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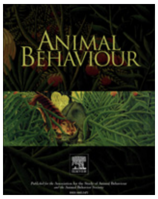

The relative prevalence of direct, indirect and generalized reciprocity in macaque grooming exchanges

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Reciprocation is thought to favour altruism among nonrelatives. Three types of reciprocity have been proposed: direct, indirect and generalized. All three are theoretically possible, but their role in real biological systems is unclear. We concurrently examined the occurrence of direct, indirect and generalized reciprocity during grooming exchanges in longtailed macaques, *Macaca fascicularis*. The occurrence of the grooming monkey A gave B predicted the latency and occurrence of the grooming B gave back to A (direct reciprocity), the latency of the grooming A received from C (indirect reciprocity), but not the grooming B gave C (generalized reciprocity). The duration of the grooming monkey A gave B predicted the latency and occurrence of the grooming B gave back to A (direct reciprocity) but not the grooming A received from C (indirect reciprocity) or the grooming B gave C (generalized reciprocity). Finally, monkeys directed overall more of their grooming to those individuals that overall groomed them more (direct reciprocity), but not to those that groomed other individuals more (indirect reciprocity); nor did monkeys that received overall more grooming groom others more (generalized reciprocity). Overall, we found strong evidence for direct reciprocity, limited support for indirect reciprocity and no evidence for generalized reciprocity. Our results support the view that direct reciprocity plays a crucial role in the life of primates and suggest indirect and generalized reciprocity are rare or absent in nonhuman animals. We argue that direct reciprocity may be driven by a system of partner-specific emotional bookkeeping of past social interactions that does not require complex cognitive capacities.

Kin selection and mutualism are two key mechanisms favouring the evolution of cooperation, that is, of behaviours benefiting other individuals (West et al. 2007a; Clutton-Brock 2009). Behaviours having lifetime fitness costs for the actor and benefits for the recipient are labelled altruistic and generally explained by kin selection. When costs and benefits are measured over shorter timescales, usage of the term 'altruism' is more controversial (West et al. 2007b). Regardless of semantic issues, an influential explanation for the evolution of short-term (i.e. not lifetime) altruism (hereafter simply altruism for brevity) is reciprocity. Altruistic interactions between nonrelatives have puzzled scientists since Darwin, as altruistic individuals risk performing a costly behaviour without receiving any benefit. Through reciprocal exchange, however, donors and recipients of the altruistic act balance benefits and costs over time, and altruism can become an evolutionarily stable strategy among nongenetically related individuals (Trivers 1971; Axelrod & Hamilton 1981). Nevertheless, while the role of kin selection in explaining the evolution of (lifetime) altruism has been essentially unchallenged (for a recent debate see Nowak et al. 2010; Boomsma et al. 2011), the role of reciprocity in explaining (shorter-term) altruism is still debated. Some authors have emphasized the paucity of convincing evidence and the likelihood of alternative explanations (e.g. Stevens & Hauser 2004; Clutton-Brock 2009; Russell & Wright 2009). Others have taken an opposite stance, arguing that reciprocity is in fact common (Schino & Aureli 2009, 2010).

Three main types of reciprocity have been proposed. Direct reciprocity is based on a tit-for-tat exchange of benefits whereby the recipient of an altruistic act is more likely to reciprocate the benefit to the former donor than to any other individual, or to cheat (i.e. by not giving any benefit). Evidence for direct reciprocity comes from studies on various species and behaviours, including defence against predators, food exchange, grooming and agonistic support (de Waal 1997; Olendorf et al. 2004; Rutte & Taborsky 2008; Schino et al. 2008; Cheney et al. 2010). Direct reciprocity has been shown to

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occur over both short (e.g. Cheney et al. 2010) and long time frames (e.g. Tiddi et al. 2011; however, in no case have benefits and costs been measured over the lifetime). More recently two additional types of reciprocity have been proposed. Indirect, or reputation, reciprocity (Nowak & Sigmund 1998) predicts that acting altruistically increases the donor's reputation and thus his or her chances of receiving an altruistic behaviour from a third individual (i.e. not the former recipient). Various studies on humans confirm the occurrence of indirect reciprocity (e.g. Wedekind & Milinski 2000). Conversely, there is mixed evidence that indirect reciprocity occurs in animals, two examples being parasite removal by cleaner fish, *Labroides dimidiatus* (Bshary & Grutter 2006; Pinto et al. 2011) and aggressive responses of song sparrows, *Melospiza melodia*, to territory intrusion (Akçay et al. 2010). Generalized reciprocity (Hamilton & Taborsky 2005; also referred to as upstream indirect reciprocity, Nowak & Roch 2007) predicts that individuals who have received an altruistic behaviour are more likely to act altruistically towards any individual, including the former donor. As such, generalized reciprocity incorporates direct reciprocity in its original definition (Hamilton & Taborsky 2005). So far, generalized reciprocity has been demonstrated in humans (Berkowitz & Daniels 1964; Bartlett & de Steno 2006) and laboratory rats, *Rattus norvegicus* (Rutte & Taborsky 2007). Generalized reciprocity is thought to be less cognitively demanding than direct and indirect reciprocity, as it does not require individual recognition, keeping track of the actions of others, or a scoring system to assess reputation or to select the best reciprocators (Stevens & Hauser 2004).

The occurrence of direct, indirect and generalized reciprocity is not mutually exclusive, and all three types of reciprocity have been shown to be theoretically plausible. Knowledge of their relative prevalence in real biological systems is thus crucial to understand the evolution of altruism and the cognitive and social constraints that the three types of reciprocity pose on animals. Our study aimed at concurrently examining the occurrence of direct, indirect and generalized reciprocity by analysing allogrooming (hereafter grooming) interactions in captive group-living longtailed macaques, *Macaca fascicularis*. To our knowledge this is the first study to analyse the relative prevalence of direct, indirect and generalized reciprocity. Grooming is considered an altruistic behaviour as it imposes various costs on the donor (Cheney & Seyfarth 1982; Dunbar 1991; Maestripieri, 1993; Scantlebury et al. 2007) and provides benefits for the recipient (Cheney & Seyfarth 1982; Schino et al. 1988; Keverne et al. 1989; Scantlebury et al. 2007). Macaques form stable mixed-sex groups and can interact repeatedly with their group companions. Moreover, in captivity all social partners are potentially available within close distance to one another. Therefore, our study setting and animals met the conditions for the three types of reciprocity to occur (Trivers 1971).

Tiddi et al. (2011) distinguished two general mechanisms that could account for the decision-making process underlying reciprocity: temporal relation between events and partner choice based on benefits received. Although originally conceived to apply to direct reciprocity, these two general mechanisms can also be applied to indirect reciprocity (where partner choice would be based on benefits received by others). Generalized reciprocity can be based on temporal relations between events but, by definition, does not allow partner choice. The emotional bookkeeping process that is hypothesized to underlie partner choice in direct and indirect reciprocity (Schino & Aureli 2009) would, for generalized reciprocity, simply make animals that receive overall more altruism also give overall more altruism.

Here we aimed at testing direct, indirect and generalized reciprocity exploring both of these mechanisms. We first focused on the temporal relation between events. If direct reciprocity plays a role in grooming interactions, we expect the occurrence and duration of the grooming monkey A gave B to be a predictor of the latency, occurrence and duration of the grooming B gave back to A. If indirect reciprocity plays a role, we expect similar effects of the grooming from A to B on the grooming A received from C. If generalized reciprocity plays a role, we expect similar effects of the grooming from A to B on the grooming B gave C. Second, we aimed at assessing partner choice based on benefits received by analysing dyadic scores of grooming regardless of the time frame of reciprocation. Direct reciprocity predicts that monkeys should direct more of their grooming to those individuals from which they receive more grooming. Indirect reciprocity predicts that monkeys should direct more grooming to those individuals that groom other individuals more. Generalized reciprocity does not allow partner choice, and predicts that monkeys that receive more grooming (from anybody) should also give more grooming (to anybody).

METHODS

Subjects and Housing

Subjects of this study belonged to a well-established group of longtailed macaques housed in an indoor–outdoor enclosure. During the observation the group had access only to the outdoor enclosure of approximately 75 m^2. At the time of the study, the group consisted of 31 monkeys: four adult males, 10 adult females, six juvenile males (i.e. <4 years old), six juvenile females (i.e. <3 years old) and five infants (three males and two females). The monkeys were fed, with fruit, vegetables and pellets, twice a day at 0900 and 1730 hours and water was available ad libitum. Shelters and ropes were available in the enclosure as enrichment devices. This study was approved by the University of Utrecht's Ethics Committee.

Data Collection

Data were collected between June and August 1989. Focal animals were two adult males (rank positions 1 and 8, respectively) and three adult females (rank positions 2, 16 and 23, respectively). To analyse the occurrence of the three types of reciprocity over a long time frame (see below) each focal animal was the subject of five 5 h continuous focal sessions (Martin & Bateson 1993). This resulted in 25 h of focal data on each of the five subjects. We collected one 5 h focal session per day, starting between 1000 and 1130 hours to avoid feeding times (see above). A minimum of 1 week passed between two focal sessions collected on the same monkey.

During focal sessions we collected data on all the occurrences of grooming interactions (defined as careful picking and/or slow brushing aside the fur of a partner with one or both hands; only grooming bouts lasting at least 10 s were considered) between the focal animal and any other adult or juvenile monkey in the group, recording the timing and the duration of the grooming interaction, the identity of the other monkey involved and any role switching (e.g. from groomer to groomee). We also recorded the time interval between two grooming interactions involving the focal animal to analyse the latency of each type of reciprocation. We determined the dominance hierarchy based on ad libitum data on dyadic agonistic interactions (i.e. threat, chase, bite, submission) with a clear winner–loser outcome. No rank reversal was observed during the study.

Data Analysis

The term 'reciprocation' is used here to refer to events of reciprocated grooming (Fig. 1), and 'reciprocity' is used to refer to