



The transfer of alternative tasks in reciprocal cooperation



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Direct reciprocity can establish stable cooperation. Nevertheless, the significance of this mechanism is yet unclear. A frequent assumption is that both commodity and context should be the same when help is exchanged between social partners. Yet, an exchange of different favours appears more likely in a natural setting. This is assumed to be cognitively demanding, however, because experienced help in one context needs to change the motivation to help by different means or in a different context. We tested whether Norway rats, *Rattus norvegicus*, transfer help from one cooperative task to another. Individuals could provide food to previously either cooperating or defecting partners by using a different mechanism to produce food for their partner than the partner had used to help them. Test subjects indeed helped previously cooperative partners more often than defecting ones by using a different provisioning mechanism. This implies that rats realize the cooperative propensity of social partners, which they consequently reward by help of a different kind; hence, they do not merely copy experienced helping behaviour. Our results suggest that animals other than primates are capable of transferring help between different contexts, which highlights new possibilities for the occurrence of reciprocal altruism involving different commodities and services in nature.

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The evolution and maintenance of cooperative interactions between unrelated individuals can be explained by the reciprocal exchange of roles between participants (Taborsky, Frommen, & Riehl, 2016; Trivers, 1971). Individuals showing direct reciprocity help those that have previously helped them (Axelrod & Hamilton, 1981). Many experimental studies have demonstrated direct reciprocity in nonhuman animals (e.g. Amici et al., 2014; Carter & Wilkinson, 2013; Rutte & Taborsky, 2008, for a review see Taborsky et al., 2016) but its importance in nature has been questioned (Clutton-Brock, 2009; Hammerstein, 2003). Usually, the concept of reciprocity is applied only to situations where the same social service or commodity is returned to the same social partner in a similar context. However, there is no reason to assume that the occurrence of reciprocity is confined to such narrowly defined conditions. More likely, help or social service received in one context should increase the propensity to help a partner also in a different context in the future. This may apply when social partners have changed, such as in generalized reciprocity (Barta, McNamara, Huszár, & Taborsky, 2011; Pfeiffer, Rutte, Killingback, Taborsky, & Bonhoeffer, 2005; Rutte & Taborsky, 2007), or when the opportunity to return a received favour to the same partner has changed,

for instance if a different task is required. Experimental studies involving given and received favours in different tasks are rare, despite growing correlative evidence (Carter & Wilkinson, 2013; Fraser & Bugnyar, 2012; Romero & Aureli, 2008).

Preconditions for direct reciprocity include individual recognition and memory of the outcome of past interactions with specific social partners, which is thought to be cognitively demanding (Brosnan, Salwiczek, & Bshary, 2010; Stevens & Hauser, 2004). In addition, cooperating across different services implies (1) an understanding of help received from a specific individual and (2) transferring this information to a different service in order to pay back the other, previously received service. There is good evidence that some nonhuman animals exchange different cooperative services reciprocally (reviewed in Taborsky et al., 2016). In monkeys, for example, grooming often seems to be traded against other social services (Borgeaud & Bshary, 2015; Cheney, Moscovice, Heesen, Mundry, & Seyfarth, 2010; Fruteau, Voelkl, van Damme, & Noë, 2009; Hemelrijk, 1994). Experiments on free-ranging vervet monkeys, *Chlorocebus pygerythrus*, showed that individuals respond more strongly to solicitations for aid of unrelated social partners that had groomed them before (Seyfarth & Cheney, 1984), and that individuals providing food to the group are subsequently groomed more often by group members (Fruteau et al., 2009).

Although trading different services is very widespread in humans and therefore seems intuitive to us, it may be cognitively

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demanding (Stevens & Gilby, 2004). When, for example, grooming is exchanged for social support (Seyfarth & Cheney, 1984), that is, individual X grooms Y (= service A) and Y will support X in a fight against Z later on (= service B), this implies both (1) the perception of somehow corresponding payoffs of services A and B, and (2) that a cooperative state is associated with a specific individual. If the association of a cooperative state with specific individuals is dynamic, that is, it is updated accordingly over a series of interactions, this would enable group members to cooperate reciprocally with specific partners over different contexts based either on associative learning or on a change in attitudes (de Waal, 2000) or emotions (Schino, di Sorrentino, & Tiddi, 2007); this works without needing to keep track of the exact outcome of every interaction. In contrast, copying the helpful behaviour of a specific partner would imply memory about, and a specific response to, every single interaction, which would hardly lead to cooperation across different contexts.

Norway rats, *Rattus norvegicus*, help social partners to obtain food if they have been helped in a similar way by the same or different individuals, that is, they show direct and generalized reciprocity in an iterated prisoner's dilemma situation (Dolivo & Taborsky, 2015b; Rutte & Taborsky, 2007, 2008; Schneeberger, Dietz, & Taborsky, 2012; Wood, Kim, & Li, 2016). Rats are highly social animals, forming groups of various sizes (McGuire, Pizzuto, Bemis, & Getz, 2006; Telle, 1966), sharing food (Barnett & Spencer, 1951) and coordinating cooperative behaviour (Schuster, 2002). There is evidence that they show transitive inference, that is, if an option A is more valuable than B and B is more valuable than C, then A is perceived to be also more valuable than C (Roberts & Phelps, 1994). Hence, Norway rats seem to be an ideal model to test for the propensity of animals to return received favours by different tasks. In this study, we expanded an established experimental paradigm where rats provide food to a social partner by pulling a movable platform by a second, similarly intuitive mechanism, through which food can be delivered to the partner by pushing a lever. Thus, focal rats experienced social partners as cooperating 'pushers' and defecting 'nonpushers', as well as cooperating 'pullers' and defecting 'nonpullers' in a full factorial design. Thereafter, the focal rats always had access to the alternative mechanism to that of their partners to provide food for them. If rats realize the difference between cooperating and defecting providers, we predicted that they should be more likely to use an alternative food-provisioning mechanism to help a previously cooperative partner than a previously defecting partner.

METHODS

Experimental Subjects and Holding Conditions

We used outbred wild-type adult (1-year-old) female Norway rats (source: Animal Physiology Department, University of Groningen, the Netherlands) weighing on average 300 g. The rats were habituated to handling right after weaning and hence did not show any signs of stress when being handled, transported to the experimental cage and exposed to the set-up. They were individually colour marked and housed with littermates in groups of five sisters in order to provide a social environment (Sharp, Zammit, Azar, & Lawson, 2003). The cages (80 × 50 cm and 37.5 cm high) were separated from each other by opaque walls to exclude visual contact between the groups. In accordance with the animal welfare legislation of Switzerland (Tierschutzverordnung Schweiz 04/2008) we enriched the cages with various materials (a wooden house and board, a tunnel, a piece of wood to nibble, a cardboard

roll to play with, digging material (wood shavings), nest-building material (hay) and a salt block, as suggested by established animal care guidelines (Forbes, Blom, Kostmitsopoulos, Moore, & Perretta, 2007). Food (conventional rat pellets) and water were provided ad libitum. In addition, rats received a corn mix, fresh fruits or vegetables once a day. The ambient temperature was 20 °C ± 1 °C, with a relative humidity of 50–60% and a 12:12 h light:dark cycle with lights on at 2000 hours and 30 min of dawn and dusk. As rats are primarily nocturnal, all training and experiments were conducted during the dark phase under red light (Norton, Culver, & Mullenix, 1975).

Pre-experimental Training

The experimental set-up was based on a two-player sequential food exchange task (Rutte & Taborsky, 2007; de Waal & Berger, 2000). Test cages (80 × 50 cm and 37.5 cm high) were divided in half by a wire mesh. All focal and partner rats experienced the following training prior to the experiment.

Pulling task

First, every rat was trained to pull a stick that was connected to a movable platform in order to receive a food item (one oat flake). The experimenter moved the platform consistently out of the cage over several training sessions, teaching the rats to pull the stick to reach the reward. In the second part of the training, a sister of the rat was placed in the second cage compartment. From then on, the rats (termed donors) did not get a reward themselves for pulling the platform; instead, only their partner (the recipient) received one. The roles of donor and recipient were regularly exchanged, and the intervals between these alternations were increased gradually from switching the roles after each pull to switching them after series of pulls lasting up to 7 min, which corresponds to the experimental period (see Dolivo & Taborsky, 2015a for a detailed plan of the training scheme). We noted the individuals pulling the most in 12 cages. Afterwards, we randomly chose six of these 12 individuals to serve as 'cooperative partners' in the experiment. In addition, six rats were trained to refrain from pulling by blocking the platform during the 7 min of exposure to the social partner in the training phase. These six rats were randomly chosen from the original population, and they served as defectors in the experiment.

Pushing task

This training was also divided into two parts. First, rats were trained to push a lever, which opened a connected trapdoor in a tube, through which a reward was delivered into the cage from above (see Appendix Fig. A1). In the second training phase, the rats were again paired with a sister. Similar to the training of the pulling task, from then on the rats never received a reward for themselves when pushing the lever. Again, the same 12 partner rats were trained to be either cooperators or defectors.

Test Procedure

During the experience phase, focal rats experienced cooperators producing rewards by either pulling the platform into the focal rat's compartment or by pushing a lever so that food dropped into the cage from above. Defectors did not produce any food. During the test phase, the roles were exchanged and focal rats could now produce food for their social partner (cooperator or defector) by pushing the lever or pulling the platform. In all cases, rats had to use the alternative mechanism to the one they had experienced before, thus making pure copying of actions impossible. Each focal

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