Reciprocity in group-living animals: partner control *versus* partner choice

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ABSTRACT

Reciprocity is probably the most debated of the evolutionary explanations for cooperation. Part of the confusion surrounding this debate stems from a failure to note that two different processes can underlie reciprocity: partner control and partner choice. We suggest that the common observation that group-living animals direct their cooperative behaviours preferentially to those individuals from which they receive most cooperation is to be interpreted as the result of the sum of the two separate processes of partner control and partner choice. We review evidence that partner choice is the prevalent process in primates and propose explanations for this pattern.

We make predictions that highlight the need for studies that separate the effects of partner control and partner choice in a broader variety of group-living taxa.

Key words: cooperation, reciprocity, partner control, partner choice, proximate mechanisms.

CONTENTS

I. INTRODUCTION

In the endless debate about reciprocity, an aspect that is often neglected is the need to distinguish between the two different processes that can underlie reciprocal exchanges of cooperative behaviours (Noë & Voelkl, 2013). The first study to distinguish these two processes was probably Bull & Rice (1991; see Eshel & Cavalli-Sforza, 1982 for an earlier insight), that named them 'partner fidelity' (later called 'partner control' by Noë, 2006) and 'partner choice'. In partner-control models (e.g. Axelrod & Hamilton, 1981) dyads of interacting individuals are conceptually isolated from other dyads and the behaviour of each subject depends only on the previous behaviour of the partner. As there is no possibility of switching partner, individuals must try to control the behaviour of the partner by rewarding cooperation and sanctioning uncooperative behaviour. In partner-choice models (e.g. Campennì & Schino, 2014) individuals choose their partners on the basis of the benefits they offer, and the need to sanction uncooperative partners is replaced by partner switching and outbidding competition. Partner choice features pre-eminently in biological market models, and proponents of biological market theory have repeatedly emphasized the distinctiveness of the two processes (Noë & Hammerstein, 1994, 1995; Noë, 2006). Empirical tests of biological market theory have however tended to focus on market effects, rather than on distinguishing and separating the effects of partner control and partner choice (e.g. Henzi & Barrett, 2002; Fruteau *et al.*, 2009).

In our opinion, the failure to distinguish and separate the two processes of partner control and partner choice has hampered empirical research and biased recognition of the presence of reciprocity, especially among group-living animals. Herein, we discuss why distinguishing the two processes is important, review the (few) attempts to quantify their relative prevalence, and make predictions about their distribution in nature.

II. THE CONSEQUENCES OF NOT DISTINGUISHING

A common assumption of research on reciprocity is that the only way actually to demonstrate reciprocity is to show the existence of a temporal contingency between the receipt of cooperation and the giving of cooperation (and/or between failure to receive cooperation and subsequent retaliation) (Hauser *et al.*, 2003; Silk, 2003). This assumption implicitly equates reciprocity with partner control and, given the relative rarity of convincing examples of true temporal contingencies between giving and receiving cooperative acts, it leads to the conclusion that reciprocity must be rare (e.g. Stevens, Cushman & Hauser, 2005; see Cheney *et al.*, 2010, and Olendorf, Getty & Scribner, 2004 for two examples of temporal contingencies studies). In fact, temporal contingencies between giving and receiving only test for partner control, and say nothing about partner choice (Carter, 2014). Thus, the emphasis on temporal contingencies, and the failure to note that they are predicted by partner control only, caused a widespread underestimation of the prevalence of reciprocity.

While empiricists focused on partner control (although apparently implying that the results apply to all forms of reciprocity), theoreticians began producing models of the evolution of cooperation by partner choice (Sherratt & Roberts, 1998; Aktipis, 2004; McNamara *et al.*, 2008; Castro & Toro, 2010; Campennì & Schino, 2014; see McNamara & Leimar, 2010 for a review on the role of variation in promoting the evolution of cooperation, especially by partner choice). It is now abundantly clear that partner choice can indeed promote the evolution of cooperation. Furthermore, theoretical models have shown that partner choice can also lead to patterns of reciprocal exchange similar to those observed in animals (see Section VII for details). Notwithstanding this new emphasis on partner choice, the contrast between the easiness with which cooperation evolves in a variety of partner-control models and the difficulties of showing empirical evidence for these models has led some authors to hypothesize that proximate constraints may limit the evolvability of reciprocity (thus again implicitly extrapolating from partner control to all forms of reciprocity; Stevens & Hauser, 2004).

A corollary of the neglect of partner choice is that evidence that animals direct their cooperative acts preferentially to those individuals from which they receive most cooperation is dismissed as showing ‘only a correlation’ (Silk, 2013). Such evidence however is (in stark contrast to the limited evidence about temporal contingencies) truly overwhelming, so that we believe it should not be dismissed lightly.

III. ACROSS-DYAD CORRELATIONS BETWEEN GIVING AND RECEIVING

One of the oldest ways of assessing the relations between giving and receiving cooperation is to carry out a correlation across dyads between cooperation given and cooperation received. Regardless of the statistical technique employed [matrix correlations or some variation of generalized linear mixed models (GLMMs)] these analyses enter dyadic values of cooperation given (i.e. cooperation given by each subject to each other subject) as the dependent variable and dyadic values of cooperation received as one of the independent variables. Kinship and/or other potential confounding factors are usually added as additional independent variables. Typically, dyadic values are calculated on the basis of a relatively long observation period (e.g. grooming rates averaged across several months of observation).

In addition to many empirical studies (e.g. Silk, 1992; Watts, 2002; Carne, Wiper & Semple, 2011), three meta-analyses have addressed the relationship between giving and receiving cooperative behaviour in primates. These meta-analyses summarized studies conducted on dozens of different primate species and hundreds of different individuals. Schino (2007; also including a single temporal relations study) assessed the relationship between grooming and agonistic support; Schino & Aureli (2008) examined the relationship between giving and receiving grooming; Jaeggi & Gurven (2013; including data on humans) investigated the relationships between grooming and food sharing and between giving and receiving food. All three of these studies found significant positive weighted average correlations across dyads between giving and receiving cooperative acts. Overall, the results of these meta-analyses provide extremely robust and convincing evidence for reciprocal exchanges in primates. Note, however, that they are silent as to the underlying processes.

Across-dyad positive correlations between cooperation given and received are not limited to primates. Recent studies have broadened the phylogenetic scope of such analyses and have obtained similar results in several other species, including jackdaws (*Corvus monedula*) that exchange food and interchange food for allopreening (De Kort, Emery & Clayton, 2006), coatis (*Nasua nasua*) that exchange agonistic support (Romero & Aureli, 2008), spotted hyenas (*Crocuta crocuta*) that interchange communal defence at carcasses for tolerance while feeding (Smith, Memenis & Holekamp, 2007), rooks (*Corvus frugileus*) that exchange food and interchange food for allopreening and agonistic support (Scheid, Schmidt & Noë, 2008), ravens (*Corvus corax*) that exchange agonistic support and interchange allopreening for support (Fraser & Bugnyar, 2012), and vampire bats (*Desmodus rotundus*) that exchange regurgitated blood and interchange blood for allogrooming (Carter & Wilkinson, 2013).

Overall, evidence that group-living animals (including humans) direct most of their cooperative acts towards those individuals from which they receive most cooperative acts seems unassailable. It is clear that we need an interpretation for such a common phenomenon.

IV. THE MEANING OF ACROSS-DYAD CORRELATIONS

We propose that across-dyad correlations between cooperative acts given and received are the result of the sum of the two separate processes of partner control and partner choice. Due to the nature of these dyadic data, no information is available on the temporal relationships between single cooperative events. In principle, it is possible to imagine two extremes of a continuum. At one end of the continuum, a significant positive dyadic correlation can result from a tight temporal relationship between giving and receiving (each act of giving is immediately returned). At the other end of the continuum, it can derive from interindividual preferences based on a comparison of the overall amount of cooperation received from each group member, in the complete absence of a temporal relationship between giving and receiving (see Section VII and Campennì & Schino, 2014, for a model showing that when partner choice is based on a comparison of the amount of cooperation received from group members, across-dyad correlations between cooperation given and received emerge). The first extreme of the continuum would correspond to strict partner control in the absence of partner choice; the other extreme would correspond to partner choice in the absence of partner control. As already noted, real animals probably use a mixture of the two strategies and the across-dyad correlations we observe empirically thus reflect the sum of these two processes.

It follows from the above reasoning that across-dyad correlations do provide evidence for reciprocity, but they do not tell us anything about the relative contributions of the two processes. The paucity of convincing evidence of partner control together with the abundance of across-dyad correlations between cooperative acts given and received suggest that partner choice may be the prevalent process, but we have relatively little quantitative evidence from studies that compare the two processes. Below, we review this evidence.

V. TRYING TO DISTINGUISH

A few studies have tried to estimate the relative contributions of partner control and partner choice in the same species and setting by evaluating both the temporal relationships between individual cooperative events and the across-dyad correlations between overall cooperation given and received. Schino, Ventura & Troisi (2003) and Schino, Polizzi di Sorrentino & Tiddi (2007) observed no short-term temporal relations between giving and receiving grooming or between grooming and agonistic support in Japanese macaques (*Macaca fuscata*). At the same time, macaques showed strong positive across-dyad correlations between grooming given and received and between grooming and support. Tiddi *et al.* (2011) observed no short-term temporal relationship between grooming and tolerance over a clumped food resource coupled with strong across-dyad correlations in wild tufted capuchin monkeys (*Cebus apella*). Kaburu & Newton-Fisher (2015) observed no short-term exchange of grooming for sexual access together with a positive across-dyad relationship between male mating success and grooming by males to females in a community of wild chimpanzees (*Pan troglodytes*) characterized by egalitarian dominance relationships. Jaeggi, Stevens & Van Schaik (2010) and Jaeggi *et al.* (2013) observed no short-term temporal relationship between grooming and food sharing in chimpanzees, while long-term food sharing given was best predicted by food sharing received. In bonobos (*Pan paniscus*) food sharing increased the short-term exchange of grooming and was also, in the long-term, best predicted by relationship quality (Jaeggi *et al*., 2010, 2013). Finally, Carter & Wilkinson (2013) conducted a fasting experiment in vampire bats. They found that, within dyads, blood given in a particular trial was not predicted by blood received in the previous trial. At the same time, blood given was strongly correlated with blood received across dyads.

In all these studies (with the possible exception of the bonobo studies of Jaeggi *et al*. (2010, 2013) partner control appeared to exert weak or no effect on cooperative behaviours (see Table 1 for details regarding the time windows used to test for immediate reciprocation) and our interpretation is therefore that the positive across-dyad correlations have to be ascribed (almost) entirely to partner choice.

Other studies used refined statistical techniques to identify (and then remove) the effects of partner control. Schino, Di Giuseppe & Visalberghi (2009), Schino & Pellegrini (2009) and Campennì *et al.* (2015) used survival analysis to identify the time window over which having received grooming increased the probability of returning grooming to the same partner, thus obtaining an objective (i.e. data-driven) estimate of immediate reciprocation (Table 1). These studies revealed significant short-term temporal relationships between giving and receiving grooming (i.e. animals showed an increased probability of immediately returning grooming, compared to their baseline). However, only 7–35% of the grooming episodes were immediately reciprocated, showing that temporal relationships between events played a limited role in guiding animal decisions about cooperation. When all the cases of immediate reciprocation were excluded from analysis (thus removing any effect of partner control), across-dyad correlations remained significant, again showing an important effect of partner choice (Schino *et al.*, 2009; Schino & Pellegrini, 2009; Campennì *et al.*, 2015). Gomes & Boesch (2009) reported similar results on exchanges of meat for sexual access in wild chimpanzees. Note also that, although it is obviously possible that an act of cooperation received can sometimes affect the likelihood of returning cooperation past the measured time window, this effect is likely to be small. It is clear that any partner-control effect of cooperation received must decrease monotonically with time, so that the magnitude of this effect after it is no longer operationally measurable must be negligible.

Applying new methods of network dynamics, Hooper *et al.* (2013) tested ‘stationary’ (i.e. long-term) and ‘dynamic’ (i.e. short-term) reciprocity in the exchange of manioc beer among Tsimane horticulturalists. They found robust long-term reciprocity, while short-term reciprocity only applied to socially distant partners.

Fruteau *et al.* (2011) found little evidence for two specific partner-control strategies (‘parcelling’ and ‘raise the stake’) in the grooming exchanges of wild mangabeys (*Cercocebus atys*) and vervet monkeys (*Chlorocebus aethiops*). Finally, Sabbatini *et al.* (2012) conducted a food-sharing experiment on tufted capuchin monkeys in which animals were tested in triads or in dyads. In triadic tests, partner choice exerted a stronger effect than partner control (effect sizes r=0.289 and r=0.194, respectively; unpublished data from Sabbatini *et al.* 2012). Interestingly, partner control appeared to play a reduced role in triadic compared to dyadic tests. This suggests a causal role for the possibility of partner choice in reducing the scope of partner control. Bshary & Grutter (2002) similarly reported that in a cleaner fish mutualism (*Labroides dimidiatus* with clients *Ctenochaetus striatus*), increased possibilities of partner choice were associated with reduced partner control.

Overall, the available evidence shows that partner choice is the prevailing process whenever both processes have been studied simultaneously.

VI. THE PROXIMATE MECHANISMS UNDERLYING RECIPROCITY

Before drawing conclusions from the evidence reviewed above, we will discuss briefly the proximate mechanisms underlying reciprocity. This topic is traditionally neglected; most authors that do discuss proximate mechanisms adopt (rather uncritically) the classification proposed by Brosnan & de Waal (2002). Below, we build on the work of Brosnan & de Waal (2002) and propose three hypothetical proximate mechanisms for reciprocity that overcome some of the difficulties encountered by their original formulation. Proximate mechanisms can be thought of as evolved answers to recurrent problems, and can therefore be expected to implement adaptive responses appropriate to the costs and benefits of the situation. The three mechanisms we discuss below are therefore likely to have evolved under different social and ecological conditions.

(1) Hard-wired reciprocity

This mechanism replaces Brosnan & de Waal's (2002) symmetry-based reciprocity that, in its original formulation, cannot be evolutionarily stable (M. Campennì & G. Schino, in preparation). Hard-wired reciprocity can be hypothesized to evolve whenever reciprocity is needed in one-shot interactions (i.e. interactions that are unlikely to be repeated). The animal responds 'instinctively' to the receipt of a cooperative act by immediately returning it. This mechanism is characterized by short delays between receiving and giving and by a one-to-one relationship in the currencies exchanged (one kind of cooperation is always exchanged with the same other kind of cooperation). It requires neither individual recognition, nor stable social relationships, and is likely to be found in cognitively unsophisticated animals (e.g. egg trading in simultaneous hermaphrodites; Fischer, 1980; Sella, 1985) or in animals that do not form stable social groups [e.g. grooming in impalas (*Aepyceros melampus*); Connor, 1995]. It is inherently a partner-control mechanism, although, in a biological market perspective, it can be conceived to allow some flexibility in exchange rates in relation to the conditions of the market place.

(2) Emotionally based reciprocity

To the extent that emotions can be conceived as task-specific computational mechanisms (LeDoux, 2012; Cosmides & Tooby, 2013), it is possible to hypothesize that a system of ‘emotional bookkeeping’ (Schino & Aureli, 2009) evolved to support reciprocity in group-living animals, i.e. under conditions of continuous social interaction with individually recognizable group mates.

Our formulation of emotionally based reciprocity is derived from Brosnan & de Waal's (2002) attitudinal reciprocity, but acts over a longer time frame. Through this mechanism, cooperation received triggers partner-specific positive emotions that promote subsequent cooperation. What motivates an animal to engage in emotionally based cooperation is the social attachment that it has developed with group companions (social attachment that itself depends also on the receipt of cooperative behaviours). Emotions thus constitute a bookkeeping system that can act over relatively long time frames and allow easy and flexible conversion among multiple currencies (Schino & Aureli, 2009). Emotionally based reciprocity requires the formation of differentiated social relationships that guide social decision-making, but no special cognitive abilities are otherwise needed. The formation of differential social relationships (from strong social bonds to simple cohabitation) is inherently a partner-choice mechanism that promotes outbidding competition (Campennì & Schino, 2014). In humans emotions associated with cooperative exchanges (e.g. anger or gratitude) presumably play a role also as a partner-control mechanism (van't Wout *et al*., 2006; McCullough, Kimeldorf & Cohen, 2008). We know very little about the short-term emotional consequences of cooperation in animals. In primates, displacement activities have been proposed as a measure of anxiety-like emotions (Maestripieri *et al*., 1992; Schino *et al*., 1996) and used to gauge the emotional consequences of receiving grooming. Overall, rather inconsistent results have been obtained (Schino *et al.*, 1988; Radford, 2012; Molesti & Majolo, 2013; Semple, Harrison & Lehmann, 2013).

(3) Calculated reciprocity

Calculated reciprocity can be hypothesized to evolve as a response to the need to be able to engage in reciprocal exchanges in rare and or/novel situations and/or when interacting with unfamiliar individuals. Alternatively, it can be conceived as a by-product of selection for the general ability to plan future actions.

An animal that engages in calculated reciprocity is supposed to be motivated by the expectation of a future return benefit (the reciprocated cooperation). Calculated reciprocity thus requires advanced cognitive abilities such as the capacity to plan social interactions or some form of ‘future thinking’. Note that, unlike Brosnan & de Waal's (2002) original formulation, we propose the defining characteristic of calculated reciprocity should not be the reliance on some computation of costs and benefits but the role played by expected benefits as the key motivating factor. This also allows calculated reciprocity to be empirically distinguished from emotionally based reciprocity (Schino & Pellegrini, 2011). Calculated reciprocity is likely to be rare outside humans (see Section VIII). It can in principle underlie both partner-control and partner-choice processes.

VII. MODELLING RECIPROCITY IN GROUP-LIVING ANIMALS

Most theoretical studies of cooperation and reciprocity focus on modelling their evolution rather than on attempting to reproduce existing patterns of exchanges of cooperative acts as observed in group-living animals (see Section II for partner-choice models and Bshary & Bronstein, 2011, for a review and classification of partner-control models). A few recent theoretical studies have used agent-based simulations to model and reproduce empirically observed patterns of social interactions. In these models, artificial agents (that may or may not be set in space) exchange positive or negative interactions based on their past experiences and/or on their spatial proximity with other agents. These models may be relevant for understanding the proximate mechanisms underlying reciprocity and its emergence from animal decision rules.

Puga-Gonzalez, Hildenbrandt & Hemelrijk (2009) and Puga-Gonzalez, Hoscheid & Hemelrijk (2015) have shown that across-dyad correlations between cooperative acts given and received can emerge as a consequence of the spatial structuring of agents. When ‘social bonds’ (in the form of a tendency to follow specific individuals) were added to these models, the pattern of reciprocity strengthened. Evers *et al.* (2014, 2015) modelled the emotional consequences of affiliation and fear, and showed that individual-specific emotional states can generate patterns of reciprocity consistent with a mechanism of emotional bookkeeping.

Although the aim of these models was only to reproduce existing patterns of reciprocal cooperation in animals, one could argue for the necessity to test also whether the strategies implemented in the agents were evolutionarily robust, i.e. if they competed successfully against other (notably, selfish) strategies. M. Campennì &

G. Schino (in preparation) found that when cooperative acts are based on interindividual proximity, reciprocal patterns of exchange emerge (thus confirming the results of Puga-Gonzalez *et al.*, 2015). Nevertheless, such a strategy was unsuccessful in an evolutionary test in which it had to compete against selfish agents that never cooperated. Generally speaking, any strategy that does not include a mechanism that controls or excludes cheaters is likely to be evolutionarily unsuccessful.

Campennì & Schino (2014) implemented the same strategy of partner choice based on benefits received in both a ‘single-generation’ and an evolutionary model. In their model, agents choose to cooperate with those partners from which they had received the most cooperation. They showed that a strategy of pure partner choice can both reproduce emergent patterns of reciprocal exchange (i.e. across-dyads correlations) and compete successfully against selfish agents in an evolutionary test. Note that in this model agents were obligate cooperators, and there was therefore no possibility of partner control. This study provided theoretical (simulation-based) support for a role of partner choice in the evolution and maintenance of reciprocal cooperation in group-living animals.

Agent-based models appear to be a promising tool for understanding the emergence of reciprocity, but they need to incorporate both tests aimed at reproducing existing patterns of behaviour as observed in real animals and tests aimed at evaluating the evolutionary plausibility of the implemented strategies.

VIII. INFERENCES AND PREDICTIONS

Two inferences can be drawn tentatively from the available evidence. First, if one accepts that across-dyad correlations between cooperative acts given and received do provide useful insight, then one must conclude that reciprocity is indeed common, at least in group-living animals. This is in sharp contrast to some commonly held opinions (Stevens *et al.*, 2005, Clutton-Brock, 2009). Second, partner choice seems to play a larger role than partner control in guiding animal decisions about cooperation. This is again in contrast to common (often implicit) assumptions.

Our focus herein is on the second of these conclusions, and thus we should ask the following questions: is this to be considered a conclusion of general applicability or is it in some way taxonomically restricted? Are there conditions or animal taxa where partner control can instead be expected to prevail?

Noë & Voelkl (2013) suggested that partner choice should prevail in one-shot interactions, while when animals engage in longer-term relationships progressively larger amounts of partner control should become apparent. We note, however, that in group-living animals (that are likely to have long-lasting relationships) the costs of partner sampling and partner switching are greatly reduced, a factor that should favour partner choice and thus promote cooperation through outbidding competition (Johnstone & Bshary, 2008). Also, stable social relationships facilitate emotionally based reciprocity that, in turn, makes partner choice an easy option for a variety of animals.

With a single exception (Carter & Wilkinson, 2013), all studies that tried to compare partner control and partner choice in the same species and setting have been conducted on primates, most concluding that partner choice is the prevalent process (see Section V). Thus, there is an urgent need for similar studies in other taxa. Group-living primate and non-primate species share two important aspects that make us suggest that partner choice may be the prevalent process across taxa. First, positive across-dyad correlations between cooperative acts given and received are common in various taxa (Section III). Second, long-term social bonds have important fitness consequences in group-living primate and non-primate species (Silk, 2007; Silk *et al.*, 2010; Cameron, Setsaas & Linklater, 2009; Frère *et al.*, 2010), suggesting that the formation of differentiated social relationships has been subject to positive selection in a variety of taxa. Long-term differentiated social relationships and emotionally based reciprocity are closely linked, and similar mechanisms of emotionally based partner choice may have been favoured by natural selection whenever animals capable of interindividual recognition came to live in permanent groups (Schino & Aureli, 2009).

By contrast, animals that do not form long-term social relationships must necessarily rely on hard-wired reciprocity for their cooperative exchanges. Under these conditions, short-term reciprocation based on partner-control processes is likely to be the prevalent process, unless it is possible and inexpensive to 'sample' different potential partners before the actual cooperative exchange takes place.

We offer two possible explanations for why partner control is comparatively rare among group-living animals, both based on an assessment of the proximate mechanisms likely to underlie reciprocity. The first explanation is that partner control may require immediate reciprocation and thus be limited in scope. Stevens & Hauser (2004) identified several possible cognitive constraints (limited memory, limited computational ability, temporal discounting) that may limit the ability of animals to engage in reciprocal cooperation. We have argued elsewhere (Schino & Aureli, 2009; see also Carter, 2014) that these proximate constraints can be easily sidestepped by a proximate mechanism based on emotional bookkeeping. Emotional bookkeeping, however, is essentially a partner-choice mechanism, and the only way to overcome the cognitive constraints identified by Stevens & Hauser (2004) in a partner-control process would be for reciprocity to be always immediate (possibly through hard-wired reciprocity).

Although immediate reciprocation does exist (e.g. immediate grooming reciprocity in primates; Barrett *et al.*, 1999), its scope is clearly limited to those cases in which the exchanged currencies are simultaneously available and needed. For example, exchanges of grooming and agonistic support can only occur when support is needed, so that a tight temporal relationship reduces dramatically the possibility of exchange. Accordingly, reciprocal exchanges of grooming and support appear to occur on a much longer time frame that involves partner choice based on overall grooming/support received rather than short-term temporal relationships between events (Schino *et al.*, 2007).

The second explanation for why partner control is relatively rare among group-living animals is that partner control may alternatively require some form of ‘planning’ of social interactions and thus be taxonomically restricted to species with advanced cognitive capacities. Partner control may occur when cooperation is proximately motivated by the expectation of a return benefit (i.e. calculated reciprocity). We are aware of only a few studies of non-human animals whose results can be interpreted as a test of calculated reciprocity (as defined above). Dufour *et al.* (2009) reported that a single pair of orang-utan (*Pongo pygmaeus*) exchanged tokens that were valuable only for the partner showing turn taking and signalling. This suggested giving was associated with the expectation that the partner returned the favour. Pelé *et al*. (2009) tested a larger number of apes in a similar setting, and did not observe systematic exchanges that could be interpreted as motivated by the expectation of a return benefit. Similarly, Pelé *et al.* (2010) did not observe systematic exchanges of tokens in tufted capuchin monkeys or Tonkean macaques (*Macaca* *tonkeana*). In a more naturalistic study, Schino & Pellegrini (2011) showed that female mandrills (*Mandrillus sphinx*) did not groom the alpha male immediately before attacking another group member (even if the male was more likely to provide support immediately after grooming), thus suggesting that the expectation to receive support did not motivate the females to groom the male. Interestingly, Sebastian-Enesco & Warneken (2015) recently showed that 5-year-old, but not 3-year-old children adjusted their sharing of a toy in anticipation of future reciprocation, thus highlighting the late development of calculated reciprocity (see also House *et al.*, 2013, for comparable results on the development of contingent reciprocity). They also suggested that the mechanisms necessary for partner choice may develop in children earlier than those necessary for partner control. Overall, we argue that partner control may be relatively rare because it is restricted either in scope (being limited to those cases where immediate reciprocation is possible) or taxonomically (being limited to humans and possibly a few other species capable of calculated reciprocity).

IX. CONCLUSIONS

(1) Distinguishing between partner-control and partner-choice processes allows a better understanding of the importance of reciprocal cooperation in animals. The available evidence seems to suggest that partner choice is the prevalent process underlying reciprocity in group-living animals. This conclusion, however, is drawn from a taxonomically biased sample of observational studies including almost only nonhuman primates.

(2) Three priorities emerge for future research. First, we need studies that quantify simultaneously partner control and partner choice in a broader variety of taxa, in order to assess the generality of our conclusions. Second, we need studies that

experimentally manipulate the occurrence of reciprocation in order to assess if and how this manipulation differentially affects parter control and partner choice. Third, we need studies that experimentally manipulate the possibility of partner control and partner choice in order to assess how one process is affected by the presence/absence of the other. Fulfilling these three needs will require the joint effort of researchers with disparate backgrounds and expertise.

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Table 1. Assumed and measured time windows for immediate reciprocation in studies of reciprocity.

Species	**Assumed/measured**	**Duration**	**Reference**
Cebus apella	Assumed	About 1 min	Sabbatini *et al.* (2012)
Cebus nigritus	Assumed	2 h	Tiddi *et al.* (2011)
Cecrocebus atys and *Chlorocebus aethiops*	Assumed	30 and 20 s, respectively	Fruteau *et al.* (2011)
Desmodus rotundus	Assumed	Unclear (about 2 weeks)	Carter & Wilkinson (2013)
Macaca fuscata	Assumed	1 min	Schino *et al.* (2003)
Macaca fuscata	Assumed	30 min	Schino *et al.* (2007)
Pan paniscus and *P. troglodytes*	Assumed	1 h	Jaeggi *et al.* (2013)
Pan troglodytes	Assumed	30 s	Kaburu & Newton-Fisher (2015)
Callithrix jaccus	Measured	2 min	Campennì *et al.* (2015)
Cebus apella	Measured	7 min	Schino *et al.* (2009)
Homo sapiens	Measured	3 days	Hooper *et al.* (2013)
Mandrillus sphinx	Measured	4.5 min	Schino & Pellegrini (2009)