

# Direct reciprocity in animals: The roles of bonding and affective processes

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The presence of direct reciprocity in animals is a debated topic, because, despite its evolutionary plausibility, it is believed to be uncommon. Some authors claim that stable reciprocal exchanges require sophisticated cognition which has acted as a constraint on its evolution across species. In contrast, a more recent trend of research has focused on the possibility that direct reciprocity occurs within long-term bonds and relies on simple as well as more complex affective mechanisms such as emotional book-keeping, rudimentary and higher forms of empathy, and inequity aversion, among others. First, we present evidence supporting the occurrence of long-term reciprocity in the context of existing bonds in social birds and mammals. Second, we discuss the evidence for affective responses which, modulated by bonding, may underlie altruistic behaviours in different species. We conclude that the mechanisms that may underlie reciprocal exchanges are diverse, and that some act in interaction with bonding processes. From simple associative learning in social contexts, through emotional contagion and behavioural mimicry, to empathy and a sense of fairness, widespread and diverse social affective mechanisms may explain why direct reciprocity may not be a rare phenomenon among social vertebrates.

**Keywords:** Prosociality; Direct reciprocity; Empathy; Fairness; Inequity aversion; Bonding; Oxytocin.

Direct reciprocity involves the sequential performance of costly behaviours that produce benefits to the interacting individuals (we here do not deal with negative—vengeful—reciprocity; Carter, 2014). This phenomenon can be distinguished from others such as indirect and generalised reciprocity: direct reciprocity is involved when A acts beneficially towards B after B benefited A; indirect reciprocity when A benefits B after knowing that B acted beneficially towards C; and generalised reciprocity when A benefited B after C benefited A (Carter, 2014). In this article, we focus on direct reciprocity only, and we discuss some of the proximal mechanisms that may underlie it.

The obstacle for direct reciprocity to become evolutionarily stable is that altruistic behaviours (costly voluntary acts that benefit others—by “costs” we mean short-term fitness costs, not life-time net fitness costs) risk being exploited by cheaters or noncooperators. The

delay between delivering a benefit to another agent and this agent’s reciprocation opens up the door to the possibility of the latter taking the benefit without reciprocating the favour received (Hauser, McAuliffe, & Blake, 2009). Despite these difficulties, some conditions may facilitate the stability of reciprocal exchanges. For instance, a prospect for repeated encounters could make nonreciprocation a less attractive alternative. This is so because mutual cooperation may provide a higher payoff when accumulated in the long run (Seyfarth & Cheney, 2012). In addition, the ability to discriminate cooperative types may allow reciprocal agents to direct their altruism in a conditional manner, thus protecting themselves from exploitation by noncooperators (Yamamoto & Takimoto, 2012).

Direct reciprocity is generally accepted to be common among people (Brosnan & de Waal, 2014; Carter, 2014). In contrast, many authors maintain that direct

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reciprocity is a rare phenomenon in the animal kingdom (e.g. Clutton-Brock, 2009; Hauser et al., 2009). On one hand, reports of direct reciprocity in non-human animals have been usually challenged on grounds of alternative explanations, such as altruism directed towards kin, interactions that produce immediate mutual benefits or situations that involve coercion, among others (see Clutton-Brock, 2009). Associated with this scepticism for animal reciprocity, it is the view that direct reciprocity relies on sophisticated cognitive abilities. Some authors claim that the delay between the altruistic act and its reciprocation requires an ability to recognise partners' identity, skill with numbers to maintain strict counting of favours given and received, as well as, inhibitory control to restrain oneself from exploiting others and spoil future cooperation (Hauser et al., 2009). Even more, providing benefits conditionally on others' past behaviour may need an adequate memory to track others' reputation and an ability to update it based on direct and indirect interactions (Hauser et al., 2009). On this view, direct reciprocity is seen as a deeply calculated affair, and, some authors think that such demanding calculations could have limited its presence across species (e.g. Clutton-Brock, 2009; Hauser et al., 2009). In this sense, a particular mechanistic hypothesis about direct reciprocity (i.e. calculated reciprocity) has reinforced the view that animal reciprocity may be a rare phenomenon.

The scepticism about animal reciprocity has, nonetheless, not been homogeneously held in the academic community (e.g. see Schino & Aureli, 2009 and Carter, 2014 for views that contrast with those of Clutton-Brock, 2009 and Hauser et al., 2009). Many authors have posited alternative mechanisms through which direct reciprocity could be sustained, and have claimed to find instances of direct reciprocity in birds and mammals, going from rats through monkeys to apes (see Carter, 2014 for a review). Indeed, many findings provide support, not so much for calculated reciprocity, but instead for a more emotionally based type of altruism (Carter, 2014; Schino & Aureli, 2009).

Many social animals establish long-term bonds within which reciprocal exchanges seemingly occur (e.g. see Schino & Aureli, 2009; Seyfarth & Cheney, 2012). In contrast to the idea of cognitive constraints on reciprocity, evolution could have shaped animals' motivations and affective responses, inclining them to engage in long-term reciprocal interactions. In this sense and contrary to the view of reciprocity as a calculated affair, direct reciprocity may not necessarily require sophisticated cognition but may rely on affective mechanisms that help to establish and regulate bonding (Schino & Aureli, 2009). These motivational processes could range in complexity from simple associative learning in social contexts, through reflexive emotional responses, such as emotional contagion and behavioural mimicry, to other-regarding

preferences, such as empathic concern and a sense of fairness (Yamamoto & Takimoto, 2012).

In short, affective mechanisms may contribute to the stability of direct reciprocity by helping to build partnerships and social bonds that protect altruistic tendencies from exploitation by selfish individuals.

In this article, we focus on the case of animal reciprocity in the context of affective bonds and relationships beyond the short term. We aim at presenting current debates on the comparative psychology of the affective mechanisms of direct reciprocity and we analyse the evidence for the modulation of these processes within bonds. The present discussion of relevant literature does not attempt to be exhaustive. For limits of space and references, we count on selected examples with a focus on the latest influential research, and also rely on other authors' reviews of related topics (and thus do not cite seminal papers if not strictly needed). Our attempt is to clarify the reach of the empirical studies cited, and to show and suggest promising avenues for future research on the topic of the affective processes underlying direct reciprocity.

The rest of the manuscript is structured as follows. In the next section, called *Reciprocity in Long-term Bonds*, we mention some of the evidence for reciprocity based on stable bonds in different species, as a nonexclusive alternative to the hypothesis of calculated reciprocity which dominated the literature in the last decade. In the following section, called *Affective Processes Modulated by Bonding*, we analyse and critically discuss the evidence for different affective responses which may help regulating altruism in the context of long-term relationships. Finally, we close with a section in which we conclude that an array of diverse mechanisms, some simple and widely present across species, others more complex and thus not as pervasive, may contribute to sustaining direct reciprocity in animals. In particular, we discuss the potential role of associative learning processes in bonding and reciprocity.

## RECIPROCITY IN LONG-TERM BONDS

Among the requirements for demonstrations of direct reciprocity, the contingent exchange of altruistic behaviours between reciprocators has been at the centre of the debate (see Clutton-Brock, 2009 and Carter, 2014 for different views). On one perspective, proof of direct reciprocity demands a short-term association between reciprocators' altruism. That is the logic underlying Tit-for-Tat (Carter, 2014). In this sense, as proof of reciprocity, some authors expect to find a short-term causal chain between an animal's altruistic behaviour and its partner reciprocation (e.g. Clutton-Brock, 2009; Hauser et al., 2009). On a contrasting view, other authors pose that favours may balance out on the long run (e.g. Carter, 2014), which is particularly sensible for long-term

relationships such as what we call friendship in humans (Seyfarth & Cheney, 2012). Indeed, long-term bonds satisfy the conditions that facilitate the stability of direct reciprocity, such as repeated encounters and conditional cooperation (Schino & Aureli, 2009).

The view of direct reciprocity as a rare cognitively demanding phenomenon was dominant in the last decade, but has receded after the recognition of animals' altruistic exchanges under field conditions and new evidence for alternative hypotheses about its underlying mechanisms. Along this line, reciprocal exchanges have been postulated to be based on affective mechanisms more than in a calculated assessment of favours given and received (see Schino & Aureli, 2009, for a review of long-term reciprocal exchanges in primates). Several examples illustrate this.

For instance, Sabbatini, De Bortoli Vizioli, Visalbergui, and Schino (2012) evaluated capuchin monkeys (*Cebus apella*) in triads and found that subjects chose who to interact with based on existing long-term bonds more than on recent food transfers among them. Schino and Aureli (2009) reviewed other studies of direct reciprocity within long-term bonds in primates. In the case of non-primates, there are suggestive cases of reciprocity in vampire bats and different bird species (Carter, 2014). The case of bats (*Desmodus rotundus*) is interesting because they commonly share meals in nature. Successful foragers regurgitate blood to feed individuals that were less successful on that day (Carter & Wilkinson, 2013). This behaviour was also studied in controlled conditions in captivity. Carter and Wilkinson (2013) found that donors approached a fasted bat, and that the food donated was better explained by the history of prior exchanges between them than by kinship. Moreover, sharing dyads showed allogrooming patterns that were consistent across long periods of time, suggesting an important role of bonding in their reciprocal altruistic behaviours.

The effect of long-term bonding on reciprocal exchanges of different currencies has been studied not only for appetitive behaviours, such as food sharing or grooming, but also for behaviours related to agonistic support. In a field study with macaques, *Macaca sylvanus*, the formation of coalitions in the reproductive season could be predicted by their bonds weeks before, suggesting that these primates cooperate in risky situations based on previously established relationships (Berghänel, Ostner, Schröder, & Schülke, 2011). Similar results have been found in a study with ravens (*Corvus corax*) in captivity (Fraser & Bugnyar, 2012). The authors recorded episodes of agonistic support and found that, besides kinship and dominance, ravens were more likely to support those that had provided agonistic support to them and preened them within the previous week. In this sense, Fraser and Bugnyar (2012) concluded that agonistic support was dependent on reciprocation within bonds more than in a short-term tit-for-tat strategy.

In synthesis, the idea that direct reciprocity may occur and be stabilised in the context of long-term bonds has attracted attention in recent years, has received empirical support in different species, and has been established as a complementary, presumably, more general (than calculated reciprocity) basis for reciprocity in the animal kingdom. These affiliative processes may in turn modulate other socio-cognitive mechanisms such as different forms of empathy and perceptions of fairness (Yamamoto & Takimoto, 2012), which may also play a role in reciprocal exchanges, as we discuss in the next section.

## AFFECTIVE PROCESSES MODULATED BY BONDING

In this section, we first discuss recent research on emotional contagion, vicarious learning, behavioural mimicry and empathic concern, as mechanisms that could underlie altruism within social bonds (see Cronin, 2012, for a recent analysis of the effect of bonding on prosociality—a concept related to altruistic behaviour, but without assumptions about costs-, especially in non-human primates). And second, we end with a critical discussion of experimental research on inequity aversion (IA) as a mechanism presumed to aid partner selection and contribute to the stability of bonds. Other relevant processes that may be modulated by bonds, such as, for example, communication and consolation behaviours, are not discussed in this review for a matter of space.

### From emotional contagion through vicarious learning to empathic concern

The concept of empathy has been associated with a broad spectrum of psychological phenomena, from the experience of emotions that match and are triggered by another's emotions, going through recognition of other's thinking and feeling, to empathic concern which may induce helping behaviours (see Panksepp & Panksepp, 2013 for a review about cross-species research on empathy).

It has been hypothesised that rudimentary and more complex forms of empathy evolved in the context of parental care and pair bonding and later expanded to affect other relationships. Indeed, authors argue that advanced forms of empathy are preceded by and grow out of more elementary ones (Panksepp & Panksepp, 2013). From a proximal perspective, the affective attunement of individuals may aid the recognition of others' needs, which, under certain circumstances, may incline individuals towards altruism (e.g. see Schneeberger, Dietz, & Taborsky, 2012). This mechanism on its own would, however, not be evolutionarily stable because nonreciprocating unempathetic individuals would be able to exploit it

in others. Accordingly, emotional contagion and different forms of empathy may be modulated by the bonding relationship between individuals, suggesting that animals are not unconditionally altruistic.

### **Emotional contagion and behavioural mimicry**

Emotional contagion is a psychological phenomenon in which the perception of an affective behavioural change automatically activates the same process in another individual (Panksepp & Panksepp, 2013). The most common example of emotional contagion in humans is infectious crying among babies (*Homo sapiens*), whereas yawning represents another paradigmatic contagious behaviour (see Palagi, Norscia, & Demuru, 2014). Indeed, contagious yawning has been shown in primates, including bonobos (*Pan paniscus*) and humans, and has been found to occur more frequently between individuals with a close social bond (e.g. Palagi et al., 2014), which is consistent with the idea of the social modulation of empathy-related abilities.

A phenomenon related to behavioural contagion, behavioural mimicry, not only occurs within pre-existing bonds but may also modulate these bonds. For instance, capuchin monkeys were exposed to two persons, one who imitated them and the other who performed contingent actions without imitation (Paukner, Suomi, Visalberghi, & Ferrari, 2009). The authors found that several of the monkeys' behaviours (looking, approaching, exchanging tokens and spending time in proximity) were preferentially directed towards the imitator and/or away from the non-imitator, suggesting a change in the monkeys' preferences after being exposed to them. Similar phenomena have been reported in humans. For instance, nonconscious mimicry in adults increased prosociality from the mimicked person (van Baaren, Holland, Kawakami, & van Knippenberg, 2004).

Vicarious learning may rely on contagious experiences as well (Panksepp & Panksepp, 2013). Many researchers studied this phenomenon using aversive conditioning in rodents. In this type of protocol, an observer watches a target individual receive a shock after the presentation of a conditioned stimulus (CS) or in a specific context. Then, when tested in the presence of the CS or in the corresponding context, the observer typically shows learned fear responses, despite having never experienced shocks in those circumstances. In agreement with results from contagious and mimicked behaviour, empathetic pain can be modulated by the pre-existing relationship between social partners (see Panksepp & Panksepp, 2013). This has led researchers to wonder whether emotional contagion, vicarious learning and other potential empathetic experiences may lead animals to act altruistically (e.g. Chang, Barter, Becket Ebitz, Watson, & Platt, 2012), as we discuss in the next subsection.

### **Empathic concern**

Empathy can be understood as the ability to recognise and share others' feelings (Panksepp & Panksepp, 2013; Singer, 2008). Demonstrations of empathy in non-human animals are debated and controversial; therefore, its existence beyond humans is not agreed (see Edgar, Nicol, Clark, & Paul, 2012 for a review and discussion of methodological issues associated with evaluating empathy in nonverbal animals). Nonetheless, some authors believe that empathy for other's distress could be a source of altruistic actions (e.g. Yamamoto & Takimoto, 2012) and have attempted to show that in animals.

Bartal, Decety, and Mason (2011) investigated whether rats showed any concern for others' welfare. In their study, pairs of rats that lived in the same cage for a few weeks before the experiment (intended to enhance their familiarity) were then tested in a rescue task. One of the rats (the trapped rat) was placed in a restraining tube, and its cage mate (the free rat) could apply a force to the restraining apparatus to open it. Indeed, free rats opened the door more frequently in the experimental than in control conditions.

The authors claimed that these findings provided evidence for a behaviour motivated by an empathic concern (Bartal et al., 2011). Nevertheless, this interpretation has been criticised on different fronts. First, similar rescue behaviour in ants (*Cataglyphis cursor*) suggests that other explanations may need to be discarded first before confidently referring to rats' behaviour as empathic (Vasconcelos, Hollis, Nowbahari, & Kacelnik, 2012). For example, rats' liberating behaviour could be simply explained by the reinforcing effect of terminating stress signals from the trapped companion (Edgar et al., 2012; Panksepp & Panksepp, 2013). Second, Bartal et al.'s (2011) findings could involve post-rescue social reinforcement associated with social contact. In fact, Silberberg et al. (2014) could not replicate Bartal et al.'s findings when they controlled for this. In their study, when the rats had not learned how to free their cage mates, they did not acquire this behaviour in a condition in which social contact was not possible (Silberberg et al., 2014). This last result suggests that a motivation for social contact may have been the main drive underlying rats' altruism.

Despite the inconclusive results of Bartal et al.'s study, other evidence points in the direction for a role of empathy-related abilities in reciprocity. Schneeberger et al. (2012) investigated whether reciprocal cooperation between unrelated Norway rats (*Rattus norvegicus*) could be modulated by the relative need of the recipient. These authors systematically varied the hunger status of the recipient rat in a generalised reciprocity paradigm. In their main treatment, the focal rat received food from an unknown trained rat, and then she had to choose whether to pull a tray to provide food for another rat (the recipient). Among other results, Schneeberger et al. found that

focal rats gave more food to lighter than heavier receivers in the food deprived condition, showing that rats were able to recognise the need state of social partners and to accommodate their altruistic helping accordingly. These results do not directly speak of the effect of empathy on direct reciprocity, but show that rats' altruism was sensitive to the recipients need state, thus suggesting a role of empathy-related capabilities on reciprocal behaviours.

To finish this subsection, we conclude that the empirical support for emotional contagion, mimicry, vicarious learning and empathic concern in animals is not homogeneous. Simple forms of shared emotionality, such as contagion and mimicry, play affiliative roles, and thus help building a context in which altruistic exchanges could thrive. More complex forms of empathy are yet to be confirmed in non-humans, but they surely play important roles in human altruism (Singer, 2008). All in all, sensitivity to others' emotional states, as a factor leading to altruism, needs to be somehow constrained so that the empathetic animal avoids being exploited by cheaters. Consistent with this view, empathy-related abilities are seemingly regulated by affiliation and bonding between individuals (Panksepp & Panksepp, 2013; Singer, 2008; Yamamoto & Takimoto, 2012).

In the next subsection, we discuss IA as another affective process that may be involved in regulating partnerships and altruism.

### Fairness and IA

IA refers to the disutility or negative emotion caused by an outcome for the agent being unequal than an outcome for other individuals in a comparable situation (see Brosnan & de Waal, 2014). As it is the case with empathy-related abilities, there is ample debate about whether non-human animals may possess some form of IA. A major part of the debate relates to experimental designs lacking appropriate controls or methodological rigour to discard alternative hypotheses (Bräuer, Call, & Tomasello, 2009). Despite this, some authors argue that non-human IA could have evolved in the context of cooperation given that a negative response to being undertreated may help the individual to stay away from non-profitable partnerships (Yamamoto & Takimoto, 2012).

One of the most used protocols to study IA in non-human animals consists of a task in which two individuals take turns (e.g. exchange tokens for food with the experimenter) and, while the partner is rewarded for its performance, the subject receives a higher or a lower reward or even no reward at all after its performance instead. Under these conditions, experimenters assess whether the subject shows signs of negative emotions, such as rejection to participate in the task or to consume its own food, given the inequality in rewards between the subject and its partner (e.g. see Brosnan, Schiff, & de Waal, 2005; Range, Leitner, & Virányi, 2012). Despite

the fact that there are no empirical studies that directly relate IA with bond-based reciprocity in non-humans, preliminary observations suggest that IA might be modulated by bonding.

In the rest of this subsection, we focused on discussing the two studies which provide evidence for the effect of bonding on IA using variations of the protocol mentioned above. It is important to have in mind although, that other non-human studies, despite finding evidence consistent with IA, have failed to find any modulation of subjects' behaviour by the relationship quality (see Brosnan & de Waal, 2014).

### IA and relationship quality

In the first of the two studies to be discussed here, Brosnan et al. (2005) evaluated IA using the token-exchange task with chimpanzees, *Pan troglodytes*. These researchers found that refusals to exchange were significantly higher in the inequity than in the equity condition, and that, importantly, IA was much stronger in animals from colonies that had a shorter history of cohabitation. The authors interpreted this last finding as a possible effect of the relationship quality on IA: the longer the bond, the lesser the IA (Brosnan et al., 2005), a result similar to that observed in humans (Clark & Grote, 2003). However, these results in chimps need to be taken with caution because years of coresidence appear to be a very crude measure of relationship quality (see also Bräuer et al., 2009, for methodological criticism on how IA was assessed). As Range et al. (2012) recognised, long acquaintances do not necessarily imply tolerant and affiliative relationships. In addition, Brosnan et al. inferred the relationship quality effect from the comparison of individuals from only three different colonies, which probably differed in many aspects besides years of cohabitation.

The effect of relationship quality on IA was also assessed in dogs that lived in the same home. Range et al. (2012) observed IA when subjects had to give their paw for no reward, while their partner was rewarded for the same performance (in this condition, dogs underperformed compared to when both dogs were not rewarded for giving the paw). By asking the owners about the relationship quality between their pets (e.g. whether they slept in body contact), the authors found that subjects with a more affiliative bond needed significantly more requests from the experimenter to give the paw in the inequity condition than dogs with a more distant relationship. Surprisingly, the effect of the relationship quality on dogs' IA was in the opposite direction to that suggested by Brosnan et al.'s (2005) results in chimps, and also to results in humans (Clark & Grote, 2003). This discrepancy suggests that different methodological aspects, such as, for example, the operational definition of "relation

quality” or “bond,” may become crucial in evaluating this phenomenon. Certainly, data are still scarce to allow satisfactory conclusions, and thus, further research is needed to clarify these matters.

To finish this section, and going beyond the difficulties in reaching strong conclusions about animals’ IA, we have shown that the potential modulation of IA by a pre-existing relationship has not been a reliable finding in terms neither of replicability (see Brosnan et al., 2005, and Bräuer et al., 2009 in chimps) nor of the sign of the effect (see Brosnan et al., 2005, and Range et al., 2012, in chimps and dogs, respectively). Despite this, the preliminary results discussed above present us with a promising avenue of research on how long-term bonds may affect the expression of reciprocal behaviour which should be deepened in the future.

## DISCUSSION

In this article, we discussed recent evidence in favour of the idea that some forms of animal reciprocity rely on stable social bonds. In accordance with this view, the search for direct reciprocity has been expanded from short-term contingent interactions to longer-term exchanges (Berghänel et al., 2011; Carter & Wilkinson, 2013; Fraser & Bugnyar, 2012; Sabbatini et al., 2012). This affective-based reciprocity contrasts with a more calculated type which has been posed to be cognitively demanding and uncommon outside humans. Indeed, this change in focus has led authors to explore the mechanisms underlying the formation and stability of social bonds (e.g. Yamamoto & Takimoto, 2012) and has stimulated the study of direct reciprocity in a larger group of species (Carter, 2014).

Bonding, even outside reproductive mates and kinship, has been shown to increase evolutionary fitness (Seyfarth & Cheney, 2012). Consistently, diverse mechanisms have been shown to underlie bonding and altruism in animals. These mechanisms vary in their nature and complexity, going, for example, from reflexive contagion and behavioural mimicry (e.g. Palagi et al., 2014) to prosocial behaviours based on recognition of others’ emotions and a concern for their welfare (e.g. Singer, 2008). Some authors even claim that animals may display IA, which may serve to avoid exploitative partnerships (Brosnan & de Waal, 2014; Yamamoto & Takimoto, 2012). According to our review of the literature, whereas the evidence for the modulation of empathy-related abilities by prior bonding is widespread (e.g. Palagi et al., 2014; Panksepp & Panksepp, 2013), support for the relationship between bonding and IA is still scarce and inconsistent in non-humans (see Brosnan et al., 2005; Range et al., 2012).

Associative learning processes can also be important mechanisms in the social life of animals. Nonetheless,

authors rarely deepen into associative learning when searching for the mechanisms involved in the origin and formation of bonds. Stable bonds are typically assessed by considering animals’ interaction patterns and their stable preferences for interacting with an individual over other members of the group. These preferences are usually measured as the frequency or the duration of interactions between animals (e.g. Berghänel et al., 2011; Fraser & Bugnyar, 2012; Sabbatini et al., 2012). Interestingly, such biased interactions might emerge as a product of reinforcement learning. For example, Carballo et al. (2015) showed that dogs developed a preference for a person who gave them food in the past, as opposed to a person who withheld food from them. Dogs’ preference was expressed as a choice to approach and spend time with the donor as opposed to the other individual. In this case, the animal may begin establishing a bond with the preferred individual based on an associative learning mechanism. If reinforcement is maintained in the long term, the bond could become stable, as it may happen in dog-human interactions. Even more, if, as suggested by Heyes (2012), social and asocial learning rely on the same processes, intermittent reinforcement in social exchanges might increase persistence and stability in bonds as it does with performance in individual learning. This is consistent with the idea of reciprocity based on emotional book-keeping in which partial reinforcement may result from imperfect short-term reciprocation (Schino & Aureli, 2009).

Other forms of learning could also take part in the formation of bonds. For instance, Owren and Rendall (1997, cited in Berghänel et al., 2011) hypothesised that the classic conditioning could have an important effect on social relationships. According to these authors, an individual’s features could become conditioned stimuli that act on its partner after repeated positive or negative interactions with it. Then, the mere presence of the partner may affect the individual’s emotional state and, therefore, trigger approach or avoidance responses. Such learning might even result in a mental representation of the bond, which could in turn modulate long-term interactions between individuals (Owren & Rendall, 1997; this notion is very close to Schino & Aureli’s emotional book-keeping). Indeed, these ideas about the role of associative learning in social behaviours could help in explaining some of the results discussed in this article. For instance, a combination of classic conditioning and operant reinforcement could explain Bartal et al.’s (2011) results which were interpreted by the authors as if rats showed empathy-induced helping. According to the associative learning perspective, the trapped rat, which shared the home-cage with the free rat, could have become an appetitive CS which thus triggered approach tendencies in the latter. With this incentive at sight, the free rat could have approached its trapped partner, and then have the chance to learn the operant response to free its cage mate.

Last, the freeing response could have been reinforced by re-establishing social contact between them, with no need to refer to empathy (Silberberg et al., 2014). Moreover, associative learning could even be behind instances of short-term direct reciprocity, which otherwise tend to be explained by presumed sophisticated cognition (Hauser et al., 2009). For example, the results of the study by Dufour et al. (2009) on orangutans' (*Pongo pygmaeus abelii*) gradual acquisition of tit-for-tat reciprocity could be interpreted along these lines. These researchers found a significant positive correlation between tokens given to and received from the partner. In fact, token exchanges increased across sessions after different phases of training, suggesting a gradual learning process. As many other associative processes, such learning would work more efficaciously if the events to be associated (i.e. the succession of prosocial exchanges) happened in short time spans. In fact, evidence for reciprocity was much less convincing in a similar protocol involving longer intervals between possible alternative exchanges (see Amici et al., 2014).

In synthesis, associative learning might play an important role in the formation and maintenance of stable bonds, and, therefore, could be a mediator of reciprocal behaviours. Despite this interesting possibility, to our knowledge, there is no empirical evidence that directly links learning with reciprocity. Future studies could attempt to shed light on this hypothesis, for example, by experimentally manipulating the formation of bonds. A possible experimental design could involve applying systematic variations in the delivery of food to subjects when in social as opposed to individual situations. This would serve to vary the extent to which nearby conspecifics become predictive of upcoming rewards. With this type of protocol, experimenters could systematically vary whether animals receive more rewards in social or individual situations while keeping the overall provision of rewards constant (nonetheless, experimenters would need to take into account dominance hierarchies and try to avoid setups in which food can be monopolised by a single individual). After a period of time in which animals are predominantly rewarded either when in pairs or when alone, subjects could take part in a task to evaluate direct reciprocity while participating with its partner or with other control subjects. If classic conditioning plays a role in bond-based reciprocity, we would expect to see more reciprocal exchanges in pairs that were usually rewarded when together than in pairs that were not.

Other investigations relevant to the mechanisms underlying social memories have been conducted on a neurochemical level. For example, oxytocin might play an important role in allowing reciprocal exchanges through bonding. Although this neurohormone is best known for its role in parturition and maternal care, it is also involved in the processing of rewards and the establishment of social memories. For example, Crockford

et al. (2013) measured oxytocin in chimpanzees' urine and found that this hormone increased after grooming sessions with bond partners, although not when grooming occurred outside bonds or in the absence of grooming. This evidence does not directly speak of direct reciprocity, although it is suggestive given the recognition that grooming is a common exchange currency in primates (Schino & Aureli, 2009). Similar results have been observed when, instead of measuring endogenous levels of oxytocin, researchers exogenously administered the hormone. For instance, 2 hours after oxytocin inhalation, rhesus macaques (*Macaca mulatta*) increased the rewards given to another individual (when the alternative was to reward no one) relative to a control group without oxytocin inhalation (Chang et al., 2012). Indeed, oxytocin increased the time subjects employed observing their partners which suggests this hormone may activate brain circuits related to social attention (Chang et al., 2012). These findings are consistent with Heyes (2012) suggestion that social learning does not require any special or demanding cognitive ability. Perceptual, attentional and motivational factors bias social animals towards information coming from conspecifics, which then predisposes them to apply their common learning mechanisms to social matters. Indeed, bonded individuals may represent special targets to gather information from. For example, ravens presented a stronger preference to interact with an object when it had been previously manipulated by a close conspecific than by a more distant partner (Schwab, Bugnyar, Schloegl, & Kotrschal, 2008).

In short, oxytocin represents a strong candidate to play a role in what Schino and Aureli (2009) have called emotional book-keeping. This affective social memory can be a crucial process in the stability of reciprocal exchanges because it allows animals to track the status of relationships without a strong cognitive burden. All in all, evidence from behavioural ecology, the psychology of animal learning and the brain neurochemistry point towards diverse socio-cognitive mechanisms that may contribute to the establishment and maintenance of direct reciprocity.

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