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Animal behaviour

Norway rats reciprocate help according to the quality of help they received

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Direct reciprocity, according to the decision rule 'help someone who has helped you before', reflects cooperation based on the principle of postponed benefits. A predominant factor influencing *Homo sapiens*' motivation to reciprocate is an individual's perceived benefit resulting from the value of received help. But hitherto it has been unclear whether other species also base their decision to cooperate on the quality of received help. Previous experiments have demonstrated that Norway rats, *Rattus norvegicus*, cooperate using direct reciprocity decision rules in a variant of the iterated Prisoner's Dilemma, where they preferentially help cooperators instead of defectors. But, as the quality of obtained benefits has not been varied, it is yet unclear whether rats use the value of received help as decision criterion to pay help back. Here, we tested whether rats distinguish between different cooperators depending purely on the quality of their help. Our data show that a rat's propensity to reciprocate help is, indeed, adjusted to the perceived quality of the partner's previous help. When cooperating with two conspecific partners expending the same effort, rats apparently rely on obtained benefit to adjust their level of returned help.

1. Introduction

Reciprocal exchange of services and commodities among conspecifics has been observed in several species, including vervet monkeys [1], baboons [2] and other primates [3], vampire bats [4], rats [5] and cichlids [6]. Laboratory experiments allow disentangling of the parameters that are important for the decision to reciprocate help, for instance when animals apply the decision rules of direct reciprocity [5]. In previous experiments, it has remained unclear, however, to what extent the propensity to return help to a social partner depends on the value of the service previously provided by this partner. This has been suggested to be important in vervet monkeys observed in the field [1]. In addition, in human economy, individuals may reciprocate help proportionally either to the effort expended by a helper [7], or to the receiver's benefit resulting from the helper's action [8]. Our goal was to clarify whether other species as well might reciprocate help differentially in response to the quality of a partner's help, by varying received benefits, whereas other parameters are controlled for.

Norway rats were chosen for this study because of their ability to perform experimental tasks under controlled laboratory conditions, their high degree of sociality in the wild and their known ability to cooperate on the basis of direct reciprocity [5]. We manipulated the quality of the partners' help by use of food items differing in value and attractiveness that were provided by two different partners in a variant of the Prisoner's Dilemma paradigm. One partner provided the focal test rat with 'high-quality' rewards, pieces of bananas, whereas the other one provided the same test rat with 'low-quality' rewards, pieces of carrots. We predicted that a perceived high-quality food reward furnished by a cooperator would enhance the propensity of test rats to reciprocate help. The quality of the offered food was the only variable parameter for test rats to distinguish between different

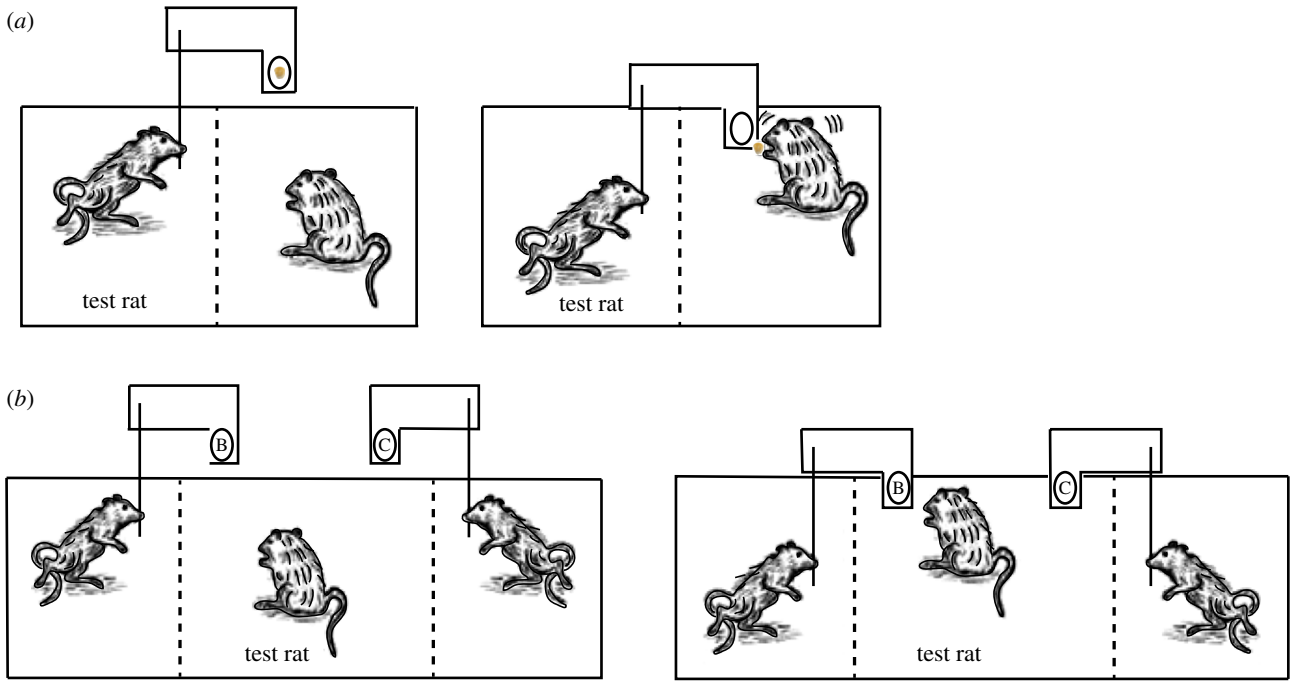

Figure 1. (*a*) Experimental set-up used for pre-experimental training and tests. Pre-experimental training: in a cage split into two compartments by wire mesh, the rats learned to pull the stick to provide food to a partner positioned in the other compartment (left). The reward could only be reached by the partner when the platform had moved inside the cage (right). Test phase: in a cage split into two compartments by wire mesh, each test rat could provide her partner (either her previous carrot provider or her previous banana provider) with cereal flakes over the course of 7 min. (*b*) Experimental set-up used for the experience phase. On two consecutive days, each test rat was placed in the middle compartment of a cage separated into three compartments by wire mesh; she was surrounded by two cooperators, each of which provided her access four times either to an appreciated treat (piece of banana), or to a less appreciated treat (piece of carrot).

cooperators. The cooperators' exerted effort was intentionally the same for all treatments in all experiments, and each cooperator was used equally as often as a 'high-quality' partner and as a 'low-quality' partner, to exclude any potential bias owing to cooperator identity.

2. Material and methods

This study involved 20 female wild-type Norway rats. The pre-experimental training followed the method developed by Rutte & Taborsky [9]. During the experiment, we used pieces of banana as attractive and pieces of carrot as less attractive rewards. More information on subjects, experimental food items and pre-experimental training is available in the electronic supplementary material.

The first experimental phase (i.e. 'experience phase') lasted for two consecutive days. Each focal rat had one experimental session per day, for which she was placed in the middle compartment of a cage separated into three compartments by wire mesh. Two cooperators were introduced into the two side compartments of this cage. The focal rats were acclimatized to the cage and to their neighbours for 1 min. Over seven subsequent minutes, one cooperator provided access four times to a preferred treat (a piece of banana), whereas the other cooperator provided access four times to a less appreciated treat (a piece of carrot; figure 1*b*). The roles of both cooperators remained unchanged during the whole experience phase, but their positions in the cage were inverted on the second day of the experience phase to avoid potential effects of a side bias. Each cooperator worked five times as a banana provider and five times as a carrot provider, in order to avoid potential effects of cooperators' individual characteristics.

During the next 2 days (i.e. 'test phase'), the 20 focal rats were tested in a cage separated into two compartments, identical to the set-up used for the pre-experimental training (figure 1*a*). After 1 min of acclimatization, each focal rat had the possibility to provide her partner (either her previous carrot provider or her previous banana provider) with cereal flakes within 7 min. Ten focal individuals were tested with the banana provider on the morning of the third day and on the afternoon of the fourth day, and with the carrot provider on the afternoon of the third day and on the morning of the fourth day. The other 10 focal rats were tested in reverse order. The total number of pulls for each former cooperator and the mean latency before the first pull were assessed for all 20 focal individuals.

The data were analysed with non-parametric statistical tests (for details, see the electronic supplementary material).

3. Results

To determine the food preference of test rats, we recorded whether they ever left even one piece of banana or carrot during the experience phase. None of the focal rats ever left a piece of banana, whereas 18 of 20 rats left a piece of carrot at least once, revealing a clear banana preference ($n = 20$, $p < 0.01$, Fisher's exact test).

The latency before the first pull (mean between both test days) was significantly longer for partners that had provided the focal test rat with carrots (Wilcoxon matched-pairs test, $n = 20$, $p = 0.02$; figure 2*a*, left panel). In addition, focal rats tended to perform more pulls for former banana than for former carrot providers (Wilcoxon test, $n = 20$, $p = 0.052$; figure 2*a*, right panel).

The rats' discrimination of their partners' quality of help increased with time. Neither the latency before the first pull nor the pulling rate significantly differed between treatments on the first test day (Wilcoxon tests, $n = 20$, $p = 0.107$ for latency before the first pull; $n = 20$, $p = 0.118$ for number of pulls; figure 2*b*), but they differed clearly on the second test day ($n = 20$, $p = 0.032$ for latency before the first pull; $n = 20$, $p = 0.013$ for number of pulls; figure 2*c*).

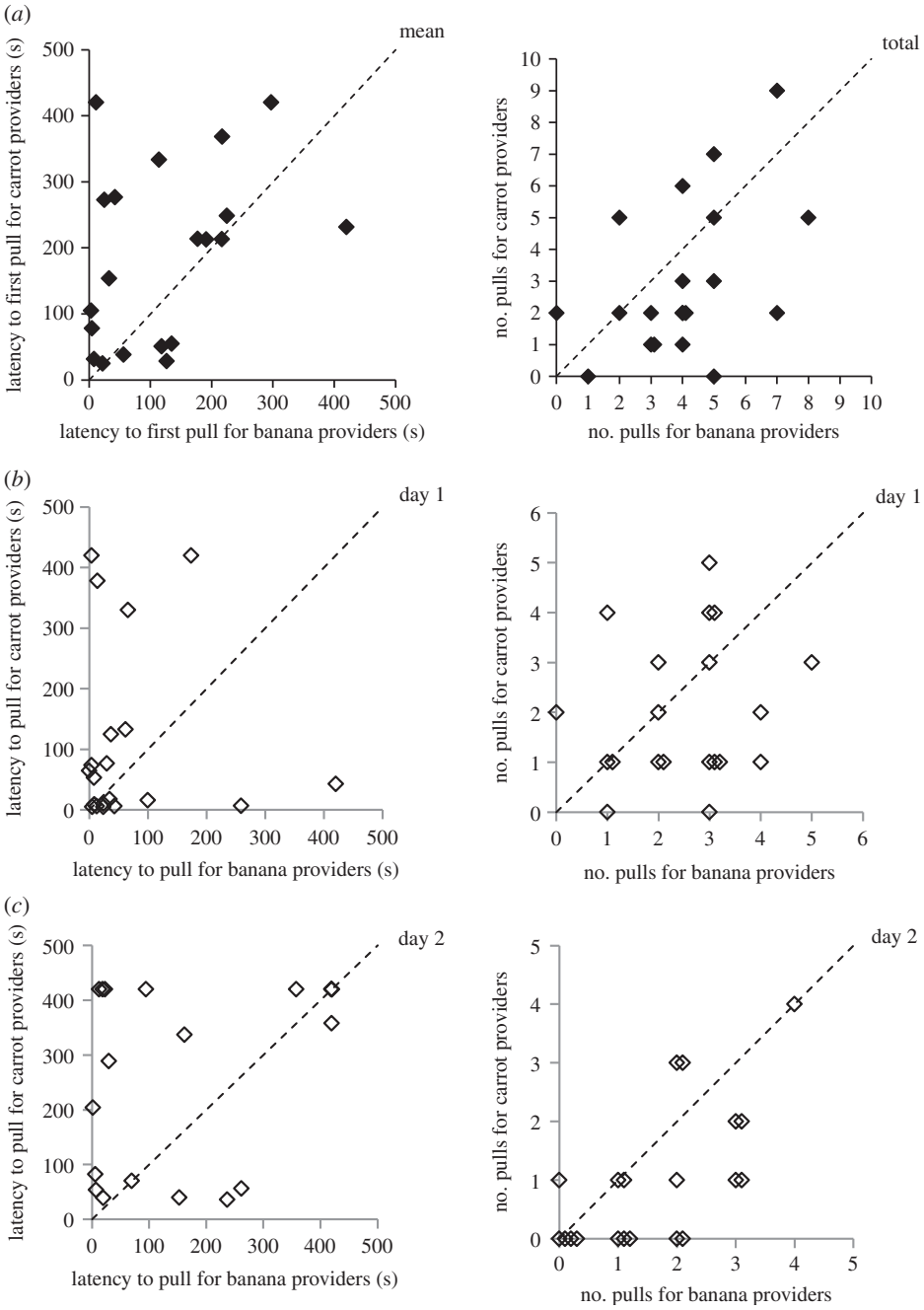

Figure 2. (*a*) Test days 1 and 2 combined. Left panel: latency before first pull of each focal rat according to treatment (mean of both test days combined). Each tested individual represented by a point above the dashed line pulled quicker for a former banana provider than for a former carrot provider, and the opposite holds for points lying below the line. Right panel: total number of pulls of each tested individual according to treatment (sum for both test days combined). Each tested individual represented by a point above the dashed line pulled less often for a former banana provider than for a former carrot provider, and the opposite holds for points lying below the line. Overlapping points were jittered around their *x*-value to increase visibility. (*b*) Latency and number of pulls on test day 1 (lines and symbols as in *a*). (*c*) Latency and number of pulls on test day 2 (lines and symbols as in *a*).

4. Discussion

Our results show that female rats adjust their help levels to the quality of help previously obtained from a social partner. Rats pulled after a shorter delay for a cooperator who had provided them with preferred bananas than for a cooperator who had provided them with the same amount of non-preferred carrots, after both cooperators had pulled for them for the same number of times.

When studying whether animals apply the decision rules of direct reciprocity, it is necessary to exclude that test individuals merely copy their partner's behaviour or attempt to pull food for themselves [9]. Previous experiments using the same experimental set-up have shown that rats differentiate clearly between situations in which they pull for a partner and situations in which the food they pull towards the cage would enter an empty compartment [5,9]. In addition, the rats differentiated between helping a known cooperator (direct reciprocity) and helping an anonymous partner after having received help (generalized reciprocity) [5]. In another study using the same experimental paradigm, the test rats were shown to strongly differentiate between pulling food for a partner and pulling food for themselves, and they differentiated between cooperators and defectors more strongly when they experienced high pulling costs

[10]. In our study, the differential reciprocation of focal individuals to cooperators providing high- or low-quality food did not decrease between test days 1 and 2, even if the general propensity to pull declined. Differentiation would be predicted to remain similar or to decline with time if mere copying was responsible for reciprocal help, but instead it increased on the second test day, despite no additional benefits or information being obtained from the experimental partners in between. This increase in differentiation between high- and low-quality partners is incompatible with any basic associative learning process and suggests reciprocal cooperation as the only consistent explanation. A possible reason for the increase in the tendency to provide more rewards for the higher-quality partner between test days might be an increased motivation of test rats to provide a signal of cooperation to the more desirable partner after not being rewarded for their help on the first test day, in order to induce future reciprocation with the high-quality partner.

In vervet monkeys, the law of supply and demand typically affects the exchange rate of goods and services between social partners. Individuals reciprocated more when the offered service was rare or when it was considered as particularly precious for them, without any obvious consideration of the relative cost paid by the donor [1]. When only one food provider was present, he received more grooming than when a second food provider was introduced [1]. In a study of human reciprocity in restaurant customers, gratitude was the factor that prompted favourable reciprocation, with food quality being related not only to satisfaction, but also to gratitude ('a positive emotion that individuals feel when others have intentionally given them something of value'; [11]).

If individuals reciprocate according to obtained benefits, prospective cooperators should provide high-quality help, for instance by investing in tasks in which they are especially competent or efficient. This reasoning might explain task specialization among members of social groups that cooperate by reciprocal commodity trading, such as in cooperatively breeding cichlids [6,12]. Reciprocity, based on the quality of exchanged services, may also affect the emergence and persistence of cooperative networks with preferential dyadic relationships in which various kinds of services can be exchanged, as observed for instance in vampire bats [4] and some primates [2,3].

In a long-term perspective, it might be interesting to test whether the effort previously expended by a partner may also influence the propensity to reciprocate help. Instead of manipulating the quality of the partners' help ('cooperative outcome') while keeping the partners' effort constant like in our experiment, the partners' expended effort should then be manipulated while keeping the cooperative outcome identical. In humans, it was indeed shown that not only the benefit received, but also the effort expended by a helping partner may affect the motivation to reciprocate [7].

A previous study of Norway rats showed that potential benefits for the recipient of a charitable act can affect the amount of help a donor will provide [10]. In this study, we have shown that, in addition, a helper is rewarded by the recipient of a cooperative act in accordance with the benefit it has previously received from the helper. Our study thereby offers new insights into complex strategic choices involved in cognitively demanding cooperation.

Ethics statement. The procedures described in this manuscript conform to the legal requirements of Switzerland and the guidelines of the University of Bern, where the work was carried out (licence no. BE98/11).

Data accessibility. All data are available in the electronic supplementary material.

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Authors' contributions. V.D. and M.T. conceived the study, V.D. collected and analysed the data, V.D. and M.T. wrote the paper.

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Conflict of interests. The authors have no competing interests.

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