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The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): direct vs generalised reciprocity

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Abstract Cooperation among non-kin has been attributed sometimes to reciprocal altruism: Two or more individuals exchange behaviour that benefits the respective partner. According to direct reciprocity, cooperation is based on past behaviour of a known partner. In contrast, in generalised reciprocity, cooperation is based on anonymous social experience where the identity of the partner is irrelevant. In a previous study, female Norway rats (*Rattus norvegicus*) were found to cooperate according to a generalised reciprocity mechanism. In this study, we tested whether Norway rats would also cooperate as predicted by a direct reciprocity mechanism and whether direct reciprocity would cause a higher propensity to cooperate than generalised reciprocity. Focal animals were experimentally manipulated to receive social experience from known or unknown, helpful or defecting partners in an instrumental cooperative task. Our first experiment shows that rats are more helpful towards a partner from which they had received help before than towards a partner that had not helped (i.e. direct reciprocity). Our second experiment revealed that after receiving help by others, rats were more helpful towards a partner from which they had received help before than towards a new partner (i.e. direct reciprocity generated a higher cooperation propensity than generalised reciprocity). We conclude that in female Norway rats, the tendency to cooperate is influenced by partner-specific information. To our knowledge, this is the first study to demonstrate direct reciprocity in rodents, and
it is the first study testing direct vs generalised reciprocity in animals.

Keywords Cooperation · Reciprocal altruism · Cognition · Rodents · Game theory

Introduction

Among evolutionary mechanisms responsible for cooperation, reciprocal altruism has achieved particular interest (Trivers 1971; Alexander 1987; Nowak and Sigmund 2005). The logic of reciprocal altruism is that the decision to pay some cost for the benefit of another individual is based on expected future help, which may be judged from past interactions. Theoretical models suggest that reciprocal altruism is either based on information about a particular partner's propensity to cooperate (direct reciprocity: Axelrod and Hamilton 1981; indirect reciprocity: Nowak and Sigmund 1998, 2005; Leimar and Hammerstein 2001) or on anonymous cooperative experience with any partner (upstream tit-for-tat: Boyd and Richerson 1989; generalised reciprocity: Hamilton and Taborsky 2005; Pfeiffer et al. 2005). According to direct reciprocity, A helps B because B has helped A before (Axelrod and Hamilton 1981). So far, experimental evidence for strategies predicted by direct reciprocity models is limited and has been often disputed (Wilkinson 1984; Milinski et al. 1990; Dugatkin and Alfieri 1991; Godard 1993; Clements and Stephens 1995; Stephens et al. 1997; Barrett et al. 2000; de Waal and Berger 2000; Krams and Krama 2002; Hauser et al. 2003; Olendorf et al. 2004). Indirect reciprocity, where A helps B because B has helped C before, which is information available to A, has been demonstrated only in humans (Wedekind and Milinski 2000; Milinski et al. 2001; Semmann et al. 2005), but see

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Bshary and Grutter (2006) for a possible example at the inter-specific level in fish. According to generalised reciprocity, A helps B because A had received help from C before, where the identities of B and C are unimportant (Hamilton and Taborsky 2005; Pfeiffer et al. 2005). Generalised reciprocity has been demonstrated to work in humans and Norway rats (Berkowitz and Daniels 1964; Rutte and Taborsky 2007).

To acquire the necessary information about a partner's likelihood to reciprocate, direct and indirect reciprocity demand that animals possess specific cognitive abilities (Stevens and Hauser 2004). For example, to play tit-for-tat, a prominent strategy found to establish cooperation in direct reciprocity models, an animal must recognise its social partner and recall what this individual had done in a previous interaction (Axelrod and Hamilton 1981). Even if animals are able to recognise conspecifics individually and to remember their behaviour, this may be difficult or costly (Milinski and Wedekind 1998), for example in large groups or when time intervals between mutual interactions are long. This may be one important reason that evidence for direct reciprocity in animals is much more limited than expected from theoretical considerations (Stevens et al. 2005). However, given the required biological and social conditions, direct reciprocity may indeed cause animals to cooperate, even if presently this mechanism may appear to be limited to primates, with few exceptions (Hauser et al. 2003). In this study, we compare the influence of individual-specific and anonymous cooperation experience on the propensity to cooperate in female Norway rats (*Rattus norvegicus*), as this species may fulfil the preconditions to cooperate according to direct reciprocity.

Norway rats are able to recognise conspecifics individually by odour (Gheusi 1997) and usually live in groups from only a few up to 200 individuals, among which, relatedness levels may vary greatly (Telle 1966). In addition, rats show a propensity to cooperate (Schuster 2002; Schuster and Perelberg 2004). In a previous study, we found that anonymous cooperative experience influences a rat's propensity to help others: A rat that was helped before by anonymous partners is more helpful towards a new partner than a rat that had received no help (generalised reciprocity; Rutte and Taborsky 2007). When testing for direct reciprocity, one needs to exclude the possibility that any positive effect of received cooperation on the propensity to help a partner would have been caused also by anonymous cooperation experience (i.e. generalised reciprocity) instead of individual-specific experience. In other words, we had to test the direct reciprocity paradigm also against a setup allowing for generalised reciprocity. In a two-step procedure, we used female rats that were not closely related and had been trained in an instrumental cooperative task (1) to test whether rats discriminate between a cooperator and a non-cooperator (defector) by showing direct reciprocity and (2) to compare the cooperative propensity of rats towards a partner that had helped them before (direct reciprocity) with that shown towards a new partner after experiencing help from others (generalised reciprocity).

Materials and methods

Subjects

The rats were bred from outbred wild-type rats (source: Animal Physiology Department, University of Groningen, Netherlands) and housed with same-sex littermates in groups of three to seven in cages ($80 \times 50 \times 37.5$ cm). We used only female rats because the dominance relationship among females is rather egalitarian compared to a marked hierarchy among males (own unpublished data). Female groups could not interact with each other between cages due to the arrangement of cages. The housing room had an average temperature of 22°C and a 12:12-h light/dark cycle with lights on at 20:00 hours. Food (conventional rat pellets) and water were provided ad libitum. Fresh vegetables (salad, carrots) were additionally provided twice a week. Rats are predominantly nocturnal, and we thus performed our experiments during the dark phase in the morning hours.

Pre-experimental training

The experimental setup (Fig. 1a) was similar to that used in tests of cooperative behaviour in primates (De Waal and Berger 2000; Hauser et al. 2003). The training of the rats in the instrumental cooperative task consisted of two steps. First, a single rat learned to pull a stick fixed to a baited platform to move it into the cage and reach the reward (one oat flake). Second, this rat learned to pull alternately with a littermate, providing access to food for each other. For this, the two rats were placed in a cage that was separated into two compartments by a wire mesh. Only one rat had access to the stick and the opportunity to move the baited platform into the cage. The pulling rat had no access to the reward, but only its partner. In a subsequent session, the roles were exchanged. Initially, the partners pulled shortly after each other (i.e. one partner had to pull four times, then the roles were exchanged immediately). The interval between the exchanges of roles was gradually increased to 2 days. All rats pulled in this cooperative situation. We assume that the focal rats in our experimental setup recognised that the partners were different individuals, as in another experiment, we found that the duration of investigative behaviour (sniffing) by rats towards a familiar and unfamiliar partner differed significantly in a similar situation (own unpublished data). The duration of investigative behaviour

towards a conspecific is an adequate method to demonstrate discrimination between familiar and unfamiliar individuals (Gheusi et al. 1994).

Experiments

In the experiments, only rats were paired that came from different cages (i.e. they were not closely related). In the first experiment (Fig. 1b), 13 focal rats alternately received help from one partner to get food (cooperator treatment) and no help from another partner (non-cooperator treatment). In this experience phase, each focal rat met each partner five times in a random sequence over a period of 20 days. In total, five helping partners that had been trained in alternated pulling were used (two were used twice, three were used three times; individual partner rats were not treated differently by the test rats in the subsequent test: Kruskal–Wallis analysis of variance (ANOVA), $df=4$, $\chi^2=6.391$, $p=0.172$). As an incentive to pull, each helping

partner had been rewarded for pulling shortly before the focal rat was put into the second compartment of the experimental cage. The session continued until the partner had pulled eight times, which, on average, was achieved within 7 min. Each time, the focal rat would receive one oat flake on the tray. The non-helping partners (in total seven; six were used twice; individual partner rats were not treated differently by the test rats in the subsequent test: Kruskal–Wallis ANOVA, $df=5$, $\chi^2=3.647$, $p=0.601$) had not been trained in pulling, and therefore, did not try to do so. As an additional security measure, the platform was mechanically prevented from moving towards the cage. Again, the duration of a trial was 7 min. During each non-cooperator session, the experimenter also baited the tray eight times with one oat flake on the side of the focal rat. After each session, the partner rat was removed first, and then the focal rat received the eight oat flakes on the tray. Note that during the entire experience phase (20 days), the focal rat did not pull herself at any stage. After the end of
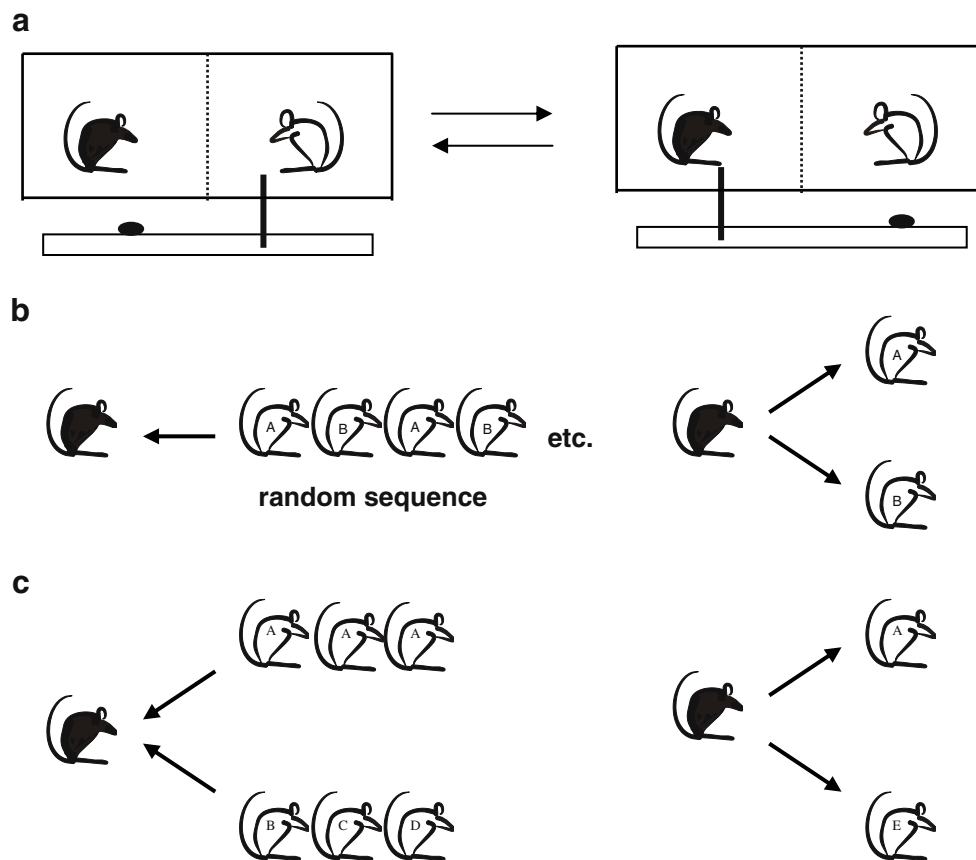

Fig. 1 Rats cooperate in an instrumental task. a Experimental setup and pre-experimental training. Two rats in the test cage are separated by a wire mesh; by pulling a stick fixed to a baited tray, one rat produces food for the partner rat, but is not rewarded herself for this behaviour. Subsequently, the roles are exchanged and the rat that had received a reward before is now in the role of the potential cooperator. b First experiment. The focal rat (black) alternately experienced help by a partner rat (A) that pulled (cooperator treatment), or no help by

another partner rat (B) that did not pull (non-cooperator treatment). Subsequently, it was tested in the role of the potential helper with both partners. c Second experiment. The focal rat (black) either repeatedly experienced help from the same partner (A) and was subsequently tested in the role of the potential helper with this partner (direct reciprocity treatment), or it repeatedly received help from three different partner rats (B, C, D) and was then tested with a new partner (E) (generalised reciprocity treatment)

the experience phase, each focal rat was paired with both partners in a random sequence on 1 day and was now in the role of the potential helper. The number of pulls performed by the focal rat in this situation was noted during a period of 7 min. The experimenter recorded the interactions on a monitor whilst sitting behind a gliding door. A new oat flake was placed on the platform 10 s after each pulling event (i.e. after the partner rat usually had consumed the food).

In the second experiment (Fig. 1c), focal rats either repeatedly received help from the same partner and were subsequently tested with this partner (direct reciprocity treatment), or they received help from three different partners and were then tested with a new partner (generalised reciprocity treatment). Four of the 14 focal rats had been used as focal rats in the first experiment. Before the experiment, each focal rat met its two respective test partners ("cooperator" and "new partner") on 3 days for 10 min each in a cage different from the experimental cage. This was done to minimise the difference in familiarity between focal rats and their test partners, which might influence the propensity to cooperate in the test situation. All focal rats were exposed to both treatments in a random sequence. In both treatments, in the experience phase, the

focal rats received help on three successive days, and on day four, they were paired, now in the role of the potential helper, either with the same partner as in the experience phase (direct reciprocity treatment; in total, six helping partners that had been trained in alternated pulling were used: one was used twice, two were used three times, one was used four times; individual partner rats were not treated differently by the test rats in the subsequent test: Kruskal–Wallis ANOVA, $df=3$, $\chi^2=3.991$, $p=0.262$) or with a new partner (generalised reciprocity treatment; in total, five helping partners that had been trained in alternated pulling were used (two were used twice, two were used three times, one was used four times; individual partner rats were treated differently by the test rats in the subsequent test: Kruskal–Wallis ANOVA, $df=4$, $\chi^2=9.778$, $p=0.044$).). Three days later, we repeated this procedure by switching the experience treatment given to the focal rats. Again, the focal rat did not pull herself in the entire experience phase. Observations and data recording were conducted in the same way as in the first experiment, but in a blind fashion such that the experimenter did not know which focal rat was in the trial. One day after this experiment, we noted the pulling rate of each focal rat

Fig. 2 Reciprocity in rats. a Direct reciprocity: rats pulled more often for a partner that had helped before (cooperator treatment, *filled dots*) than for a partner that had not helped before (non-cooperator treatment, *open triangles*). b Direct vs generalised reciprocity: the pulling frequency of rats was higher when paired with a partner that had helped before (direct reciprocity treatment, *filled dots*) than when having received help from others (generalised reciprocity treatment, *open triangles*). *Numbers* on the abscissa with the same first digit denote individuals from the same family (e.g. 10, 11 and 12 were siblings), and the same numbers in both graphs indicate the same individual (e.g. 50 was used in both experiments)
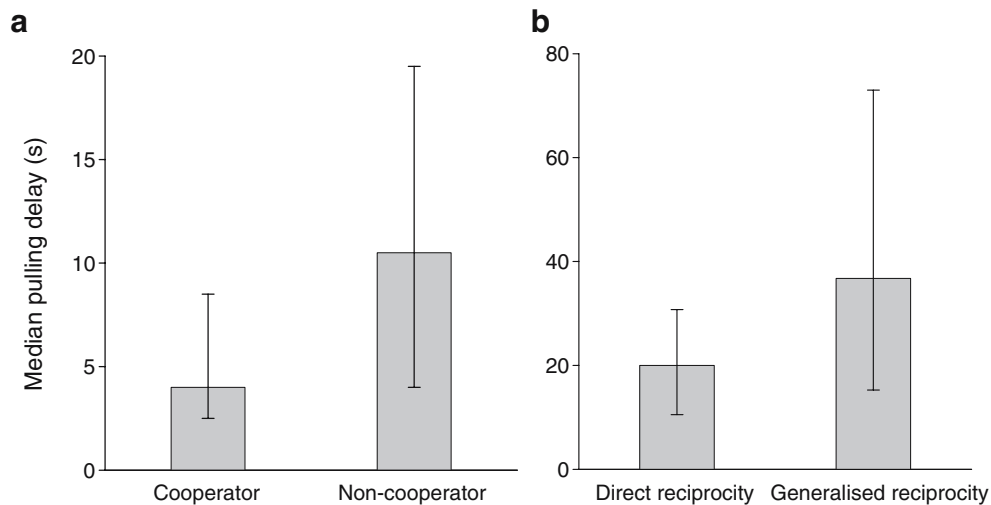
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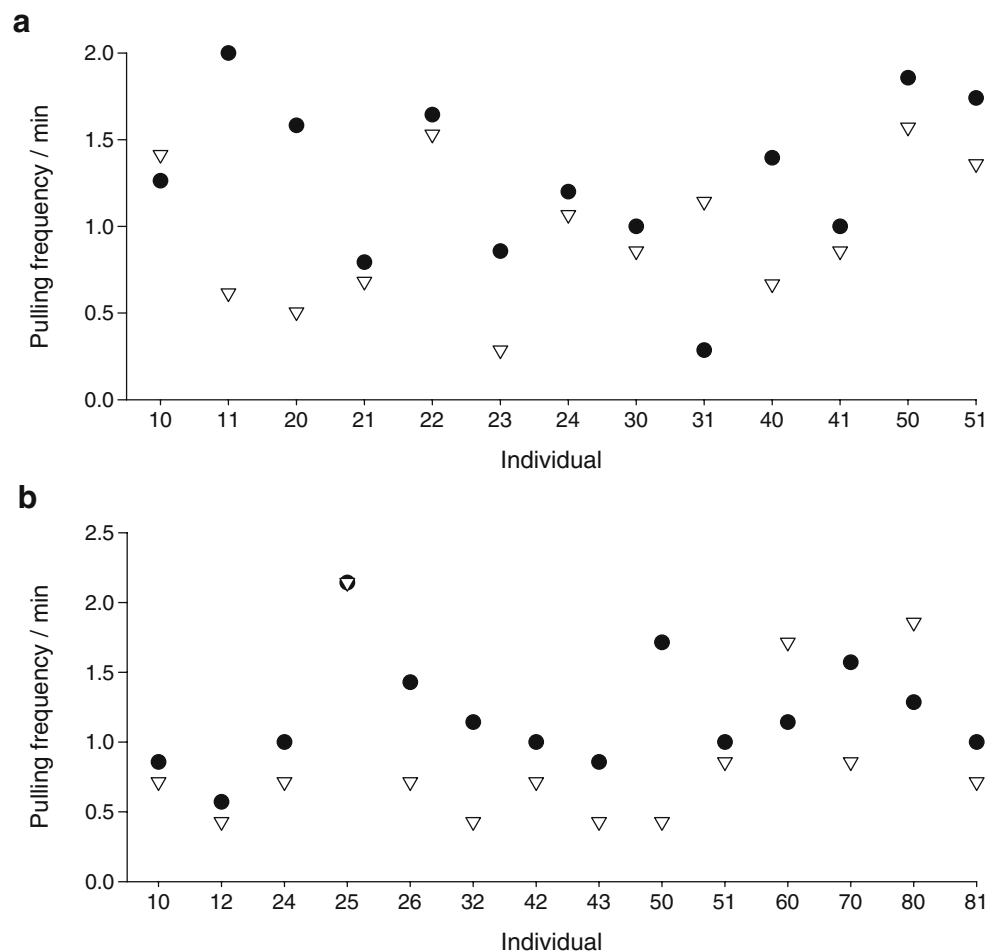
Fig. 3 Reaction times. **a** The median delay (±quartiles) when pulling for a cooperator (cooperator treatment) was shorter than when pulling for a partner that had not helped before (non-cooperator treatment).

b When pulling for a partner that had helped before, the median delay was shorter (direct reciprocity) than when pulling for a new partner after receiving help from others (generalised reciprocity)

when alone in the experimental cage to check for intrinsic differences in pulling frequency. The situation was equivalent to the experiment where the rat could move the platform into the cage by pulling, but she was unable to reach the reward, and no partner was present.

Statistics

The data were analysed with non-parametric statistics using the software package SPSS 11.0 (SPSS, Chicago, IL, USA). We compared treatment effects of individuals using two-tailed Wilcoxon matched-pairs signed-ranks tests. For analysing differences in baseline pulling frequency after the second experiment, we used the Mann–Whitney U test.

Results

In the first experiment, rats pulled more often for a partner that had pulled for them in previous interactions than for a partner that had not done so (medians: cooperator treatment, 1.26 pulls/min, non-cooperator treatment, 0.86 pulls/min; $n=13$, $Z=-2.200$, $p<0.05$; Fig. 2a). The median interval between placing an oat flake on the platform and pulling by the rat was shorter in tests with the cooperator than in tests with the non-cooperator ($n=13$, $Z=-2.062$, $p<0.05$; Fig. 3a). In the second experiment, the pulling frequency was higher for the partner that had helped before than for a new partner after having received help from others (medians: direct reciprocity, 1.07 pulls/min, generalised reciprocity, 0.71 pulls/min; $n=14$, $Z=-1.996$, $p<0.05$; Fig. 2b). The median pulling delay was shorter when the test rat was paired with a known cooperator than when meeting a new partner who was not known from previous

cooperative interactions ($n=14$, $Z=-2.543$, $p=0.01$; Fig. 3b). The baseline pulling frequency recorded 1 day after the experiment when rats were alone in the cage was lower than in the direct reciprocity treatment (Mann–Whitney U test, $p=0.001$) and in the generalised reciprocity treatment (Mann–Whitney U test, $p=0.002$), respectively, but it did not differ significantly between the treatments (direct reciprocity: median=0.57, $n=8$; generalised reciprocity: median=0.43, $n=6$; $U=14.0$, $p=0.23$). Therefore, there is no indication that the intrinsic tendency to pull had been influenced by the experimental treatments.

Discussion

The data of our first experiment indicate that rats reciprocate help in this cooperative situation. To our knowledge, this is the first experimental demonstration that animals show direct reciprocity in an instrumental cooperative task below the level of primates. Focal rats discriminated between a partner that provided help and a partner that did not and based their own helping behaviour on previous interactions with a particular partner. Social learning as an alternative explanation for this result is unlikely, as the focal rats were exposed to both treatments (receiving help and receiving no help) in an alternating sequence during the experience phase. Thus, each focal rat was exposed to a pulling partner and a non-pulling partner, but showed a clear difference in her subsequent pulling behaviour towards the two different partners. It remains to be tested whether rats would be able to distinguish between more than two partners. This would be interesting with respect to their natural social system and the associated frequency of social interactions. The strategy used by the rats may be

compatible with generous tit-for-tat (GTFT), which is one of the direct reciprocity strategies found to establish cooperation in game theory models of the iterated Prisoner's Dilemma (Nowak and Sigmund 1994). A GTFT player always cooperates after the partner cooperated, irrespective of its own last move, and cooperates with a small probability after the partner defected. Our rats also pulled for a partner that had not provided help before, but at a significantly lower frequency than for a cooperator. The pulling rate for a non-cooperator was still higher than the pulling rate of a rat that was alone in the experimental cage, i.e. with no partner present (unpublished results). The rats pulling for a non-cooperator might have been influenced by the help experience they had received during the experience phase (generalised reciprocity effect), as both the cooperator and non-cooperator treatment were applied alternately.

In the second experiment, the helping behaviour of rats after having received help was lower towards a new partner than towards a known cooperator, although the received amount of help had been the same in both treatments. This shows that the effect of receiving help from a cooperator on the propensity to help this individual in the future was not due to generalised reciprocity. Such control against generalised reciprocity was necessary because in a previous study, we found that after receiving help from anonymous partners, the propensity of Norway rats to help an unknown partner increased by more than 20% (Rutte and Taborsky 2007). Anonymous social experience has been found to influence behavioural decisions also in the agonistic context (the winner and loser effects; Hsu and Wolf 1999; Rutte et al. 2006), which also holds for Norway rats (S. Lehner, M. Taborsky and C. Rutte, unpublished data). Note that the pulling rates should not be compared between the first and second experiment of this study, as the rats differed in their individual pulling performance, and for the most part, different individuals were used in both experiments (see "Materials and methods"). However, within each experiment, the propensity to help a previous cooperator increased by 46.5 and 50.7% compared to the respective control situations, which may be viewed as additional evidence that direct reciprocity does generate higher levels of cooperation in Norway rats than generalised reciprocity.

Our results suggest that rats remember cooperative interactions with individuals and use this specific information about a present partner in future interactions, if it is available (direct reciprocity). This shows that rats may act similar to primates in an instrumental cooperative task. Experimental studies on food sharing in monkeys that used a similar setup showed that cotton-top tamarins pulled more often for an altruist (i.e. an individual that had pulled before although it did not receive a reward for this action) than for a defector (that never pulled; Hauser et al. 2003), and capuchin monkeys shared food with a partner more readily who had cooperated

with them before (de Waal and Berger 2000). The capuchin behaviour suggests that a positive attitude towards the partner who had helped resulted in attraction, social tolerance and a propensity to cooperate (de Waal 1997), which might be a mechanism explaining the behaviour of Norway rats as well (see Brosnan and de Waal 2002 for a discussion of proximate mechanisms of reciprocal cooperation).

Direct reciprocity can only evolve if specific information about a partner can be used or if individuals interact exclusively with one partner for an extended period (Dugatkin 1997). If the latter does not apply, direct reciprocity involves individual recognition and specific memory about previous interactions with individual partners. For species lacking the cognitive abilities to either identify all possible partners or to remember all relevant interactions with different partners, cooperation based on specific social information may be constrained. In rats, it has been suggested that social and individual recognition is based on olfactory cues (Gheusi et al. 1994). However, memory of the identity of a conspecific in laboratory rats was reduced when a third individual was introduced between interactions (Burman and Mendl 2000). Thus, even if a species evolved the ability to recognise conspecifics individually, memory capacity may not always suffice to keep track of frequent interactions with changing partners. In contrast, for generalised reciprocity to work, an individual needs to base its future behaviour solely on social experience with any member of a group (unspecific information). No higher cognitive setup is necessary for this mechanism, but it may be mediated by neurological or hormonal changes (Uvnas-Moberg 1998; White and Hiroi 1998; Rilling et al. 2002; Kosfeld et al. 2005). It remains an exciting challenge for future studies to clarify how these and other physiological mechanisms might differ between cooperative behaviour based on direct and generalised reciprocity.

Our data show that Norway rats use individual-specific (this study) and unspecific (Rutte and Taborsky 2007) information when deciding to help a conspecific. If a partner's tendency to cooperate is known from previous interactions, rats appear to make use of this information. Using unspecific information if specific information is not available may still be better than using no information. According to this "hierarchical information hypothesis", we would expect that cooperative behaviour towards a partner whose cooperative propensity is known is not influenced by anonymous prior experience, as specific information can be used. Only if such information is lacking should generalised reciprocity be employed. Our results are consistent with this prediction. Future studies should help to unravel whether such hierarchical information processing is more generally involved in decisions of animals to cooperate or not. Importantly, the possibility to make use of any cooperation experience (even if resulting from anonymous partners)

should be incorporated also in studies of more specific reciprocity mechanisms. Otherwise, the existence of direct reciprocity cannot be unequivocally assumed if animals are more likely to help a partner after having received help, even if it was from this very individual. To our knowledge, this is the first study that has taken care of this precaution.

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