluntary food sharing with both kin and non-kin, allo-maternal child care, division of labour, care for the sick, injured and elderly, information donation (teaching), cooperative hunting, collective warfare, etc. (Gurven 2004; Kaplan & Gurven 2005;

Marlowe 2007; Gurven & Hill 2009; Hrdy 2009; Kaplan *et al.* 2009; Burkart & van Schaik 2010). Prosocial acts occur within family units, including pair-bonded partners and their offspring, and also among family units within local groups. Their pervasiveness suggests that they return high fitness benefits to actors.

Among great apes, cooperation is less common and prosocial acts are less pervasive (see also Melis & Semmann 2010). Food sharing is generally reluctant and rarely active, even among kin (figure 2, discussed in detail below), there is little evidence for teaching (reviewed by Humle *et al.* 2009; Jaeggi *et al.* 2010a) and allo-maternal child care is virtually absent, as is care for the disabled beyond grooming (Hrdy 2009; van Schaik & Burkart 2010). Among chimpanzees, the most common forms of cooperation involve closely bonded males, such as in mutual support in conflicts (Watts 2002; Gilby *et al.* 2009), cooperative hunting (Boesch & Boesch 1989; Boesch 1994; Watts & Mitani 2002) and inter-community warfare (Manson & Wrangham 1991). This indicates that prosocial acts among great apes on average yield lower fitness benefits to actors, with the possible exception of chimpanzee males, who seem to profit more from cooperation. Probably, this is due to the relatively low average relatedness of chimpanzees and the resulting reliance on direct reciprocity for many aspects of cooperation (Langergraber *et al.* 2007, 2009), as well as the absence of strong pair-bonds.

Species other than great apes show more parallels with humans with respect to the natural history of cooperation. In particular, voluntary food sharing, teaching, allo-maternal care and care for the injured are more common in cooperative breeders such as callitrichid monkeys or social carnivores (Kühme 1965; Brotherton *et al.* 2001; Clutton-Brock *et al.* 2001; MacDonald & Sillero-Zubiri 2004; Thornton & Raihani 2008; Hrdy 2009; Burkart & van Schaik 2010). This indicates that cooperative breeders enjoy higher return benefits from prosocial acts and are more prone to engage in them. Could this similarity with humans reflect convergent evolution?

Humans can also be called cooperative breeders, since they show high levels of infant care by older siblings, husbands and grandmothers (reviewed by van Schaik & Burkart 2010). In contrast, great ape females are independent breeders who receive no help in rearing their young (Hrdy 2009). While most great apes, and in particular females with offspring, are relatively solitary in order to avoid feeding competition (van Schaik 1999; Stumpf 2007), cooperative breeders typically form family groups, including at least one bonded pair and multiple offspring, both dependent and independent (Clutton-Brock 2002; Chapais 2008). Within this expanded kin network, prosocial acts should be under more positive selection and the underlying psychology could change accordingly. Thus, the Cooperative Breeding Hypothesis states that some convergent evolution between humans and other cooperative breeders explains the emergence of psychological and cognitive features in humans not shared by the other apes (Burkart *et al.* 2009; Hrdy 2009; Burkart & van Schaik 2010).

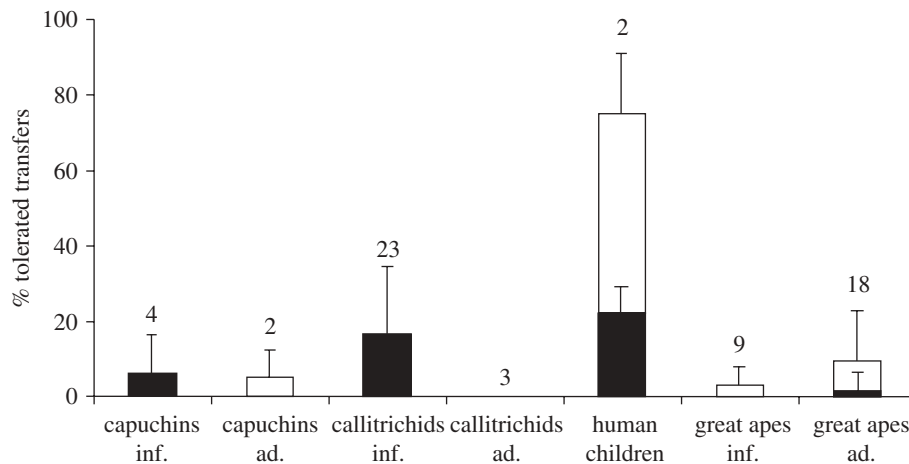


Figure 2. Percentages of all tolerated food transfers among different primate species in which the owner shared proactively (offering) or reactively (active giving or facilitated taking upon begging). The remaining transfers were passive (tolerated taking). See electronic supplementary material, tables S1 for operational definitions and S2 for a full reference list including additional species. Bars represent means of different studies, i.e. the percentage of transfer from each study, or the independent study group is counted as one data point. The numbers above the bars indicate the number of independent data points contributing to these means, inf., sharing with infants; ad., sharing among adults. Black bars, proactive; white bars, reactive.

Humans may also differ from chimpanzees in two other important aspects of cooperation. Firstly, there is substantial *interdependence* among foragers, because the returns from individual foraging are smaller than the ones from cooperative foraging and hunting returns are large but so unpredictable that sharing became a survival necessity (Kaplan *et al.* 2009). Thus, a solitary human forager, in stark contrast to a solitary chimpanzee, is always worse off than a cooperative forager. Furthermore, the fission–fusion dynamics of foragers allow for considerable partner choice, thus restraining selfish tendencies owing to the risk of losing valuable cooperation partners (Kaplan *et al.* 2009). These two aspects combined caused the necessity to establish and maintain a cooperative reputation. Thus, non-cooperative individuals may face substantial costs imposed by the ‘moral community’ (Boehm 1999), ranging from shunning over overt accusations to ostracism and violence (Boehm 1999; Gurven 2004; Marlowe 2009). These potentially high costs exerted by others on cheaters probably lead to a hyper-awareness of the risk of being detected, i.e. a *conscience* (Trivers 1971; DeScioli & Kurzban 2009), functioning to anticipate others’ reactions and thus avoid these costs. Combined with large group sizes and the possibility to spread reputations through language as gossip in a fission–fusion society (Dunbar 2004), concern for reputation should thus have led to an increased sensitivity to being watched by others. Secondly, individuals, and in particular men, may signal cooperative tendencies and their own qualities to large audiences in order to increase their chances of being chosen as cooperation partners or mates (Smith & Bliege Bird 2005). Thus, costly signalling theory also predicts sensitivity to the presence and size of an audience, in order to maximize the broadcasting efficiency of costly signals.

Hence, some aspects of human cooperation are probably homologous with our closest relatives, in particular with regard to mutualism and direct reciprocity

(hunting, warfare, agonistic support), whereas others are better explained by convergence with cooperative breeders, probably owing to increased kin networks and strong pair-bonds, and yet others are probably uniquely derived, viz. concern for reputation and the broadcasting of prosocial acts to large audiences. These aspects of the natural history of cooperation are likely to affect the psychological rules regulating prosocial acts.

3. PSYCHOLOGICAL RULES UNDERLYING PROSOCIALITY

As indicated in figure 1, we propose that prosocial behaviour can be *reactive*, i.e. triggered by extrinsic stimuli (with a positive slope (a)), or *proactive*, i.e. in the absence of any obvious extrinsic stimuli, indicated by the intrinsic motivation (b). Note that common definitions of altruism in other fields, such as in psychology (Batson 1991) or philosophy (Kitcher 1998), mainly refer to proactive prosociality and may not consider prosocial behaviour in response to explicit stimuli altruistic.

In general, the steepness of the response (a) will have been moulded by natural selection according to the average probability of return benefits to the actor. As both kin selection and reciprocity theory predict that prosocial acts should be adjusted to the recipient’s need in order to achieve the greatest potential benefit (Hamilton 1964; Trivers 1971), actors should be sensitive to signals or signs of need. Note that responding to *signals* of need usually requires no special abilities, because they are directed at the actor and have specifically evolved in a form that most successfully elicited the desired response (Zahavi 1987). However, the ability to correctly read *signs* of need (not directed to actor) may often depend on theory-of-mind capacities. Thus, actors with a well-developed theory of mind may be better at perceiving adequate situations for prosocial acts, which should lead to a steeper slope (a).

Table 1. Summary of experimental outcomes measuring prosocial tendencies in primates.

paradigm	chimpanzees	macaques	capuchins	callitrichids
provisioning games	negative ^a	positive, ^b negative ^c	positive ^d	positive, ^e negative ^f
unilateral cooperation	tends to break down ^g		reciprocal ^h	reciprocal, ⁱ sustained ^j
targeted helping	positive ^k		positive ^l	

^aSilk *et al.* (2005), Jensen *et al.* (2006), Vonk *et al.* (2008) and Yamamoto & Tanaka (2010).

^bBut no control for simpler explanations; Massen *et al.* (2010).

^cMason & Hollis (1962), Colman *et al.* (1969) and Schaub (1996).

^dLakshminarayanan & Santos (2008), de Waal *et al.* (2008) and Takimoto *et al.* (2010).

^eBurkart *et al.* (2007), Cronin *et al.* (submitted) and Hauser *et al.* (2003).

^fCronin *et al.* (2009) and Stevens (2010).

^gReviewed by Snowdon & Cronin (2007) and Warneken & Tomasello (2009).

^hde Waal & Berger (2000) and Hattori *et al.* (2005).

ⁱHauser *et al.* (2003).

^jCronin & Snowdon (2008).

^kWarneken & Tomasello (2006), Warneken *et al.* (2007) and Yamamoto *et al.* (2009).

^lBarnes *et al.* (2008).

Furthermore, the importance of maintaining a co-operative reputation and the opportunities for costly signalling predict that actors should be sensitive to the (perceived) presence and size of an audience (Trivers 1971; Smith & Bliege Bird 2005; DeScioli & Kurzban 2009; Earley 2010). Hence, an increase in either perceived need and/or perceived signalling opportunities (along the *x*-axis of figure 1) should lead to increased prosocial behaviour. Finally, the social distance to the recipient should function as a modifier of the prosocial response. Thus, all other things being equal (same *x*-value), close kin and reciprocating partners (friends) should elicit a higher prosocial response, because the average return benefit to the actor is greater.

4. IDENTIFYING PSYCHOLOGICAL RULES

In humans, the presence of prosocial behaviour in response to specific stimuli can be shown with so-called 'titration experiments', by keeping all other stimuli constant and only changing the one of interest. For instance, dictator games, in which a dictator can allocate any amount of received money to a potential recipient, can be played under varying conditions, e.g. including subtle cues of being watched (Haley & Fessler 2005; Rigdon *et al.* 2009). The increase in contribution when a dictator feels observed allows us to conclude that they are sensitive to having an audience, even though this sensitivity may be entirely subconscious.

A prosocial act in the absence of extrinsic stimuli may be called *proactive* prosociality (*b* in figure 1). This is more controversial, since the notion that all extrinsic stimuli can be excluded in controlled experiments can be questioned (e.g. Trivers 2006; Bardsley 2008). Thus, it may be safer to assume that experiments take place at 0' rather than 0 (figure 1), where extrinsic stimuli have been excluded or controlled for as much as possible, but some residual stimuli may remain. Hence, there may be a grey area where prosocial acts can be provoked by either a high intrinsic motivation and/or a very strong response to subtle stimuli (high *a* in figure 1). In particular, in the case of an audience, the awareness of the risk of detection may be so strong that actors respond

prosocially to subtle cues of being watched or just the *idea* of being watched. In this view, conscience thus functions to anticipate reactions by a potential audience (Trivers 1971; DeScioli & Kurzban 2009). Similarly, in the case of need, actors could respond to just the slightest signs of need in a potential recipient if their theory of mind capacities are well developed, or they could respond to the *idea* of the recipient being in need. If this is the case, many humans may never actually reach the 0 level, i.e. no experimental setting can exclude all social influences and make actors decide out of purely selfish considerations (Trivers 2006).

Among animals, and in particular non-human primates, similar experimental approaches have been followed. Provisioning experiments were often designed to reflect economic games played with humans, and have mainly focused on *proactive* prosociality. A fundamental constraint on them is that they cannot be played anonymously, but nonetheless, if prosocial behaviour occurs in the absence of or regardless of any measurable stimuli from the recipients, the plausible conclusion would be to infer a high intrinsic motivation (*b*) or a very high sensitivity to residual stimuli (*a*). Other experiments investigated prosocial acts in response to signs or signals of need, such as so-called targeted helping experiments. Table 1 gives an overview over the types of experiments we discuss below, as well as their main findings. In all these experiments, one should be aware of the risk of false positives or false negatives owing to possible confounding effects on the subjects' behaviour. This risk is especially high in experiments with low ecological validity, since they may not be understood by the subjects in the same way as conceived by the experimenters. Hence, one should examine the pattern of results as a whole, without over-emphasizing single studies, and validate them through consistency with the natural history.

Another line of evidence we therefore examine is naturally occurring food sharing. Defined as the tolerated transfer of food from A (the owner) to B (the recipient), food sharing is a common form of prosocial behaviour among primates (Feistner & McGrew 1989; Brown *et al.* 2004; Rapaport & Brown 2008). However, food sharing is clearly not homogeneous among

primates with respect to the underlying psychology. In most species, transfers are mainly passive, even among kin, while in others, food owners may actively promote transfers by ‘offering’ (Feistner & McGrew 1989), thus showing stronger prosocial dispositions. Here, we present a quantification of these ways in which food is transferred (figure 2; see electronic supplementary material, table S1, for operational definitions), focusing on the best-studied taxa: great apes, capuchins and callitrichids (see electronic supplementary material, table S2, for complete list of species). In particular, we will discuss food offering, i.e. transfers initiated by the owner in the absence of begging, as reflecting *proactive* prosociality and active sharing upon begging as reflecting *reactive* prosociality, in response to signals of need. Tolerated taking or *passive* sharing, the most common form of food sharing among primates (figure 2), is more ambiguous with regard to the underlying psychology since the lack of overt action could represent no prosocial response or an explicit absence of a negative response to the beggar. However, parsimony suggests that no overt action mostly reflects the absence of a psychological response.

5. EVIDENCE FOR PSYCHOLOGICAL RULES

This section summarizes empirical evidence for the proposed psychological rules underlying prosocial acts in humans and other primates. First, we examine reactive prosociality (§5*a*), in response to perceived need (§5*a*(i)) or audience (§5*a*(ii)) and as modified by social distance to the recipient (§5*a*(iii)). Then, we discuss the possibility of proactive prosociality (§5*b*), i.e. in the absence of extrinsic stimuli. In each subsection, we first present the evidence on (I) humans and then (II) on primates, as inferred from experimental evidence and food sharing. The primate evidence focuses on great apes as our closest living relatives, and in particular chimpanzees as the best-studied species, but other species, in particular capuchin monkeys and callitrichid monkeys, are mentioned throughout to illustrate parallels with humans.

(a) *Reactive prosociality*

(i) *Need*

(I) Humans routinely respond with prosocial acts to the need of the recipient as signalled by the latter, e.g. through an outstretched hand in a begging gesture and/or vocalizations, and start doing so at young ages (Eisenberg & Mussen 1989; Brownell *et al.* 2009). This is illustrated by the frequent reactive food sharing of young children (figure 2). The underlying motivation is probably empathy or sympathy (Trivers 1971; Eisenberg & Mussen 1989; Silk 2007; de Waal & Suchak 2010). Furthermore, even in the absence of explicit *signals* of need (in the form of a directed solicitation), an actor can respond to *signs* of need. For instance, if an individual is trying to reach an object, an actor may respond by retrieving and handing over the object (Warneken & Tomasello 2006). Note that the correct interpretation of such signs of need depends on the specific theory of mind

capacities particularly well developed in humans (Burkart *et al.* 2009), which may explain why in children helping is elicited faster and in a broader range of contexts than in chimpanzees (Warneken & Tomasello 2006; Warneken *et al.* 2007).

(II) Among great apes, and in particular chimpanzees, signals of need can be seen in solicitation of grooming (Pika & Mitani 2006), of agonistic support (de Waal 1982) or of food. Begging for food may sometimes elicit *reactive* sharing, but most often there is no overt response and food is shared passively (if at all), suggesting a low sensitivity to need (figure 2). Indeed, reactive sharing may often serve to get rid of the beggar, even the actor’s own offspring, by giving scraps while withholding more valuable food (Kuroda 1984; Bard 1992; Ueno & Matsuzawa 2004), thus reflecting selfishness rather than prosociality. However, among adults, and in particular chimpanzee males, reactive sharing is somewhat more common (figure 2) and may sometimes include large quantities of meat (Boesch & Boesch 1989; D. Watts 2009, personal communication), suggesting higher sharing motivation.

Great apes, especially chimpanzees, are known to have relatively well-developed theory of mind capacities (Call & Tomasello 2008) and could thus be expected to read and respond to recipient need. Yet, crucially, *signs* of need, such as approaching and peering at a food owner without begging hardly ever lead to sharing (Kuroda 1984; Jaeggi *et al.* 2008, 2010*b*), suggesting that explicit signals are required for a prosocial response.

We now turn to the experimental evidence. Begging did not induce food donation in provisioning games among chimpanzees (Silk *et al.* 2005; Jensen *et al.* 2006), which may reflect low sensitivity to these signals if they are not made in immediate proximity. However, helping behaviour in response to explicit signals of need has been reported for chimpanzees (Warneken & Tomasello 2006; Warneken *et al.* 2007; Yamamoto *et al.* 2009) and capuchin monkeys (Barnes *et al.* 2008) in targeted helping experiments (table 1). Crucially, signs of need such as struggling to solve a task (Yamamoto *et al.* 2009) or reaching for an object without calling the subject’s name (Warneken *et al.* 2007) mostly did not induce helping in chimpanzees, unless they were well enculturated by humans (Warneken & Tomasello 2006).

Cooperative breeders, such as callitrichids and social carnivores, may use signals of need in the form of specific begging calls that usually increase begging success (Kühme 1965; Feistner & McGrew 1989; Mech *et al.* 1999; Manser & Avey 2000; Brown *et al.* 2004). There is also good experimental evidence that the response to these vocalizations is adjusted to the beggar’s skill level (Thornton & McAuliffe 2006; Humle & Snowdon 2008). Signs of need (reaching) also did not induce a prosocial response in callitrichids (Burkart *et al.* 2007; Cronin *et al.* 2009). Thus, cooperative breeders generally show reactive prosociality to signals of need, but not to signs of need.

Taken together, the most striking result is not the response to signals of need, but rather its often reluctant nature or even absence in many species, in particular in the food-sharing context (figure 2 and

electronic supplementary material, table S2), as well as the unresponsiveness to *signs* of need. These findings and the fact that, at least among chimpanzees, theory of mind capacities is better developed in competitive rather than in cooperative situations (Hare & Tomasello 2004) suggest that in this species, prosocial responses to signals and signs of need have not been under the same positive selection as in humans, i.e. that the slope (a) in figure 1 is shallower.

(ii) *Audience*

(I) The (perceived) presence and size of an audience can increase prosocial behaviour among humans in natural situations (Smith & Bliege Bird 2005) as well as in various experiments, where subtle eye cues or actual audiences increased contributions in dictator games (Marlowe 2004; Haley & Fessler 2005; Rigdon *et al.* 2009), public goods games (Milinski *et al.* 2002; Bateson *et al.* 2006; Burnham & Hare 2007) and trust games (Fehr & Schneider 2010). This adjustment to a potential audience may be largely unconscious (cf. Bateson *et al.* 2006). Finally, the fact that some of the effects are entirely driven by men (e.g. Rigdon *et al.* 2009) may indicate costly signalling, while the response to more explicit reputation incentives (e.g. Fehr & Schneider 2010) may indicate a general concern for reputation.

(II) Among animals, sensitivity to the presence of an audience is expected when individuals have to maintain a cooperative reputation or advertise their own qualities in the face of considerable partner choice. While this has been nicely shown in fish (Bshary & Grutter 2006), only anecdotal observations suggest that chimpanzee males rising in rank may use food sharing to signal generosity to the whole group (de Waal 1982). The number of beggars positively affects the amount of food shared among chimpanzees and bonobos (Fruth & Hohmann 2002; Gilby 2006), but this has been interpreted as reflecting increased harassment rather than signalling generosity. So far, no controlled experiments have been done to investigate the role of an audience on prosocial behaviour.

A precondition for audience effects on cooperative behaviour is that the potential audience actually attends to interactions between others and uses this information to build reputations. There is much evidence that animals eavesdrop on others' interactions (e.g. Bshary & Grutter 2006), but among primates, eavesdropping mainly concerns dominance interactions (Bergman *et al.* 2003) or sexual behaviour (Crockford *et al.* 2007) rather than prosocial acts (see Earley 2010). Recent experiments have shown that chimpanzees, but not capuchins (Brosnan & de Waal 2009), can learn to distinguish between a prosocial and a selfish human experimenter (Russell *et al.* 2008; Subiaul *et al.* 2008), suggesting that the audience can build prosocial reputations. However, as noted above, no experiments have tested whether actors respond to a greater number of observers with more prosociality. Furthermore, there is hardly any evidence that non-cooperative behaviour is punished by others (Jensen 2010). Thus, more studies are

clearly needed to investigate audience effects in non-human primates in the context of prosociality.

(iii) *Social distance*

(I) In humans, all other things being equal, partners with whom the actor has a strong affiliative bond based on either kinship or friendship can elicit more prosocial acts than enemies or neutral persons (e.g. Birch & Billman 1986; Eisenberg & Mussen 1989; Majolo *et al.* 2006) and in-group members are favoured over out-group members (Goette *et al.* 2006; Fehr *et al.* 2008). There is also clear evidence that these prosocial acts are further influenced by the recent history of interactions, taking, e.g. indebtedness into account (e.g. Eisenberg & Mussen 1989). The underlying emotions here are probably feelings of gratitude or guilt (Trivers 1971), which can thus have short-term effects on perceived social distance.

(II) Many animals have some way of recognizing or preferentially interacting with their close kin if they have the opportunity to do so (Chapais 2006; Silk 2006). Furthermore, unrelated individuals in many species of primates form long-term social bonds, called friendships (Silk 2002), characterized by reciprocal exchange of grooming and other social commodities such as coalitionary support or food sharing (Brown *et al.* 2004; Schino 2007; Schino & Aureli 2008, 2009; Jaeggi & van Schaik in preparation). Hence, there is a clear preference among primates to direct prosocial acts to kin or reciprocating partners (friends). The recent history of interactions, i.e. indebtedness, may also sometimes be taken into account (e.g. de Waal 1997; de Waal 2000; Hemelrijk 1994).

Nonetheless, controlled experiments in which subjects were given a choice to act prosocially towards a relative, friend or a neutral partner were largely inconclusive. Chimpanzees did not provide more food to kin than to non-kin (Jensen *et al.* 2006; Yamamoto & Tanaka 2010) and neither did macaques (Schaub 1996). Only capuchin monkeys differentiated between kin, familiar and unfamiliar partners (de Waal *et al.* 2008). Thus, even though natural observations clearly indicate partner specificity in prosociality, as predicted by kin selection or reciprocity, many provisioning experiments surprisingly indicated a complete absence of prosociality. This may again indicate that prosocial acts among many primates, even to relatives or friends, need to be elicited by immediate and salient stimuli, such as continuous begging (cf. Yamamoto & Tanaka 2009b), which was not possible in these experiments. This notion is supported by the fact that among most primates virtually all food sharing, even with infants, is in response to begging (figure 2 and electronic supplementary material, table S2).

(b) *Proactive prosociality*

(I) Proactive sharing or helping occurs in experiments with human children (Birch & Billman 1986; Rao & Stewart 1999; Warneken & Tomasello 2006), but it is difficult to exclude possible signs or signals of need in these paradigms. In one-shot dictator games

in which anonymity and large social distance are ensured as much as possible and the need of the recipient is unknown, the average contributions are always above zero (although many players actually do give zero), indicating that at least a subset of individuals is prosocial in the absence of any stimuli (see Camerer 2003, table 2.3, for a compilation of various studies). These experiments thus lead to the conclusion that humans are at least occasionally motivated by other-regarding preferences (Camerer 2003).

(II) Among non-human primates, proactive prosociality can be seen in food offering, i.e. when food owners initiate sharing in the absence of begging or other signs of interest by the recipient (Feistner & McGrew 1989). Offering has been reported occasionally for a number of species (see figure 2 and electronic supplementary material, table S2, for species not in the figure). However, regular offering is only seen among callitrichids, where parents and helpers give specific food calls to invite transfers to the infants (figure 2). This indicates a strong motivation to share and suppression of own feeding motivations among callitrichids, which is further supported by the facts that preferred food is more likely to be offered (Feistner & Chamove 1986; Ferrari 1987), animals offer more when infants are out of sight (e.g. Ferrari 1987; contrary to capuchins: de Waal *et al.* 2008) and they offer food to other adults (Rapaport 2001) or even to infants of different species (Feistner & Price 1999). This strong sharing motivation among callitrichids is in line with the high motivation to carry infants (Hrdy 2009), despite the substantial cost associated with it (Schradin & Anzenberger 2001). Non-primate cooperative breeders may show similarly high motivations to help and share (Kühme 1965; Clutton-Brock *et al.* 2001).

Since proactive prosociality has been claimed for humans mainly on the basis of non-zero contributions in dictator games (Camerer 2003), similar games have been designed to test primates (see provisioning games in table 1). In chimpanzees, four studies did not find any evidence for proactive prosociality, even in mother–offspring dyads (Silk *et al.* 2005; Jensen *et al.* 2006; Vonk *et al.* 2008; Yamamoto & Tanaka 2010). In macaques, there was also hardly any evidence for prosociality in provisioning games (Mason & Hollis 1962; Colman *et al.* 1969; Schaub 1996). (A recent study did report provisioning from dominants to subordinates; Massen *et al.* 2010). However, it did not find sharing in the opposite direction, and the experimental set-up did not rule out the simpler explanation that dominants prefer to sit close to subordinates (e.g. so as to induce being groomed), whereas the latter avoid the former (to avoid aggression). Furthermore, generous behaviour by dominants is in stark contrast to the natural history of this despotic species, where most grooming is directed up the hierarchy (Schino & Aureli 2008) and food sharing is virtually absent (Jaeggi & van Schaik *in preparation*). Hence, the null model of no proactive prosociality is not convincingly rejected. In capuchin monkeys, mainly positive evidence has been reported (de Waal *et al.* 2008; Lakshminarayanan & Santos 2008; Takimoto *et al.* 2010). In callitrichids, some studies report positive

evidence for common marmosets (Burkart *et al.* 2007) and cotton-top tamarins (Hauser *et al.* 2003; Cronin *et al.* submitted), but others do not (Cronin *et al.* 2009; Stevens 2010). Because the positive evidence is less easily explained away and here is consistent with the natural history, the preliminary conclusion that callitrichids show proactive prosociality seems warranted.

A high intrinsic motivation to act prosocially may also be expressed in so-called unilateral cooperation games (table 1), in which only one of two individuals is rewarded for a task solved by both. In these games, cooperation tends to break down among chimpanzees (reviewed by Warneken & Tomasello 2009). Among capuchins, unilateral cooperation works if the role of recipient is alternated (de Waal & Berger 2000; Hattori *et al.* 2005), allowing for immediate reciprocation. Among tamarins, in contrast, it is sustained over long periods without alteration of rewards or signals of need (Cronin & Snowdon 2008). Thus, a high intrinsic prosocial motivation apparently allows them to keep cooperation going in the absence of immediate rewards.

6. DISCUSSION

(a) *Methodological issues*

Before drawing conclusions from the evidence reviewed above, it is important to eliminate potential confounding effects. In particular, we discuss the possibilities that primates may be more prosocial in non-food versus food tasks and that rearing and housing conditions may affect levels of prosociality.

Firstly, it has been suggested that prosociality is more pronounced in non-food contexts (e.g. de Waal *et al.* 2008; Warneken & Tomasello 2009; Yamamoto & Tanaka 2009b), perhaps owing to an obsession with food and the associated lack of inhibitory control in provisioning experiments. The evidence for non-food prosociality among chimpanzees includes targeted helping (table 1) as well as other contexts such as adoption of orphans (Boesch *et al.* 2010). However, in these contexts, prosociality is also mainly reactive, thus not contradicting the main findings here. Furthermore, tool sharing by great ape mothers, a non-food context, seems to be equally reactive as food sharing, happening virtually only upon request by the infant (Hirata & Celli 2003; Lonsdorf 2006; Sanz *et al.* *in preparation*; cf. figure 2). Hence, the psychological regulation of prosociality seems similar in food or non-food contexts.

Secondly, rearing and housing conditions may affect subjects' performance in experiments (Boesch 2007). For instance, the degree of enculturation, through hand-rearing or daily interactions with animal keepers, is likely to affect subjects' psychology. In particular, since many prosociality paradigms reflect typical human interactions, sometimes with little ecological validity for the primates, enculturated individuals are more likely to grasp the idea of the paradigm. For instance, the subjects of Warneken *et al.* (2007) were housed in the chimpanzee sanctuary of Ngamba Island, where the chimpanzees receive their daily food in bowls, which they have to actively *hand* to the keepers. This may well have influenced

Table 2. Summary of the main findings regarding the proximate regulation of prosocial acts in the best-studied species. ++, Regular in experimental and natural context; +, regular in at least one context; --, absent in both contexts; (-), possibly absent but no controlled experiments (cf. table 1, figure 2 and text).

rule	humans	chimpanzees	capuchins	callitrichids	evolutionary status
need ^a	++ (signs and signals) ^b	+ (signals)	+ (signals)	+ (signals)	homologous
audience ^c	++	(-)	(-)	(-)	uniquely derived
social distance ^d	++	+	++	+	homologous
proactive ^e	++	-	+	++	convergence

^aDo actors adjust prosociality to the perceived need of the recipient?

^bSigns of need by the recipient, such as reaching for an object or struggling with a task, are not directed at the actor and probably require some theory of mind capacities to be correctly read; signals of need, such as begging or calling, on the other hand, are explicitly directed at the actor and evolved in a form most successful at eliciting a response.

^cDo actors adjust prosociality to the perceived presence and size of an audience?

^dDo actors adjust prosociality to the social distance to the recipient?

^eDo prosocial acts occur in the absence of obvious extrinsic stimuli, thus reflecting a high intrinsic prosocial motivation?

their performance in a very similar experiment in which they had to retrieve an object and hand it to a human experimenter (Warneken *et al.* 2007). This is not to say that the experimental results are flawed, but they may reflect the species' *potential* rather than species-typical behaviour. Thus, if enculturated chimpanzees can learn to be more prosocial, the conditions under which this is the case may help explain how our own species came to evolve in this direction, but it need not necessarily inform us about chimpanzee-typical prosociality.

(b) *Reconstructing the evolution of human prosociality*

Despite these uncertainties, some general conclusions about similarities and differences in the psychological regulation of prosociality in the best-studied species can be drawn. These are summarized in table 2. We infer the presence of three components with different evolutionary histories: one shared with other apes, especially chimpanzees, a second acquired owing to the adoption of cooperative breeding and probably shared with other cooperative breeders, and a third one acquired uniquely owing to living in large, fission–fusion societies with high interdependence among individuals.

Humans are both regularly proactively prosocial, thus reflecting a high intrinsic prosocial motivation, and highly responsive to extrinsic stimuli. Chimpanzees, in contrast, are hardly ever proactively prosocial and their reactive prosociality generally depends on salient and immediate signals of need, such as continuous solicitations (cf. Yamamoto & Tanaka 2009b). This agrees with the notion that chimpanzee cooperation among adults mainly rests on direct reciprocity, which is clearly indicated by the presence of long-term social bonds (friendships; Silk 2002) within which favours are exchanged symmetrically (e.g. Watts 2002; Mitani 2006) and by the low average relatedness within these cooperative relationships (Langergraber *et al.* 2007, 2009). Hence, chimpanzees are a good example for both the scope and limits of cooperation based on direct reciprocity. The establishment of long-term friendships and the corresponding attachment allows chimpanzees to engage in various forms of cooperation such as cooperative hunting

(Boesch & Boesch 1989; Boesch 1994), agonistic support (e.g. Watts 2002; Mitani 2006) and collective warfare (Manson & Wrangham 1991). Thus, prosocial acts are particularly common among males, who profit most from cooperation (Boesch & Boesch 1989; Nishida *et al.* 1992; Watts 2002). On the other hand, cooperation is subject to opportunistic fluctuations (de Waal 1982; Gilby *et al.* 2009) and in experiments has difficulty getting started (Brosnan & Beran 2009; Brosnan *et al.* 2009; Yamamoto & Tanaka 2009a) or tends to break down in the absence of immediate rewards (reviewed by Warneken & Tomasello 2009) or explicit solicitations (Yamamoto & Tanaka 2009b). These difficulties of experimental reciprocity may further indicate that reciprocity among chimpanzees (and indeed most animals) is mainly symmetry-based rather than calculated (Brosnan & de Waal 2002), i.e. prosocial acts are averaged out on a long-term basis mediated by affiliative emotions rather than exchanged contingently in a tit-for-tat manner requiring substantial cognitive effort (Stevens & Hauser 2004; see discussion by Brosnan *et al.* 2010). While it is parsimonious to assume that human ancestors shared these aspects of cooperation based on direct reciprocity with chimpanzees, humans seem to have acquired several derived features, some of which may have evolved convergently with other taxa. These derived features combined to make human cooperation more stable relative to chimpanzees.

The regular proactive element of human prosociality almost certainly shared with callitrichids suggests that a high intrinsic prosocial motivation evolved convergently in cooperative breeders, probably because of the risk of neglect of unattended offspring (Hrdy 2009; Burkart & van Schaik 2010), and the need for active provisioning to maintain fast growth levels (Brown *et al.* 2004; Gurven & Hill 2009). This proactive element could also explain why teaching is more common among cooperative breeders (Rapaport 2006; Rapaport & Brown 2008; Burkart & van Schaik 2010), whereas great apes often do not take advantage of low-cost opportunities to teach (Hirata & Celli 2003; Lonsdorf 2006; Jaeggi *et al.* 2010a; Sanz *et al.* in preparation). Furthermore, the adoption of cooperative breeding typically leads to the formation of family units, within which prosocial acts are dispensed more freely because they generally benefit

close kin or pair-bonded partners (Chapais 2008; Hrdy 2009; Burkart & van Schaik 2010). Thus, a high intrinsic prosocial motivation would not be counterselected if applied within the family. Finally, within human societies, kin networks extend far beyond the family unit (Chapais 2008), and even when applied to non-relatives, a high prosocial motivation may be beneficial if it sends a costly signal or serves to maintain one's good reputation (see below).

Capuchin monkeys may, on the face of it, not fit this picture. One could argue that the more stable group composition relative to chimpanzees, as well as increased paternity concentration and female philopatry (Fragaszy et al. 2004) could have led to more stable reciprocal relationships and higher average relatedness, thus favouring prosocial motivations. However, the same is true for most macaques, probably without increasing prosociality. Another explanation could be that capuchins also evolved higher prosocial motivations, because they, like many New World monkeys, engage in allo-maternal care, such as infant carrying and regular food sharing from males to infants (Fragaszy et al. 2004). At the moment, no other convincing hypotheses exist for the taxonomic distribution of the components of prosociality among primates.

Finally, humans seem to have acquired a strong sensitivity to the (perceived) presence and size of an audience. There are two explanations for this. Firstly, the potentially high costs imposed on cheaters in a society of interdependent individuals (Boehm 1999; Gurven 2004; Kaplan et al. 2009; Marlowe 2009), which we have internalized as 'conscience', functioning to anticipate others' reactions (Trivers 1971; DeScioli & Kurzban 2009), have led to an increase in prosocial behaviour in the presence of subtle cues of being watched. Secondly, individuals (mainly men) may send costly signals in the presence of large audiences, thus advertising themselves as valuable cooperation partners or mates (Smith & Bliege Bird 2005). This new sensitivity to being watched and to the size of the audience may lead to strong reactive prosociality, in the presence of subtle extrinsic stimuli (0'), or even to proactive prosociality, if the conscience effectively internalized the possibility that extrinsic stimuli are present (0). Finally, the recent rise of anonymous market societies with their need for larger scale cooperation may have further modified psychology (Henrich et al. 2010).

In conclusion, we note that humans differ from their closest living relatives, the great apes, in two key aspects of the psychological regulation of cooperation: humans are *proactive*, i.e. they act prosocially in the absence of obvious extrinsic stimuli, and more *reactive*, i.e. they respond more strongly to extrinsic stimuli and to a wider range of such stimuli. Thus, the parameters *a* (response to extrinsic stimuli) and *b* (intrinsic motivation) in figure 1 differ between humans and great apes, indicating that prosociality has been under stronger positive selection during human evolution.

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