Rats play tit-for-tat instead of integrating social experience over multiple interactions

Manon K. Schweinfurth[1,2] * and Michael Taborsky[2]

[1] School of Psychology and Neuroscience, University of St Andrews, St Mary's Quad, KY16 9JP St Andrews, UK

[2] Behavioural Ecology, University of Bern, Wohlenstr. 50a, 3032 Hinterkappelen, Switzerland

* Corresponding author: ms397@st-andrews.ac.uk / phone: +44 (0)1334 46346

Theoretical models of cooperation typically assume that agents use simple rules based on last encounters, such as "tit-for-tat", to reciprocate help. In contrast, empiricists generally suppose that animals integrate multiple experiences over longer timespans. Here we compared these two alternative hypotheses by exposing Norway rats to partners that cooperated on three consecutive days but failed to cooperate on the fourth day, and to partners that did the exact opposite. In additional controls, focal rats experienced cooperating and defecting partners only once. In a bar-pulling setup, focal rats based their decision to provide partners with food on last encounters instead of overall cooperation levels. To check whether this might be due to a lack of memory capacity, we tested whether rats remember the outcome of encounters that had happened three days before. Cooperation was not diminished by the intermediate time interval. We conclude that rats reciprocate help mainly based on most recent encounters instead of integrating social experience over longer timespans.

Keywords: *Rattus norvegicus*, cooperation, reciprocity, tit-for-tat, memory, food sharing

Introduction

Evolutionary mechanisms underlying cooperative behaviour between unrelated individuals are hotly debated (1,2). If helping others involves fitness costs, future benefits must compensate for this loss for cooperation to evolve (3). The reciprocal exchange of help between social partners can lead to stable cooperation by taking turns (4). The sequential iterated Prisoner's dilemma game is a mathematical paradigm used to model the prerequisites for evolutionarily stable decision rules of reciprocal cooperation in such social dilemmas (5–7). Here, two players can decide either to cooperate with a partner or to defect. The dilemma is caused by the payoff matrix. Defecting individuals receive the highest benefit in a single interaction, because they receive help without paying any costs of helping others. At the same time, if both partners cooperate, they gain more than, if both are defecting. Helping a partner while the latter is defecting will deliver the lowest reward, i.e. the "suckers payoff" (5). Consequently, if players meet only once, defection is the optimal choice. If partners meet repeatedly, however, mutual repeated cooperation between the partners may evolve, leading to the highest payoffs.

Hundreds of behavioural strategies have been modelled to clarify when cooperation can evolve under these adverse conditions (5,8). Computer simulations revealed that one of the simplest successful strategies in the iterated Prisoner's dilemma game is tit-for-tat (5). Here, players start cooperatively and subsequently copy the last behaviour of their social partner. In order to decide whom to help, donors need to remember the identity of the partner in combination with the outcome of their last interaction. A problem for the tit-for-tat strategy is that mistakes can easily abolish reciprocal cooperation. One accidental defection can lead to continued mutual defection, as tit-for-tat is not meant to correct mistakes (9). However, memory mistakes may occur. A study of human subjects, for instance, showed between 10 and 24% memory errors when subjects were asked to remember only the last encounter in an iterated Prisoner's dilemma game played in groups of 5 to 15 individuals (10). This caused cooperation to collapse and the only stable strategy remaining was "always defecting". A possible solution to this problem is a modification of the response strategy, where individuals

sometimes cooperate even if the last move of their partner was "defecting"; This modified strategy has been referred to as "generous tit-for-tat" (11). Another successful variant of the response strategy is "win-stay, lose-shift", where individuals repeat their previous move if doing well, but change otherwise (12).

Generally, strategies taking into account only the last experience can be outcompeted by strategies integrating several experiences, e.g. "tit-for-2tats" (13). In nature, animals typically interact more than once with each other. By experiencing a partner repeatedly, animals can learn their behavioural strategies more easily (14) and response errors are less likely to occur. However, presently it is unclear how animals memorize and use previous social experiences in social situations, and whether multiple, instead of single, experiences with the same partner are integrated to trigger an appropriate response (15).

Here we ask whether wild-type female Norway rats (*Rattus norvegicus*) base their decision to reciprocate help on long-term cooperative experiences with a social partner, or whether they respond to the last encounter. We used rats because they form social groups of various sizes (16) and show kin (17,18) and individual recognition (19,20). Importantly for our study, rats show a high propensity to cooperate (reviewed in: (21,22)). For example, rats prefer to work with a partner, even if they could achieve the same reward individually (23). Further, if they can choose between a prosocial option that rewards their partner and themselves or a selfish option, they opt for the prosocial option (24). Rats have been shown to help conspecifics in different situations. For instance, they were found to free trapped partners (25) and to allogroom conspecifics (26), whereby they apply decision rules reflecting direct reciprocity (27). They were frequently shown to help conspecifics by donating food to a social partner (22), and they exchange different tasks and commodities with each other (28). Previous experiments demonstrated that wild-type female Norway rats exchange food according to both direct and generalised reciprocity rules (29,30), whereas male Norway rats apparently only apply direct reciprocity (31).

To test the importance of integrated versus last social experiences for the helping propensity of rats, focal rats experienced help by partners that cooperated in three successive encounters on three consecutive days, but a lack of cooperation in the last encounter before focal rats could provide food to their partner. The same focal rats experienced a second partner that defected in all but the last trial before the focal rats could repay favours. In addition, focal rats experienced short-term cooperating and defecting partners that were experienced only once before they could provide them with food. In order to test for a potential limitation of memory capacity, we additionally investigated the focal rats' ability to remember the cooperating and defecting behaviour of partners experienced one or three days prior to the test.

Cooperation in our experiments involved providing food to a partner with the help of the bar-pulling paradigm (Fig. 1), reflecting a variant of the iterated sequential Prisoner's dilemma game (29,32–34). We predicted that if rats integrate multiple successive experiences, they will provide more food to partners that were cooperating compared to defecting on several consecutive events, even if their last experience with the respective partners was opposite. However, if rats base their decision mostly on their last encounter, they should provide more food to previously defecting partners that were cooperating in the last encounter than to previously cooperating partners that were defecting in their last move. Furthermore, in that case their helping propensity should not differ between partners experienced only once, or several times.

Materials and methods

Experimental subjects and housing conditions

We used female adult outbred wild-type Norway rats, weighing on average 350 g. The rats were obtained from the Animal Physiology Department at the University of Groningen (Netherlands) and were habituated to handling right after weaning. Rats were individually marked by ear punches. The cages (80 x 50 x 37, 5 cm, housing littermates in groups of up to five sisters) were separated from each

other through opaque walls to exclude interactions between the groups. The housing rooms had a temperature of 20°C ± 1°C and a relative humidity of 50 - 60%. The rats were kept under an inversed 12:12 h light/dark cycle with lights on at 20:00 hours and 30 minutes of dawn and dusk. Rats are nocturnal and cannot see the colour red (35,36). Therefore, all trainings and experiments were conducted during the dark phase of the daily cycle and under red light.

Pre-experimental training for food sharing

Rats were individually trained to use the bar-pulling paradigm (see (37) for a detailed description of the procedure). The setup consisted of a test cage (80x 50x 37.5 cm), which was divided by a wire mesh into two compartments and a movable tray connected to a stick (Fig. 1). By pulling the stick, the platform moved towards the cage and provided food (an oat flake) only to the partner of the pulling individual (29). To ensure task understanding, every rat was first trained to pull the tray for itself (solo-pulling training). After the learning criterion of at least eight pulls within seven minutes was reached, we switched to the next stage. From now on, rats were always trained with a sister as training partner, and pulling individuals never received a reward for pulling the tray any more (social-pulling training). The roles between training partners (donor, recipient) were exchanged and the intervals between these switches were increased gradually over 18 sessions, from switching after each pull to switching after series of pulls lasting up to seven minutes (i.e., the later experimental period).

Reciprocity test

Each focal rat (n= 21) received four experimental treatments (Fig. 2), each consisting of an experience and a test phase. During the long-term experience phase, focal rats were exposed to the same social partner four times on consecutive days. During the short-term experience phase, focal rats were exposed to a social partner only once. In one treatment, the social partner provided food to the focal rat by pulling the platform towards the latter on three consecutive days. On the last day of the experience phase (t_4) the platform was blocked with a string and therefore the partner did not provide food to the focal rat (hence called treatment CCCD, where C = cooperation and D = defection). On the following day, the roles were reversed so that the focal rat could now pull the platform with food into

reach of its partner. In a second treatment, the platform was blocked on the first three days so that the partner rat did not provide any food to the focal rat. On the 4th day of the experience phase, the platform was unblocked and the social partner now provided food to the focal rat (DDDC). Again, on day five the focal rat was enabled to provide food to its partner in return. In a third treatment, focal rats experienced a social partner once as being a cooperator (C) before they could donate food to it during the test phase on the next day. In treatment 4, rats experienced a social partner once as being a defector (D) before they could donate food to it during the test phase on the next day. All experience and test phases lasted for seven minutes, with one minute of acclimatisation prior to start (30). Rats only experienced one trial per day.

The focal rats' partners (n= 33) were used several times during the experiment, but we ensured that focal rats only met partners that they had not met before the experiment. Each focal rat experienced four different unrelated and unfamiliar partners serving as either long-term cooperator, long-term defector, short-term cooperator, or short-term defector. We ensured that experimental partners of focal rats continued to cooperate with them over several days during the experience phase by making use of the fact that rats show generalised reciprocity, i.e. they help others if they received help by someone (29). For this purpose we paired partners of focal rats with trained cooperators in the evening after they had provided food to the test animals, and these trained cooperators provided food to them quasi as a return benefit for their previous cooperation. This procedure ensured that the motivation of partners of test animals persisted over the days where they donated food to them without receiving any favours from them in return. Focal rats and their partners, the test order of focal rats, and the order of treatments were selected randomly using the Excel command RAND().

Test of memory capacity

In order to test the memory capacity of rats, we exposed 25 randomly selected individuals to four treatments in a randomized order. Each rat experienced either a cooperating or defecting partner during 7 minutes as described in the reciprocity experiment, but this experience happened only once. Either one or three days later, the test rats were enabled to provide food for their partner. To make

the conditions of this memory test as similar to the reciprocity experiment as possible, we provided the test rats with similar handling conditions by placing them in an empty cage containing the pulling apparatus for the same period (1+7 min) on the two days on which they did not experience help by a partner (see Fig. S1).

The cooperating and defecting partners used in the memory capacity experiment were trained to perform their divergent roles. Cooperators (n= 6) were randomly selected amongst individuals with good pulling performance after training. They received additional social pulling sessions in which they were always paired with another cooperator and thus always cooperated during the experience phases. Defectors (n= 6) were randomly selected and did not receive any solo pulling training. They experienced the same number of social pulling sessions as the focal rats did, but they were paired with other defectors so that they did not learn how to pull.

Statistical analyses

All statistical analyses were performed using R (version 2.15.2; with R studio, packages: MASS, lme4, TOSTER). In all phases of these experiments, the numbers of pulls (i.e., the numbers of provisions for the respective partner) were counted.

To compare the focal rats' tendency to help previously experienced partners during the test situation, we performed a generalized linear mixed model, assuming a Poisson distribution (GLMM; R command: glmer). We tested the model for overdispersion, which was not detected, hence showing an appropriate fit. As explanatory variables, we included the last cooperation level by the partner ('cooperating' or 'defecting') and the amount of experiences ('several' or 'one'). As we tested each focal rat four times, we included the identity as random variable. Further, we included the partner's identity in the model as a random effect because they served several times as a partner of different focal rats. We excluded the non-significant interaction between both explanatory variables (GLMM: β = 0.09 ± 0.22, n= 21, *p*= 0.67) and report the reduced model. Further, we tested which conditions were different and were equal to each other by conducting posthoc TOST Paired Samples T-Tests (R

command: dataTOSTpaired). Additional information on this test can be found in the supplementary material. Furthermore, using Spearman rank correlation analyses, we tested the relationship between the number of pulls of cooperating partners during their last encounter with the focal subject and the number of pulls of the latter during the test phase.

To compare the focal rats' ability to remember cooperators and defectors for 1 or 3 days, we analysed the total number of pulls for the respective partners using a generalized linear mixed model. We included the pulls of focal rats as response variable, the focal and partner rats' identity as random variable to account for multiple testing of the same individuals, and cooperation level of the partners ('cooperating' or 'defecting') as well as the time delay between experience and test phase ('one' or 'three' days) as fixed factors. We excluded the non-significant interaction between both explanatory variables (GLMM: β= -0.16 ± 0.19, X^2= 0.68, *p*= 0.41) and report the reduced model. We also tested for overdispersion of the data, which was not the case.

Results

Reciprocity test

Focal rats donated food less often to partners that were defecting on the day before the test (treatment CCCD and D vs DDDC and C; GLMM: β = -0.35 ± 0.11, n= 21, *p*= 0.001; Fig. 3). Their pulling rates were lower for partners that they had experienced for four days with conflicting cooperation experiences (CCCD or DDDC) than for partners that they only met cooperating or defecting once (treatments C and D; GLMM: β = -0.40 ± 0.11, n= 21, *p*= 0.0003). It should be noted that two rats showed high donation rates only in the single experience treatments (C and D; fig. S2). If these two rats were removed from the sample, the first effect was still significant (CCCD and D vs. DDDC and C; GLMM: β = -0.36 ± 0.12, n= 19, *p*= 0.003), whereas the latter effect disappeared (CCCD and DDDC vs. D and C; GLMM: β = -0.15 ± 0.12, n= 19, *p*= 0.22). Nevertheless we report the result from the full sample as there is no reason to believe that these two rats differed from the others due to reasons suggesting their removal from analysis.

Posthoc analyses revealed that focal rats cooperated more often with C than D partners (Paired Samples T-Test: t_{20}= 2.59, *p*= 0.018). The same was true for DDDC vs. CCCD partners (Paired Samples T-Test: t_{20}= 2.29, *p*= 0.033). Although we did not detect a significant difference between the focal rats' pulling frequency for D and CCCD partners (Paired Samples T-Test: t_{20}= 1.56, *p*= 0.14), it cannot be concluded that focal rats provided equal levels of help to them; the equivalence test did not detect equivalence either (TOST Paired Samples T-Test: t_{20}= -0.74, *p*= 0.24). There was a non-significant trend that C partners received more help than DDDC partners (Paired Samples T-Test: t_{20}= 1.85, *p*= 0.08; detailed test results are provided in tab. S1). The number of food donations by focal rats during the test phase did not correlate with the number of pulls of partners cooperating during the last experience encounters (Spearman rank correlation: S= 1426.3, rho= 0.07, n= 21, *p*= 0.75).

Test of memory capacity

Again, the rats pulled more often for cooperating than for defecting partners (GLMM for number of pulls: β= -0.42 ± 0.11, n= 25, *p*= 0.006; Fig. 4). Notably, this applied irrespectively of whether they had experienced their respective partners one or three days prior to the test phase (GLMM: β= -0.01 ± 0.09, X^2= 0.01, n= 25, *p*= 0.94; Fig. 4).

Discussion

Rats provided food more often to partners that had been cooperating during the last encounter prior to the test than to partners that had been defecting during the last encounter. This suggests that rats mainly cooperate according to their last experience with a partner instead of responding to the latter's overall cooperation level. While the last encounter dramatically changed their response towards conspecifics, cumulative experience may still have some effect, as in direct comparisons DDDC and C partners, as well as CCCD and D partners, were not treated equally. The trend that rats cooperated more often with C than DDDC partners might suggest some integration, as DDDC partners were previously not always cooperative, whereas C partners were, because they were experienced only

once and only as cooperators. Hence, rats might consider information of previous encounters as well. Overall, however, rats clearly weigh the last experience disproportionally.

The fact that rats base their decision to reciprocate help mainly on their last interaction with a partner, which happened one day before the test, might suggest that they are unable to remember interactions that had occurred in a more distant past. However, our second experiment of the rats' ability to remember the behaviour of partners for one or for three days did not indicate a decline of memory during this time span. The rats provided more food when facing a previous cooperator than a previous defector independently of the time span that had passed between experience and test phase. The rats were thus able to remember the outcome of their social interactions with a partner at least for three days. These results suggest that rats have access to social information spanning several days. Nevertheless, they consider mainly the most recent experience when deciding to help a partner.

Importantly, the results cannot be explained by memory extinction, memory interference or conditioning. (i) Memory extinction denotes the loss of a conditioned response that is not rewarded anymore. Theoretically, rats might simply associate the movement of the platform with a reward. If a defector did not pull the stick, focal rats may have reduced pulling the platform in the test phase merely because of the lack of a rewarding movement in the previous experience phase. However, rats can remember the behaviour of two (30,31) and four partners (38) that were experienced in a sequence and help previous cooperators more often than previous defectors, independently of the last experience before being tested. Thus, despite the last experience differing from their test partners' cooperation levels, rats are able to distinguish between previous cooperators and defectors. Therefore, the rats' cooperation decisions are apparently not constrained by memory extinction. (ii) Memory interference describes that new information interferes with earlier information, causing the latter's devaluation. According to this logic newly available information may replace previous information, which might explain why rats cooperated according to the last experience. This possibility can also be excluded, however. A study, based on a similar experimental design as reported here, that presented rats with a sequence of different cooperating or defecting partners, showed that focal rats

responded to each individual partner according to its previous behaviour, despite the fact that the last interaction with a different partner provided the opposite cooperation experience (38). Hence, the last experience did not interfere with the memory of previous interactions with other partners. (iii) Conditioning cannot explain our results either, because in the same experimental setup rats have been repeatedly shown to refrain from pulling food towards the neighbouring cage compartment after experiencing cooperating partners if that compartment is empty, whereas they do pull food towards it when the previous cooperator is present in that compartment (29,30,39,40). Furthermore, previous experiments revealed that rats do not merely copy their partner's behaviour in the experimental paradigm we used, because they successfully transfer between different actions of help, e.g. pushing a lever or pulling a tray to deliver food to a partner (41), and they exchange different commodities with a partner such as allogrooming for food (28). In addition they also exchange services that do not involve any instrumental training, such as reciprocal allogrooming (27). In summary, rats seem to base their decisions to help primarily on the last encounters with their partner, which seems not to be affected by any memory constraints and cannot be explained by conditioning (cf.(42)).

Under natural conditions, rats live in groups of various sizes ranging up to 200 individuals (43). In such large colonies, it may be difficult to keep track of previous encounters with different social partners, even if these are biased towards members of a limited subgroup. Living in large groups is assumed to make strategies that monitor several encounters with different interaction partners cognitively demanding (44). Although the occurrence of mistakes could be lowered if several encounters were considered, applying simpler decision rules might be better when exposed to complex social challenges (45–48). For instance, humans cooperating in an iterated Prisoner's dilemma game were shown to switch to using only the information of the last encounter when challenged with a working memory task between interactions (49). In addition, while cooperation in iterated Prisoner's dilemma games is modelled as an all-or-nothing response, cooperation in the real world is more likely a continuous response, i.e. cooperating more or less. Under this condition, providing some help to defectors, even if considerably less than for cooperators, could act as a buffer for memory mistakes or provide

incentives to social partners to start cooperating (11). Rats helped defectors less than cooperators, but they provisioned defectors to some extent too. Hence their strategy seems to be more forgiving than the narrow tit-for-tat strategy characterized by an all-or-nothing response.

Our results are consistent with the observation that female Norway rats apparently lack social bonds (50). Instead of incorporating information over several encounters into a stable social bond, rats seem to continuously replace information by each interaction. This may be a cognitively less demanding way to cope with a multitude of interactions involving many different social partners, which seems to be the natural situation in Norway rats (see above). Nevertheless, this recency effect might also be important for animals exhibiting social bonds that are influenced by cooperation. The more animals weigh the last experience, the more likely social bonds change over time. In fact, many decisions of animals both in sociopositive and socionegative contexts might be driven only or primarily by last experiences (51), which may be memorised over extended periods. Hence, we urge that more manipulative studies are needed to carefully disentangle the relative importance of last from integrative information on social partners in a range of different animals and contexts.

Previous experiments testing for contingent responses in repeated donation games using fish (e.g. (52–54)), birds (e.g. (55–57)), and primates (e.g. (58–60)) did not allow distinguishing between immediate and cumulative responses to cooperation or defection of their partners. Therefore, to the best of our knowledge this study is the first to test for these alternative possibilities. Given the scepticism that animals use decision rules based on last encounters, similar to tit-for-tat, in mutual cooperation (10,15), our results prompt a re-evaluation of the behavioural mechanisms involved in reciprocal cooperation.

Various proximate mechanisms have been suggested to underlie reciprocal cooperation. These include decisions based on symmetrical traits ("symmetry-based reciprocity"), recollection of the quantity or quality of received help and consequential attribution of appropriate returns ("calculated reciprocity"), remembrance of prior short-term attitudes or long-term emotions associated with a particular partner

("attitudinal reciprocity" and "emotional bookkeeping"), or a response to physiological changes caused by received help (61,62). Calculated reciprocity is probably the most contended among these mechanisms, because it implies scorekeeping of received help. We did not find an association between the numbers of donations received and given, which is at variance with the assumptions of this mechanism. This finding is in line with other studies ((59,63) but see (64)). Decision making in cooperative contexts can be explained by short-term physiological changes (reviewed in: (65)). In our study, this is rather unlikely to have strongly affected the results, because rats were tested 24 hours after the last encounter (during the memory capacity test even three days after meeting the partner). A memory of emotions or attitudes associated with a certain partner might have been involved in the regulation of reciprocal cooperation in our experiment, as emotions are known to bias decisions (66) and reduce memory errors (67), which is an important precondition for successful application of a tit-for-tat like strategy.

In conclusion, our results show that rats cooperate more often with social partners that have been cooperative in their latest interaction. Apparently, Norway rats use a simple heuristic based primarily on the outcome of their last interaction, resembling a tit-for-tat like strategy that cannot be attributed to a lack of memory capacity as suggested by the results of our memory capacity test. As this is the first study disentangling recent from cumulative information on the cooperation propensity of social partners, more research is needed to test such decision rules in different social contexts and in a variety of species.

Ethics

Rats were housed in cages (80x 50x 37.5 cm), enriched with a wooden house and board, a channel, a piece of wood to nibble, a loo roll to play with, digging-material (wood shavings), nest-building material (hay) and a salt block. Food (conventional rat pellets and corn mix alternating with fresh fruits and vegetables) and water were provided *ad libitum*. The rats were never food deprived, nor did injuries occur during this study. The housing of the animals and the experimental procedure were authorized by the Swiss Federal Veterinary Office under license BE25/14.

Data accessibility

The data reported in the paper will be made available in the electronic supplementary material.

Authors' contributions

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

Competing interests

The authors declare no competing interests.

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Fig. 1: Apparatus to provide food to each other

Rats could provide food to each other by pulling a stick connected to a movable platform. By pulling the stick, the platform moves into the experimental cage and provides food only to the recipients. During the experience phase, focal rats experienced partners as cooperating food providers or defecting non-providers. During the test phase, the roles were exchanged and focal rats could pull the stick to deliver food to their social partner.
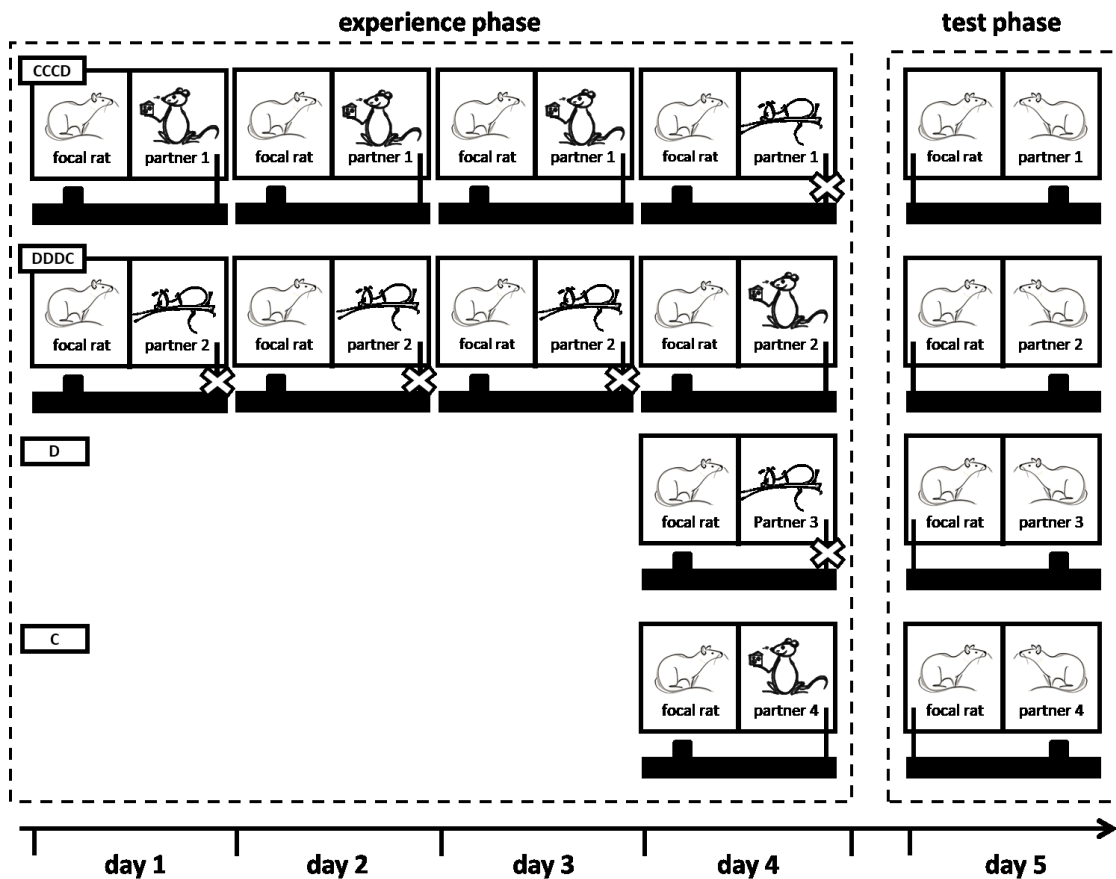
Fig. 2: Experimental set-up

During the experience phase, focal rats received help from a partner that pulled a platform towards them, which provided a food reward. In the CCCD treatment, the partner provided food on 3 consecutive days ("cooperation experience", C), but failed on day 4 ("defection experience", D; platform blocked, indicated by a cross across the pulling stick). During the DDDC treatment, the platform was blocked during the first 3 days so that the focal rats did not receive help from the partner. On day 4, the platform was unblocked and the partner delivered food to the focal individual. In the D treatment, the partner was only experienced once as a defector not providing any food. Finally, in the C treatment, the partner was only experienced once as a cooperator providing food to the focal subject. During the test phase (day 5), the focal rat got access to the platform and could provide food to the partner it had experienced on the previous 4 days. Each focal rat was tested in all four treatments.
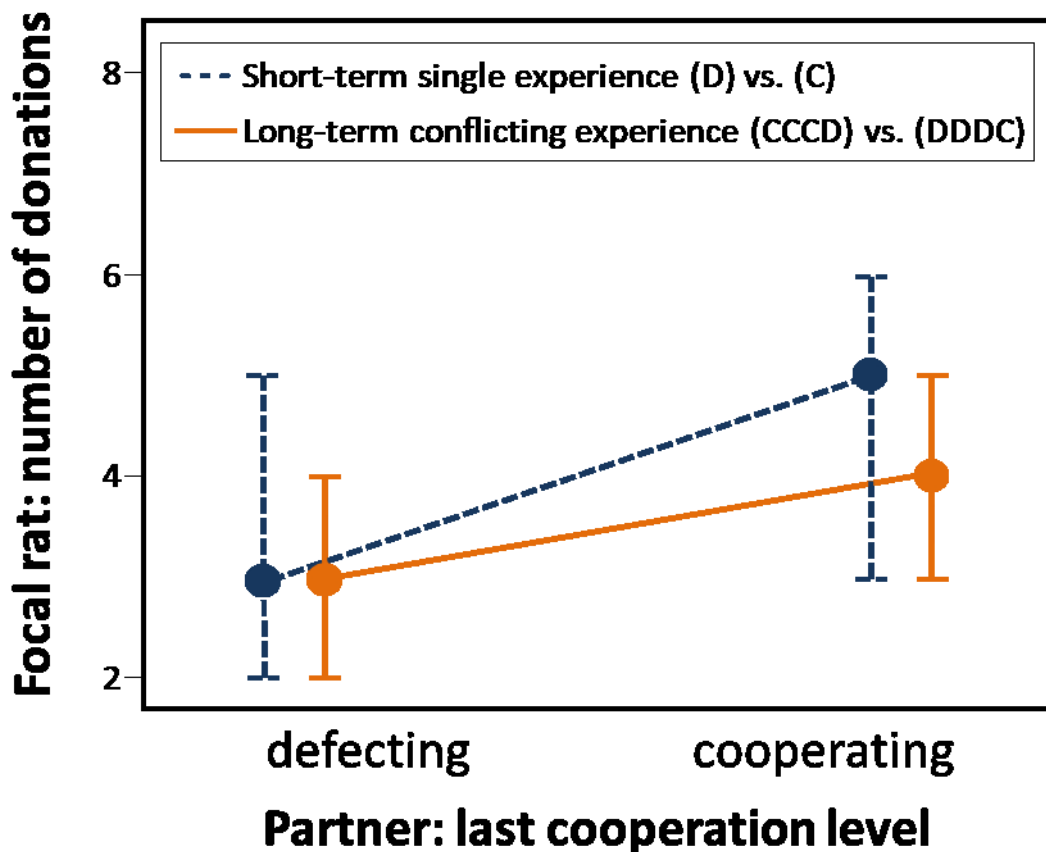
Fig. 3: Food donations of focal rats to their social partners depending on the latter's previous long-term or short-term cooperation propensity.

Focal rats pulled more often for partners (DDDC) that had defected for three days but cooperated on the last day prior the test phase, compared to partners (CCCD) that had cooperated for three days but defected on the last day (indicated by continuous orange line). Likewise, rats provided more food to cooperating (C) than to defecting partners (D) that had been encountered only once, i.e. on the day before they could provide them with food (indicated by dashed blue line). Median frequencies with interquartile ranges are shown. The individual donation rates are shown in Fig. S2.
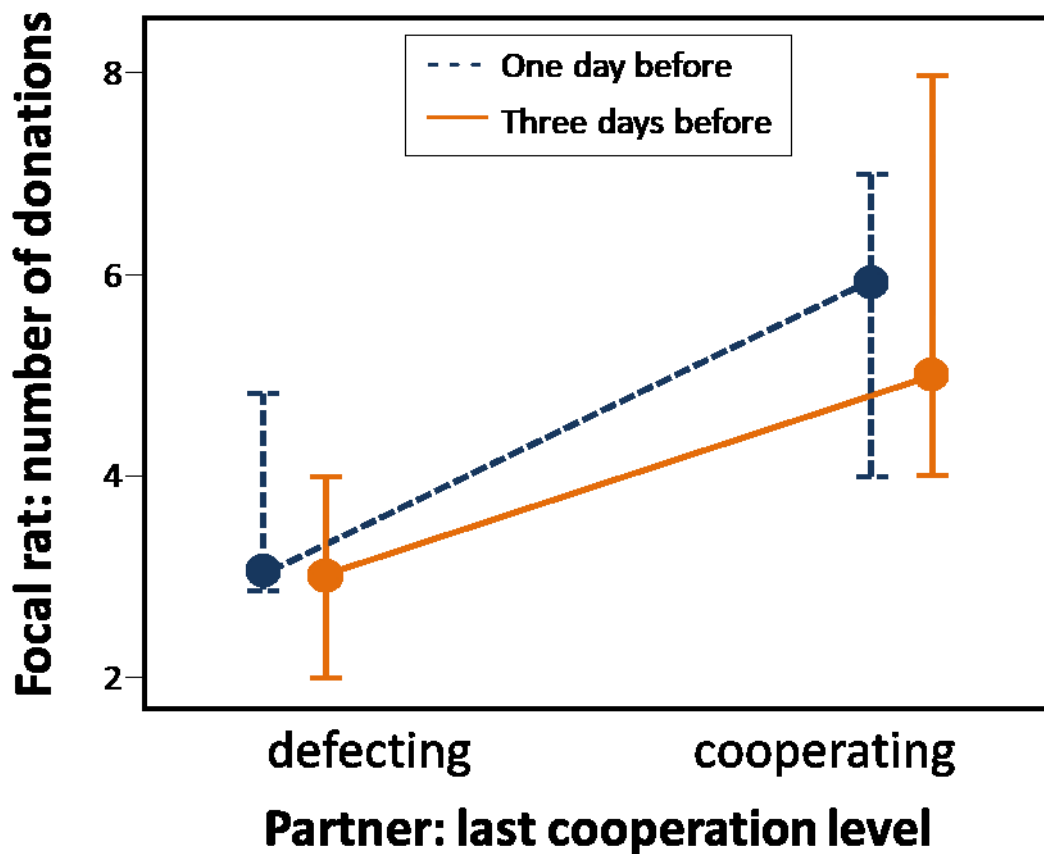
Fig. 4: Total number of pulls of focal rats for cooperators and defectors experienced once, either one or three days prior to the test

Rats provided more food to cooperative than to defective partners, irrespective of whether the partners' helpfulness was experienced one or three days prior to the test. Median frequencies of pulls with interquartile ranges are shown.

Appendix: Comparisons between the four experimental conditions

We performed TOST Paired Samples T-Test to examine potential differences and equivalences between conditions (tab. S1) by reversing the roles of H_0 and H_1, taking into account that the data are paired, i.e. the same focal rats were tested repeatedly (1). This test is based on a parametric t-test, whereas our data were not normally distributed. However, based on our sample size this assumption violation does not impact the detection rate of this test (2). Further, we validated this approach by comparing our results to a permutated Paired Samples T-Test (R package: RVAideMemoire, code: perm.t.test with 5000 permutations). The results did not deviate from the results obtained with TOST Paired Samples T-Tests, which seems therefore a valid test for our data (3).

This TOST Paired Samples T-Test requires defining a threshold above which two conditions are considered as equal. A medium sized effect size is d= 0.5, i.e. two groups differ by half the standard deviation, which is commonly used for equivalence tests (4). Hence, we set the upper and lower equivalence boundaries symmetrically to ± 0.5. If the true effect (± 90% confidence interval) was within this boundary, it was considered to be equal. To test whether the effect is within the boundaries, two one-sided tests are conducted. If both one-sided tests are significant, H_0 can be rejected, i.e. the conditions can be considered to be equal.

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Tab. S1 Comparisons between the four experimental conditions

Condition	Dissimilarity	Similarity	
		TOST upper boundary	TOST lower boundary
C vs. D	t_{20}= 2.59, *p*= **0.02**	t_{20}= -0.30, *p*= 0.61	t_{20}= 4.88, *p*< 0.001
DDDC vs. CCCD	t_{20}= 2.29, *p*= **0.03**	t_{20}= -0.01, *p*= 0.50	t_{20}= 4.58, *p*< 0.001
D vs CCCD	t_{20}= 1.56, *p*= 0.14	t_{20}= -0.74, *p*= 0.24	t_{20}= 3.85, *p*< 0.001
C vs. DDDC	t_{20}= 1.85, *p*= 0.08	t_{20}= -0.44, *p*= 0.33	t_{20}= 4.14, *p*< 0.001

Focal rats experienced four partners that were experienced once as cooperators (C) and defectors (D), as well as four times as overall cooperators that were defecting in the last round (CCCD) and overall defectors that cooperated in the last round (DDDC). Comparisons were made using the TOST Paired Samples T-Test, testing for differences and similarities between conditions.
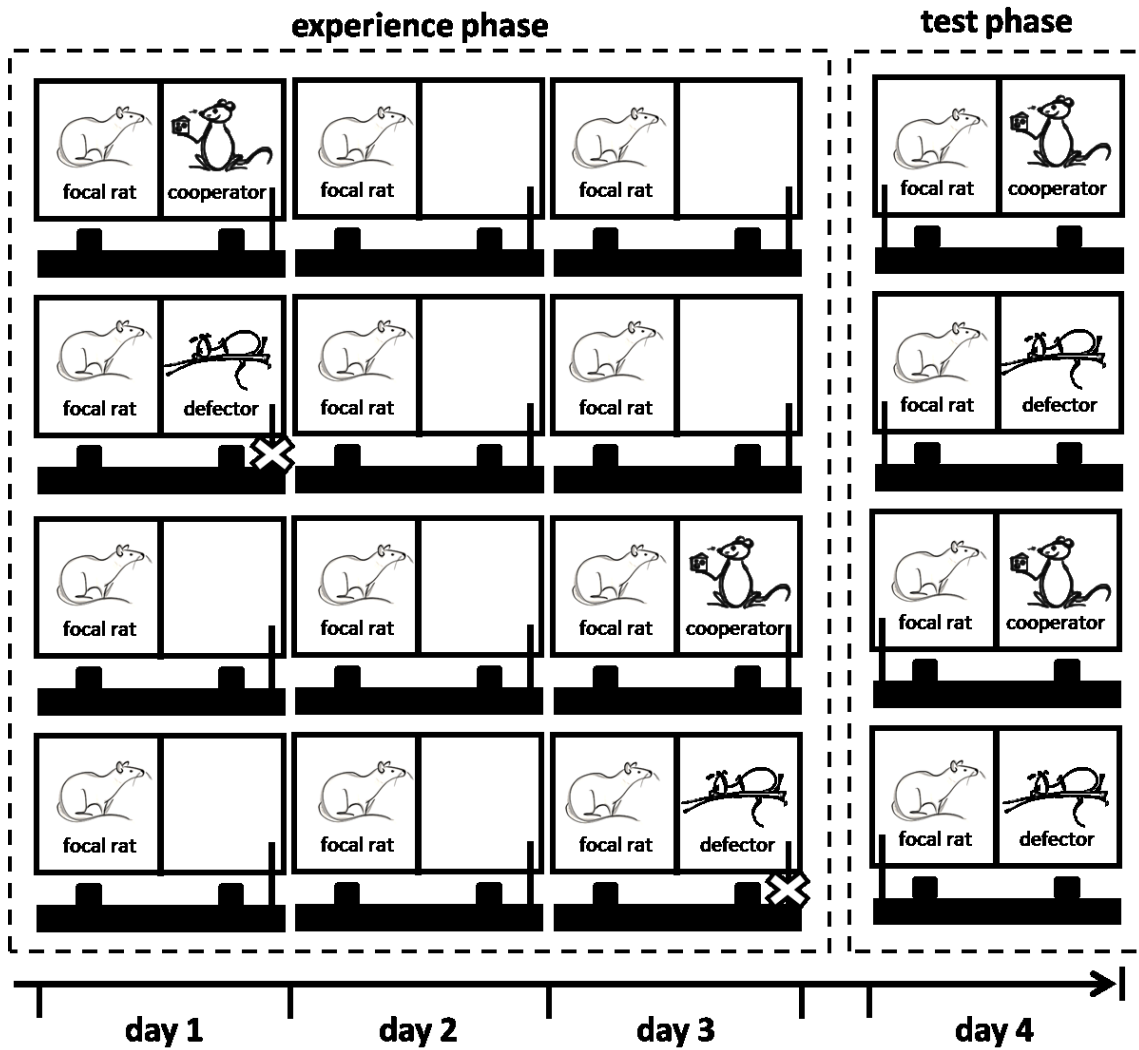
Fig. S1: Experimental setup of the memory capacity test

Focal rats experienced either cooperating (provided food) or defecting (did not provide food, indicated by a cross across the pulling stick) social partners one or three days prior to the test phase. In the test phase (day 4), focal rats were enabled to provide food to their partners.
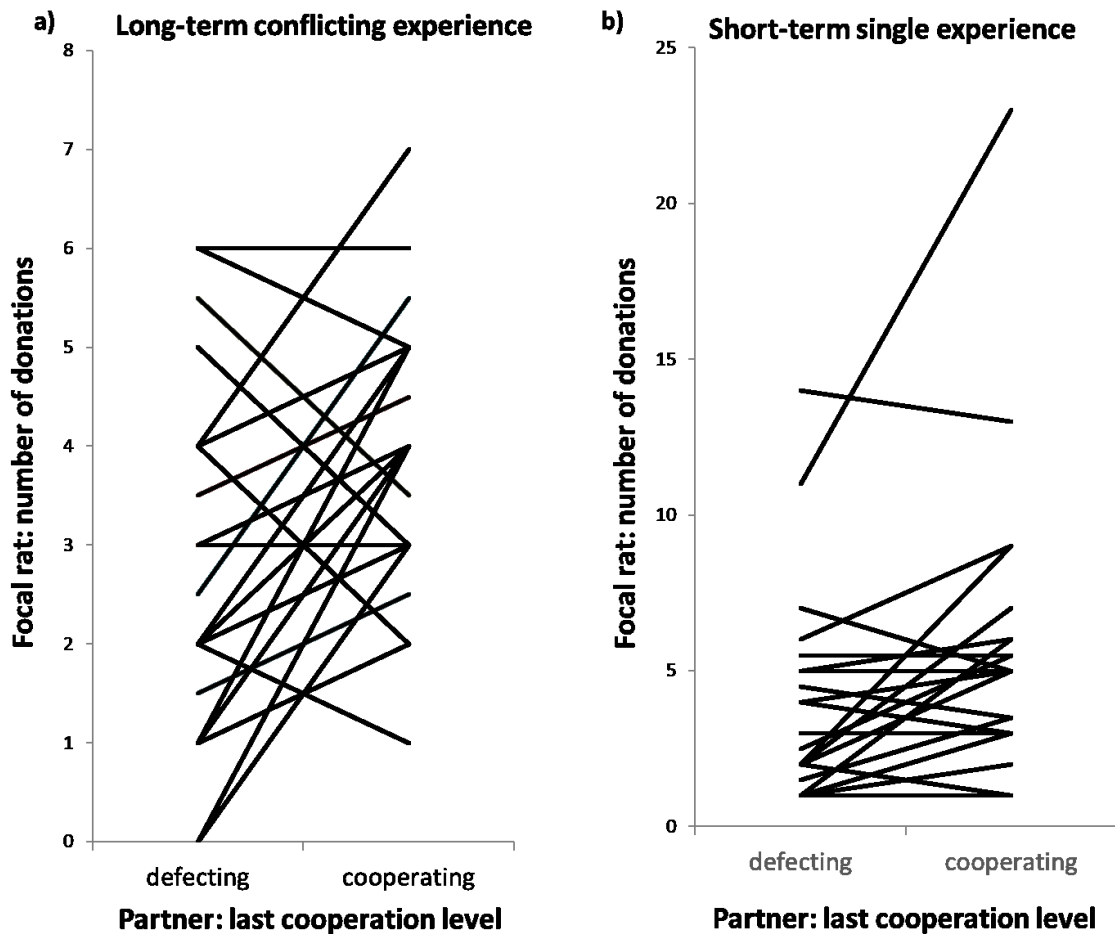
Fig. S2: Food donations of focal rats to their social partners depending on the latter's previous long-term or short-term cooperation propensity.

Focal rats pulled more often for partners (DDDC) that had defected for three days but cooperated on the last day prior the test phase, compared to partners (CCCD) that had cooperated for three days but defected on the last day (panel a, long-term conflicting experience). Likewise, rats provided more food to cooperating (C) than to defecting partners (D) that had been encountered only once, i.e. on the day before they could provide them with food (panel b, short-term consistent experience). Every line represents the raw data for a single focal rat towards its partner. To avoid overlap of data, we raised the respective lines of 4 individuals in (a) and in (b) by 0.5 units on the ordinate for better visibility. The slopes of lines were not affected by this measure.