

Reciprocal trading of different commodities in Norway rats

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The prevalence of reciprocal cooperation in non-human animals is hotly debated [1,2]. Part of this dispute rests on the assumption that reciprocity means paying like with like [3]. However, exchanges between social partners may involve different commodities and services. Hitherto, there is no experimental evidence that animals other than primates exchange different commodities among conspecifics based on the decision rules of direct reciprocity. Here we show that Norway rats (*Rattus norvegicus*) apply direct reciprocity rules when exchanging two different social services, food provisioning and allogrooming. Focal rats were made to experience partners either cooperating or non-cooperating in one of the two commodities. Afterwards they had the opportunity to reciprocate favours by the alternative service. Test rats traded allogrooming against food provisioning and vice versa, thereby acting by the rules of direct reciprocity. This might indicate that reciprocal altruism among non-human animals is much more widespread than currently assumed.

Keywords: reciprocity, *Rattus norvegicus*, allogrooming, food provisioning

Results and Discussion

The evolution and maintenance of cooperative interactions between unrelated individuals can be explained by the reciprocal trading of given and received help [4]. Theoretical models of several forms of reciprocal cooperation have revealed evolutionary stability of simple exchange rules such as tit-for-tat or generalised reciprocity [5]. Numerous empirical examples suggest that reciprocal cooperation is widespread in nature (reviewed in: [1]), albeit formal experimental analyses of the decision rules involved in reciprocal trading are hitherto lacking. Behavioural biologists have doubted that the assumptions of theoretical models of direct reciprocity are reflecting natural conditions [6], which has caused scepticism regarding the importance of reciprocal cooperation in nature [2]. This scepticism is partly caused by the common assumption that reciprocity involves an exchange of a single commodity. However, the concept of reciprocal altruism is based on the contingency between any services traded between two or more individuals [4]. Many studies from fish to great apes have shown that social partners reciprocate favours in different commodities and contexts (reviewed in: [1]). The vast majority of these studies made use of naturally occurring variation of the respective behaviours, which spawned criticism because of the correlative nature of reported evidence [2]. To rule out the influence of confounding effects, fully controlled manipulative experiments are required. In an elegant field experiment, food provisioning of vervet monkeys was manipulated and the consequent increase in allogrooming of food providers by other group members hinted at a contingent return of a different service, allogrooming for getting access to a food supply [7]. It was not tested, however, if allogrooming in turn affected the propensity to supply food to a previous groomer. In addition, the behavioural manipulation was confined to low-ranking individuals, so potential effects of social hierarchy on this exchange could not be excluded. Hence, it is currently not clear whether and how reciprocal trading of different commodities in animals may work by the rules of direct reciprocal cooperation as predicted by evolutionary theory.

Contingency between received and given help in divergent commodities

We therefore investigated whether two social commodities, food provisioning (Figure 1) and allogrooming, are reciprocally exchanged in Norway rats (*Rattus norvegicus*) by manipulating both the behaviour of partners and the sequence of their social services in a full factorial design (Figure 2). Norway rats are an ideal model system to study reciprocal exchanges because they naturally share food and groom conspecifics [8], and they were experimentally shown to reciprocally trade food for food [9,10] and allogrooming for allogrooming [11]. Rats

live in burrows and form mixed social groups containing up to 200 individuals, which frequently interact among one another [12]. It is yet unknown whether they also trade different commodities with each other. In our experiment, 37 dyads of female wild-type rats were tested in four different situations, each consisting of an experience and a test phase (Figure 2). During the experience phase, focal rats experienced their partner as cooperating or non-cooperating in one commodity (either allogrooming, which was induced by applying saline solution to the neck of the focal rat [11]; or food provisioning, which was induced by enabling a potential donor to pull a tray with food into the focal rat's reach). During the following test phase, focal individuals were enabled to return the received service to the same partner by using the opposite commodity than their partner had used in the experience phase. We recorded the delay until focal rats provided help to their partner for the first time, and how often they helped their partner during the test phase. Allogrooming is a naturally occurring affiliative behaviour where no training was involved. In contrast, rats had been taught at young age how to donate food to a social partner by pulling a tray loaded with food into its reach (see Methods below; [9,13])

We tested whether a received service would change the focal rats' propensity to provide the same partner with a different service, and if so, whether such exchange would work in both directions. Results showed that focal rats indeed provided more help for previously cooperating than for previously non-cooperating partners (GLMM: $\beta = -0.24 \pm 0.007$, $X^2 = 11.82$, $n = 37$, $p < 0.001$, Figures 3a & 3b), and that this occurred similarly in both directions of commodity trading (GLMM, non-significant interaction term: $\beta = 0.11 \pm 0.15$, $X^2 = 0.53$, $n = 37$, $p = 0.47$). The effect was not driven by one of the two directions of commodity exchange, because when the two datasets were analysed separately, we found the same effects. Focal rats groomed previously cooperative food providers more often than non-cooperative ones (GLMM: $\beta = 0.17 \pm 0.05$, $X^2 = 10.77$, $n = 37$, $p = 0.001$), and focal rats provided more food to previously cooperating high groomers than to low groomers (GLMM: $\beta = -0.20 \pm 0.08$, $X^2 = 5.93$, $n = 37$, $p = 0.015$). In response to increased allogrooming, 20 rats increased whereas 11 decreased their food provisioning. In response to receiving food donations, 21 increased whereas 11 decreased their allogrooming rate (see Figure 3). The time until test rats started to provide the respective service to their partners did not differ significantly between previously cooperative and previously non-cooperative partners (Cox-regression model: $\beta = -0.43 \pm 0.17$, $X^2 = 6.24$, $n = 37$, $p = 0.16$, Figure S1).

The results cannot be explained by an unconditional increase in activity or help after receiving food, as rats do not show a "good mood effect" after receiving food in this experimental paradigm [14]. Furthermore, food

donations in this experimental paradigm are not an undirected act, as no or very few attempts to pull the stick are shown when the partner compartment is empty [9,15,16]. In addition, rats tested in a similar paradigm have been shown to respond to the need of their partner when donating food, which may hint on some understanding of their role in this food-provisioning task [17]. Moreover, our study showed that a naturally occurring behaviour (allogrooming) is traded against a previously trained behaviour (food provisioning), hence the reciprocal trading cannot be explained by mere conditioning processes during the pre-training phase [cf. 18], or by other factors such as response facilitation, stimulus enhancement or proximity, because the two tasks differed drastically (for potential alternative explanations and additional information, see Supplemental Information (SI “Alternative Concepts”)).

Focal rats that had experienced a non-cooperative partner also provided help to them, even if it was significantly less than that provided to cooperators. In theoretical treatments of the Prisoner’s dilemma game, usually an “all or nothing response” to experienced behaviour is modelled, which is unrealistic in natural interactions [1,19]. Instead, a continuous response to received cooperation or defection as shown by our rats is much more likely and has been found also in numerous other studies of reciprocal cooperation (including rats; reviewed in [1]). Theoretical models have shown that (i) some unconditional cooperation propensity at first move is required for the establishment of direct reciprocity in a population [5], and (ii) ‘generous’ or ‘forgiving’ reciprocal cooperation, or simply ‘errors’ can significantly enhance the emergence and evolutionary stability of reciprocity [19–21].

Reciprocation of services differing in currency or value has been argued to be cognitively highly demanding. Therefore, it has been assumed that a limitation of such capabilities in non-human animals may prevent the occurrence of reciprocal cooperation among social partners [3]. This applies only, however, if we assume that the payoffs are somewhat calculated, i.e. if decisions follow the rules of ‘calculated reciprocity’ ([22,23], reviewed in: [24,25]). In contrast, trading different services may not be cognitively more challenging than an exchange of the same commodity if simple cognitive mechanisms are applied such as ‘attitudinal reciprocity’ ([26]. reviewed in [24]). As rats apparently apply decision rules denoting direct reciprocity when they trade food donations against allogrooming, reciprocal exchange of different commodities among social partners cannot be cheated. If rats are able to establish cheat-proof commodity trading among one another, our results might indicate that transfers between different commodities could be common in nature. Indeed, our findings are

consistent with a large body of observational data indicating reciprocal exchange between different commodities under natural or semi-natural conditions (reviewed in: [1]). It would be interesting to scrutinize in future studies whether rats and other animals would exchange different commodities also based on generalised reciprocity decision rules that is “help anyone if helped by someone”. Several species including rats, dogs, monkeys and humans have been shown to apply such rules when exchanging the same commodity among one another [16,27–29].

Demonstrating reciprocal trading when several commodities are involved might be difficult under natural conditions, because different commodities can interact with each other, and divergent commodity values and the social setting may additionally increase complexity [30]. A manipulative approach is important also because observational studies cannot control for the potential integration of past social experiences. Experimental manipulation can elucidate underlying mechanisms, but the ecological validity may be unclear [31,32]. Using allogrooming and food provisioning, our study combined a natural with a trained altruistic behaviour, thereby demonstrating that the application of artificial devices can translate into ecological meaningful behaviours, as the rats traded both services against each other in both directions. Moreover, by using two different services with always the same pairs of individuals, mere symmetry-based reciprocity [23], where decisions are based on symmetrical traits like proximity or rank, cannot explain our results. This is difficult to exclude in observational studies.

In our experiment we used randomly chosen dyads of female rats that were familiar to each other. Male rats also apply direct reciprocity decision rules when providing food for each other [10], but it is currently not known whether they would also trade alternative services among one another like females did in our study. Furthermore, it would be interesting to test in future studies whether Norway rats prefer particular partners for cooperative interactions when given the choice, thereby adopting decision rules characteristic of a biological market [7,33,34]. Rats of both sexes form dominance hierarchies, and dominant rats receive more affiliation from subordinates than the other way around. However, reciprocal service works in both directions [11]. In primates, helping decisions may depend on bonding status [1,35], but Norway rats apparently do not form social bonds within their group [36].

Different service values

Focal rats groomed their social partners more often than they provided food for them (GLMM: $\beta = 0.77 \pm 0.07$, $\chi^2 = 114.6$, $n = 37$, $p < 0.001$) and they started grooming them earlier than they started donating food (Cox-regression model: $\beta = -0.79 \pm 0.18$, $\chi^2 = 19.99$, $n = 37$, $p = 0.019$, Figure S1). Both allogrooming and food provisioning involves costs to the donor [11,17]. A preference to groom instead of to provision a partner might have two adaptive explanations. First, rats may prefer allogrooming over providing food because it is the cheaper or more natural behaviour. A previous study has shown that wild-type Norway rats take into account the costs of cooperation when reciprocating received help [17]. Second, the perceived value of grooming and food donations may differ, with receiving food being experienced as a more valuable resource than being groomed. Different values of the exchanged commodities, thus, may lead to more grooming bouts being reciprocated for fewer, more valuable food donations. Previous work has shown that rats take the relative value of received help into account when returning a favour to social partners [37]. Finally, the difference between cooperative and non-cooperative behaviour of the social partner during the experience phase was greater when the latter's role was food provisioning than when it was allogrooming (Figure S2). This may have enhanced the propensity of focal rats to return the previously received service asymmetrically.

We used allogrooming and food sharing because both cooperative behaviours are widespread in animals under natural conditions [1,2,38], and, as our study shows, they can be easily manipulated. Hence our approach enables promising opportunities to experimentally evaluate the general importance of reciprocal trading of diverse commodities in different animals. In addition to the services we chose, other commodities might be reciprocated, such as infant handling [39], sex [40], support in aggressive encounters [41], and tolerance [42]. Recognizing the potential of organisms to exchange different commodities and services among one another is an important step towards understanding the evolution of reciprocal cooperation at large.

Implications

Humans have been termed "ultra-social" because they help others in diverse situations and are highly dependent on each other [43]. This ultrasociality has been suggested to be the key for our ecological success [44], and unlike any other animal humans trade different commodities on a global level. Yet the evolutionary roots of commodity trading are largely unclear [45]. As humans are great apes, primates have often been used as model to study the phylogenetic roots of human reciprocal cooperation. Indeed, there is good observational

evidence for trading different services in primates. Chimpanzees, for instance, trade grooming against support, support for meat and meat for sex [40], whereas Barbary macaques trade grooming for agonistic support and tolerance while feeding [46]. It has not yet been studied experimentally, however, if individuals apply direct reciprocity decision rules in such exchanges, which is required to prevent exploitation by being cheated and hence constitutes a precondition for the evolutionary stability of reciprocal cooperation. Our data show that Norway rats apply such rules when reciprocally trading alternative commodities among one another. This capability is hence not limited to primates but may have originated much earlier in vertebrate evolution. Hence, reciprocal trading of different commodities might be widespread in nature. In fact, evidence from cooperatively breeding fish suggests that they may exchange alloparental brood care for access to resources in a safe territory [47], and reciprocal exchange of commodities may occur also in interspecific relationships such as symbioses [48,49].

Trading goods and services against each other may render fitness benefits. Allogrooming is a frequently occurring natural service in Norway rats [8,50]. Furthermore, Norway rats were previously shown to reciprocate help also within the same type of service, i.e. food for food [9,10] and grooming for grooming [11], and rats initiating as much allogrooming as they receive over their lifetime were shown to survive longer [51]. Hence, the reciprocal exchange of different commodities may reflect an evolved, fitness enhancing behavioural response. Primates have also been shown to live longer when having close bonds with partners that trade favours with them reciprocally [35].

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Author contributions

M. T. and M. K. S. designed the experiment and wrote the paper, M. K. S. collected and analysed the data.

Declarations of interests

The authors declare no competing interests.



Figure 1: Apparatus used for the reciprocal exchange of food

Rats could provide food for a partner by pulling a stick connected to a movable platform. By pulling the stick, the platform moved into the experimental cage and provided food only to the partner, not to the puller. During the experience phase of the experiment, focal rats experienced partners as cooperative food providers or uncooperative non-providers. During the test phase, the roles were exchanged, and focal rats could now pull the stick to deliver food to their experimental partner.

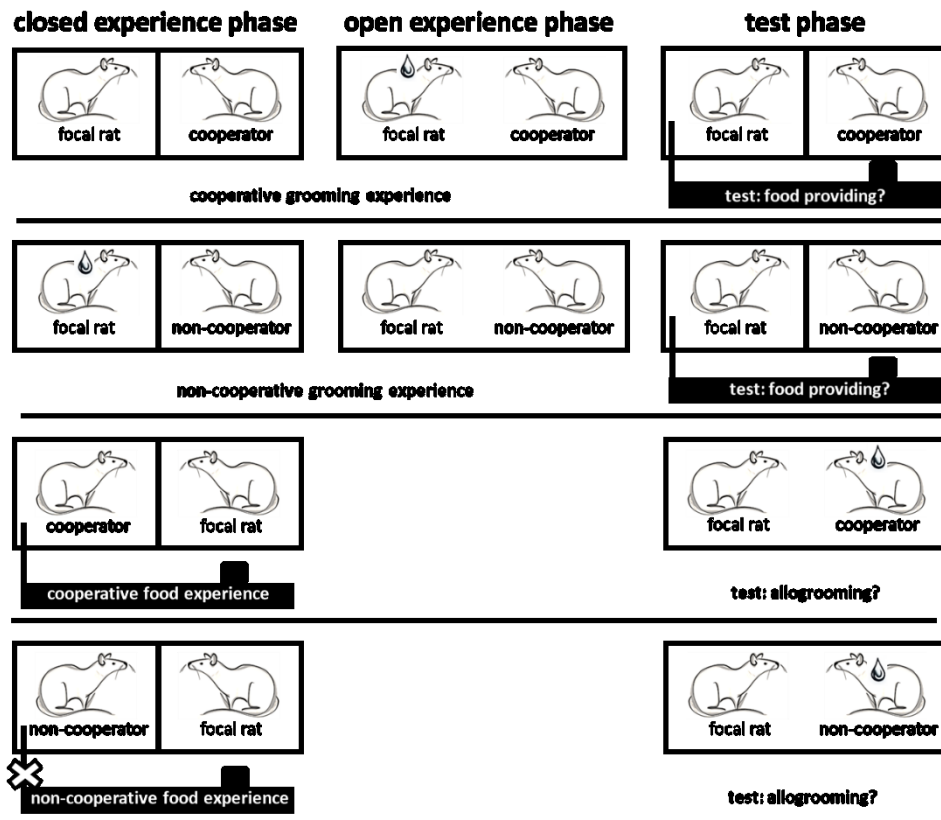


Figure 2: Experimental set-up

The experiment consisted of an experience phase and a test phase. Every focal individual experienced all four treatments with the same social partner, in a randomized sequence. The partner was either cooperating or non-cooperating in one of two tasks, providing food for or allogrooming the focal rat. Afterwards focal rats could benefit the social partner by the alternative social service. In order to produce cooperative grooming partners, we applied a saltwater solution on the focal rat's neck (= drop symbol in figure) when both rats could freely interact. During the associated test phase, focal rats had the possibility to pull a stick that was connected to a movable platform to provide food to the previously experienced grooming partner. In contrast, during the non-cooperative treatment we applied saltwater to the focal rat's neck when the rats were separated from each other by a wire mesh, so the partner could not groom the focal rat. Again, the focal rat was able to benefit the partner thereafter by providing it with food. Importantly, focal rats directly interacted with their respective partners both when these were cooperative or non-cooperative during the open experience phase, and they were separated from them in both situations during the closed experience phase. Hence experiencing cooperation or not, and not the possibility to physically interact, differed between the treatments. In the reversed experimental sequence, focal rats experienced a cooperative, food-providing partner and afterwards

we applied saltwater on the partner's neck to test whether the focal animal's propensity to help the partner removing unpleasant saltwater is enhanced by the previously experienced food donations of the partner. During the control trials simulating defection, we blocked the platform so that the uncooperative partner was unable to provide food to focal individuals; again, during the test phase, focal rats could groom the partner on which saltwater had been applied. (See also Figure S2)

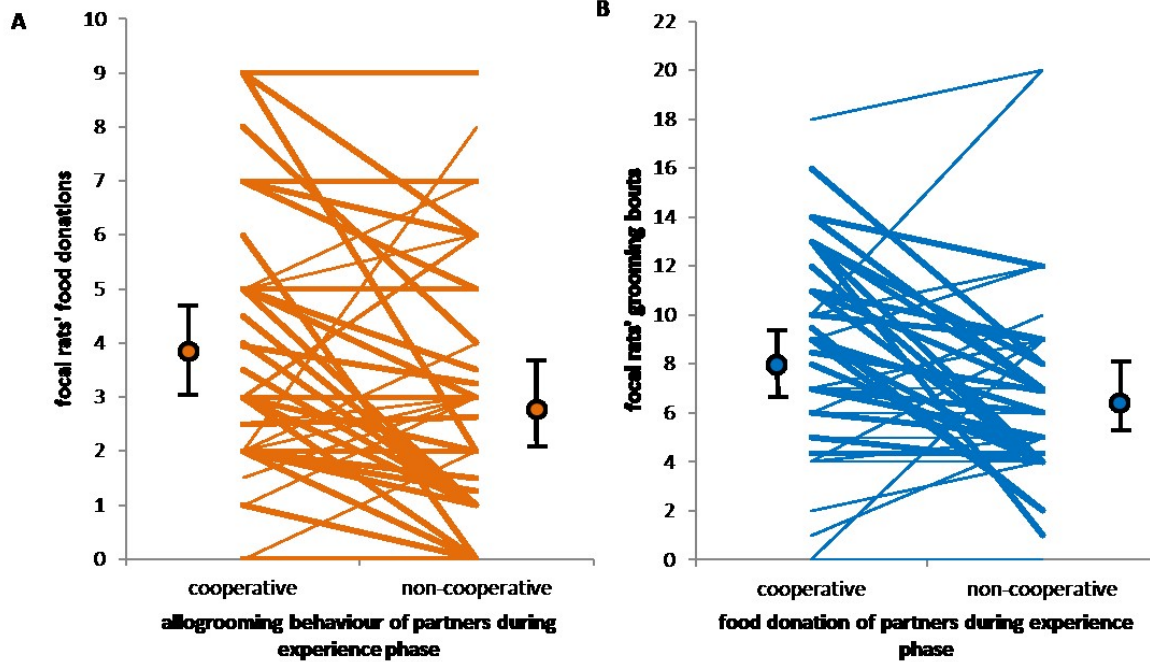


Figure 3: Numbers of helpful acts during the test phase

Focal rats provided more food (a) to previously experienced cooperative grooming partners than to non-cooperative grooming partners. Focal rats also reciprocated in the reversed situation (b), where they groomed more often food providers than non-providers. The inserts depict the respective behaviours. Every line represents the raw data for a single focal rat towards its partner. To avoid overlap of data, we raised the respective lines in 7 cases by 0.5 and in 1 case by 0.25 units on the ordinate for better visibility. The data are summarized by arithmetic means with 95% confidence intervals on each side of the plot. (See also Figure S1)

STAR Methods

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Manon K. Schweinfurth (manon.schweinfurth@iee.unibe.ch).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Experimental subjects and holding conditions

We used 74 adult female outbred wild-type Norway rats (*Rattus norvegicus*; source: Animal Physiology Department, University of Groningen, Netherlands) weighing on average 300g. 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 setup and an observer. They were individually marked by ear punches and housed with littermates in groups of three to five sisters. The cages (80x 50x 37.5cm) were separated from each other by opaque dividers to exclude interactions between the groups. The ambient temperature was 20°C ± 1°C, with a relative humidity of 50 - 60%. The light/dark cycle was set to 12:12 h with lights on at 20:00 hours and 30 minutes of dawn and dusk. As rats are nocturnal and lack receptors for red light all trainings and experiments were conducted during the dark phase of the daily cycle under red light.

Ethical note

In accordance with animal welfare legislation of Switzerland (Tierschutzverordnung Schweiz 04/2008) rats were housed in enriched cages (80cm x 50cm x 37.5cm). Each cage contained a wooden house and board, a plastic tube, a piece of wood to nibble, a paper roll to play, digging-material (wood shavings), nest-building material (shredded and crumbled paper) and a salt block. Food (conventional rat pellets and corn mix) and water were provided *ad libitum*.

The housing of the animals and the experimental procedure were authorized by the Swiss Federal Veterinary Office under license BE98/11. During the experiment, no injuries occurred. In addition, the animals were constantly monitored during all experiments, and if any deviant behavior or unexpected physical reactions had occurred, the experiments could have been stopped immediately.

METHOD DETAILS

Pre-experimental training of food sharing

The experimental setup [16] was based on a two-player sequential food-exchange task. Test cages (80x 50x 37.5cm) were divided into two equal-sized chambers by a wire mesh. A movable platform connected to a stick was installed in front of this cage. By pulling the stick, the rat was able to move the platform towards the test cage, delivering a food reward (one oat flake) to the partner (see [16], Figure 1). All test and partner rats experienced the following training prior to the test. First, each rat was trained to pull a reward for itself (solo-pulling training). Once the rats had learned this task successfully, the second part of the training began. Now the rats were paired with a sister (social-pulling training). From now on, they never receive a reward for pulling the platform anymore. Instead, by pulling alternately for each other the rats experienced that not they but only their social partner received a treat if they pulled the platform. The roles (donor or recipient) were regularly exchanged, and the intervals between these switches were increased gradually from switching after each pull to switching after series of pulls lasting up to seven minutes (i.e., the length of the experimental period). More details on the exact training procedure are described in [37].

Manipulation of grooming rates

Grooming between social partners was induced by applying a salt-water solution (applied 4 times using a cotton bud soaked with a saltwater solution consisting of 250g salt/ 1l water) on the focal rat's neck; see details in [11]). We chose saltwater because rats were shown to avoid eating salty food, and a pilot experiment revealed that they avoided saltwater of the concentration used in our experiment [11]. Hence we enhanced grooming costs beyond the inevitable expense of saliva loss [50], thereby ensuring that allogrooming was **not a merely** self-serving behaviour. In order to experimentally manipulate allogrooming rates and produce cooperating 'high groomers' and non-cooperating 'low groomers', we divided the experience phase into two parts. In the 'closed' experience phase, the pair was separated from each other by a wire mesh. In the 'open' experience phase, both rats could freely interact. Each dyad passed both parts of the experience phase, 'open' and 'closed', in random sequence, each lasting 20 minutes. By providing experience with both phases, we ensured that the degree of separation did not differ between treatments.

Test procedure

We tested in total 37 dyads of rats ($n = 37$). All experimental pairs comprised full sister cage mates. Focal rats tested with cooperating and non-cooperating grooming partners met their partner during both the open and closed experience phases (see above). The only difference between the treatments was that we applied saltwater once during the closed and once during the open experience phase. Therefore, saltwater was applied in both treatments and rats interacted in both treatments with each other, but once they could allogroom after saltwater application (when saltwater was applied in the 'open phase') and once they could not (when saltwater was applied in the 'closed phase'), thereby creating 'cooperating' (i.e., allogrooming) and 'non-cooperating' (i.e., not allogrooming) partners.

Immediately after the last grooming phase, both rats were placed into the food-exchange paradigm and the focal rat had access to the stick in order to pull food within reach of the partner. In 7 out of 37 cases partners groomed focal rats that received saltwater during the open phase less often compared to when no saltwater was applied. In these 7 cases, we switched the treatments to ensure that all partners groomed more often during the cooperating than during the non-cooperating treatment, independently of the previous saltwater application. Importantly, excluding these 7 trials from the analyses did not qualitatively change the results.

We also tested this paradigm in the reversed order. Focal individuals experienced partners as either cooperator or non-cooperator in the food provisioning task. In the cooperative treatment, social partners could provide food to the focal rat during 7 minutes. The number of food items provided was at the partner rat's discretion; i.e. it was not predetermined by the experimenter (see also Figure S2). **After a rat pulled the platform within reach of its partner to eat the oat flake, the platform was pulled back by the experimenter and reloaded.** In the non-cooperative treatment, we blocked the platform to prevent partners from provisioning food to the focal rats. Everything else was the same as in the cooperative treatment, which means that the stick was protruding into the partner's compartment and the platform was loaded with an oat flake. Directly after the experience phase, the focal rat and its partner were placed in the grooming arena for 20 minutes. Here, the partner received a saltwater application (application as above; see Figure 2).

Each phase, where grooming was either experienced or tested, lasted 20 minutes and took place in a glass box measuring 80x 40x 40cm. The food provisioning phase lasted 7 minutes, with one additional minute of prior

habituation. This phase took place in the same cage as the pre-experimental training for food sharing. To minimize the effect of individual differences between experimental partners on the focal rats' behaviour, we used a repeated measures design presenting focal rats always with the same partner. The choice of focal individuals and their partners, as well as the order of focal individuals, treatments, and the order of closed and open experience phases were selected randomly using the Excel command RAND(). However, we ensured (i) that all possible treatment combinations were tested equally often to avoid detrimental sequence effects, (ii) that in the grooming experience phases half of the rats experienced the 'open phase' first and the other half second, and (iii) that the random sequence of focal individuals was kept constant over the different testing days.

Alternatives to contingent reciprocity

The assumption of contingent reciprocation of received help might be challenged by alternative concepts. However, the experimental procedures used in this and similar studies of Norway rats render alternative explanations unlikely:

Potential influence of food receipt or intake

Rats that received a treat might show a general increase in activity, which could translate into increased food provisioning levels. To exclude that this could cause a difference in response to received cooperation versus non-cooperation, experiments have been conducted in which focal rats received the *same* amount of food, once given by the cooperating partner rat and once given by the experimenter after the non-cooperating partner rat had not provided any food. In these experiments, rats generally provided more help to cooperating than to non-cooperating partners even when receiving the same amount of food in the different experience phases [9,16,17]. Conversely, when focal rats received *different* amounts of food in the experience phase which was not due to the behaviour of the present partner rat, but instead brought about by a remotely controlled food dispenser, focal rats did *not* make a difference between previously receiving rewards or not [14]. Apparently, neither receiving treats nor food intake can by itself explain the enhanced helping propensity of Norway rats after experiencing cooperation.

Social context

Pulling the tray towards the cage might reflect conditioned behaviour notwithstanding the social context. Hence, this possibility was scrutinized by providing focal rats with four different situations [9,15,16]. Rats received food

by a cooperating partner or they experienced a non-cooperating partner that did not provide food to them. Afterwards they could decide to donate food to these partners or to an empty cage. Focal rats pulled more often for cooperators than for an empty cage, but they did not pull more often for a non-cooperating partner than for an empty cage [15]. In addition, rats showed no difference in pulling for an empty cage after they had experienced a cooperating or a non-cooperating partner [15]. This indicates that rats take into account whether their food provisioning is received by a partner rat.

Imitation

It might be argued that rats simply copy their partners' behaviour from the experience phase when returning received favour in the respective test, even if there is a time delay between these phases of the experiment. To exclude this possibility, an experiment was conducted in which the focal individuals could return received favour with a different mechanism [52]. Here, focal rats experienced either a partner cooperating by pushing down a lever that delivered food to them, or a partner cooperating by pulling a loaded platform into their reach. Afterwards, focal rats could donate food to their partner by using the alternative device, thereby making copying impossible. The results were compared to the behaviour of focal rats towards respective uncooperative partners. Focal rats provided more food to cooperating than to non-cooperating partners, independently of the device they operated [52]. This shows that rats in such situation do not merely copy the helping behaviour of the partner when returning a received service.

Effects of training

Rats might reciprocate help only because they had been trained in mutual alternation of receiver and donor roles. To check for this possibility, an experiment was performed using a natural behaviour that did not include any training. Here, focal rats experienced partners as cooperating high-level groomers and non-cooperating low-level groomers [11]. Thereafter, focal rats could allogroom their social partner. Focal rats groomed partners more often than had groomed them at enhanced levels before [11]. This illustrates that rats reciprocate favours also by a behaviour for which no pre-training had been provided. Arguments refuting the apprehension that mere *Pavlovian association processes* might be sufficient to explain reciprocal cooperation among Norway rats were outlined in Dolivo et al. [53].

QUANTIFICATION AND STATISTICAL ANALYSIS

Behavioural data

All grooming and pulling events were counted, and the latency to the first grooming and food provisioning event was measured. An allogrooming bout was defined as one individual repeatedly nibbling and licking the body surface of the other except the anal region. A new event was recorded if the allogrooming had been interrupted for at least 10 sec. As most grooming events were invariably short, we chose to analyse the frequency instead of the duration of allogrooming. Grooming phases ('open' experience phases and grooming test phases) were videotaped using a handheld camera mounted on a tripod in front of the experimental arena (Sony: HDR-CX550, using the night vision mode). Video recordings were analysed using the Solomon Coder software (version beta: 14.10.2004).

Statistical analyses

All statistical analyses were performed using R (version 2.15.2, <http://www.r-project.org>; with R studio and packages 'lme4' & 'survival'). To test for reciprocal exchange of commodities, we performed a generalized linear mixed model (GLMM). We included the number of events by the focal rat during the four test phases as a response variable. As explanatory variables, we included the cooperation level by the partner ('cooperating' or 'non-cooperating', see also fig S2) and the order of commodities ('providing food → grooming' or 'grooming → providing food'). As we tested each dyad four times, we included pair identity as random variable. We tested the model for overdispersion, which was not detected, and assumed Poisson distribution of data. We excluded the non-significant interaction between both explanatory variables (GLMM: $\beta = 0.11 \pm 0.15$, $X^2 = 0.53$, $p = 0.47$) and report the reduced model. Because two non-robust datasets could be combined to form a single robust dataset without a significant interaction, we also tested the two datasets ('providing food → grooming' and 'grooming → providing food') separately by following the above described model structure. We applied the same model structure to the latency data using a Cox proportional hazards regression model. Again, we removed the non-significant interaction (Cox-model: $\beta = 0.32 \pm 0.34$, $X^2 = 0.88$, $p = 0.99$). $p < 0.05$ is reported as significant.

DATA AND SOFTWARE AVAILABILITY

Data and software can be obtained from the first author on request.

Appendix

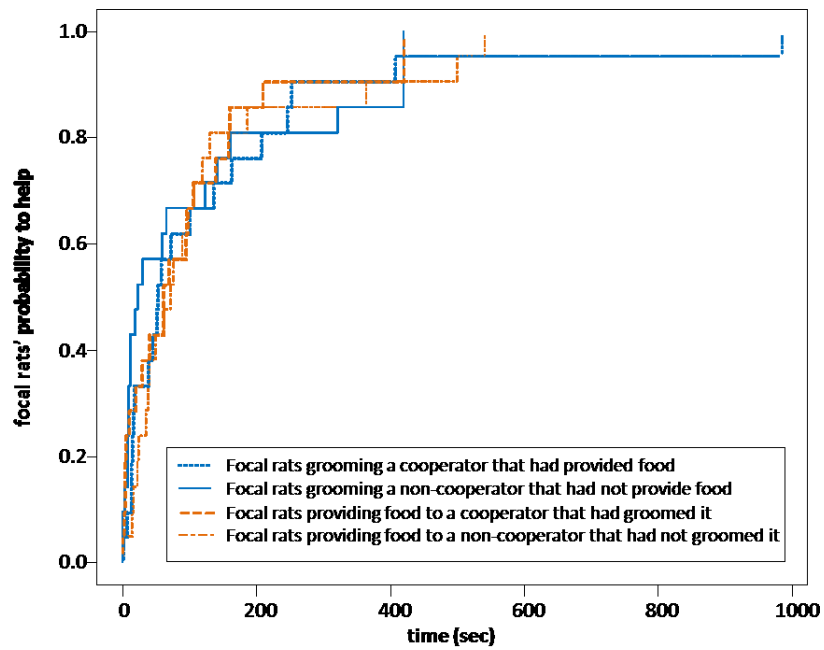


Figure S1: Probability of focal rats to start providing service to their partner during the test phase. Related to

Figure 3

Focal rats did not distinguish between previously cooperating or non-cooperating partners in their latency to provide service, but they generally groomed them earlier than they provided food for them.

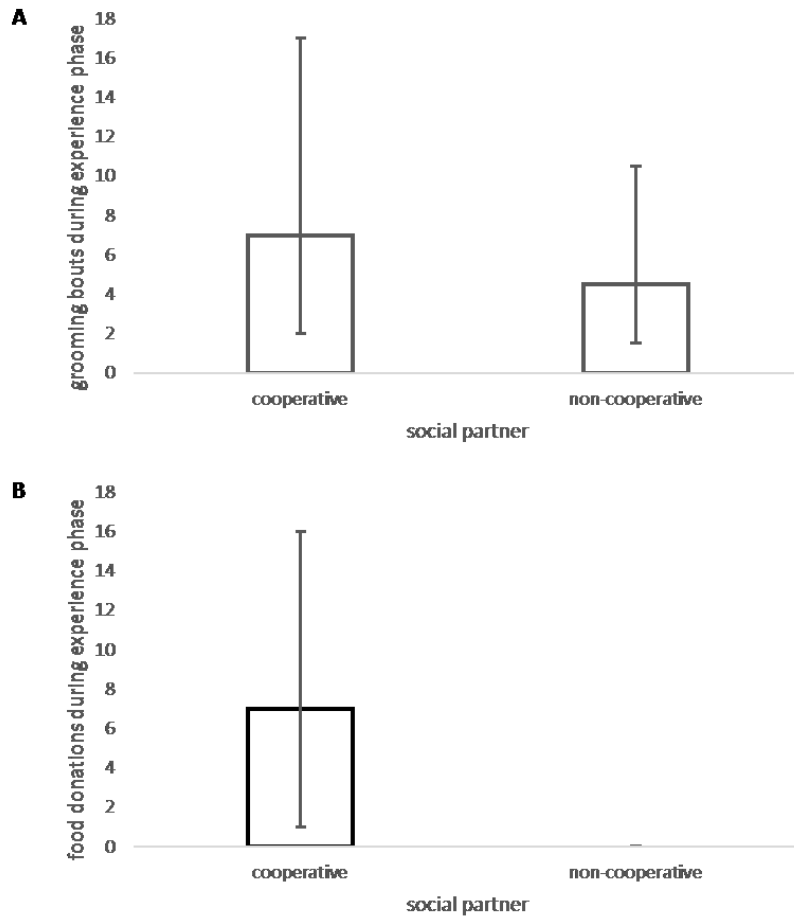


Figure S2: Help provided by partner rats during the experience phase. Related to Figure 2

Focal rats experienced one partner in four different situations during the respective experience phases. Their social partner either groomed them at enhanced levels (cooperative) because saltwater was applied on the focal rat's neck, or at normal levels (non-cooperative) because no saltwater was applied (panel a; difference in grooming rates between the 'cooperative' and 'non-cooperative' situation: Wilcoxon matched-pairs signed-ranks test, $V = 231$, $p < 0.0001$). In addition, focal rats experienced their partner as a cooperating food donor by bringing a loaded platform into their reach, or as non-cooperating 'defector' because the platform was blocked and hence the partner did not donate food to them (panel b). Here shown are the median frequencies \pm interquartile ranges.