No evidence for audience effects in reciprocal cooperation of Norway rats

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Rats (*Rattus norvegicus*) cooperate according to indirect reciprocity, which implies involvement of a reputation mechanism. Here we test whether rats employ such mechanism in repeated cooperative interactions. Focal subjects were first trained individually to pull food towards a social partner. During the experiment, focal rats were confronted with two types of trained social partners: one always cooperated and the other one always defected, either in presence or absence of an audience. Based on the hypotheses that rats possess a reputation mechanism involving image scoring, we predicted them to be more helpful in presence of an audience, independently of the partner's cooperative behaviour. If, in contrast, reputation involved a standing strategy, we predicted rats to distinguish more between cooperators and defectors in the presence of an audience than in its absence. Rats helped cooperative partners more than defectors, but against both predictions the presence or absence of an audience did not influence their helping propensity. This indicates that either reputation is not included in the decision of rats to help an individual that has helped others, or that reputation is neither involving image scoring nor a standing strategy. Although rats have been shown to modulate their decision to help a social partner based on its helpful behaviour towards others, they do not seem to adjust their behaviour strategically to the presence of an audience.

Keywords: indirect reciprocity, altruism, reputation, image scoring, standing strategy

Introduction

Three forms of reciprocal cooperation among animals have been described. Direct reciprocity (Axelrod & Hamilton, 1981), where individuals help those that have helped them before. Generalized reciprocity (Boyd & Richerson, 1989; Pfeiffer et al. 2005; Rankin & Taborsky, 2009), where the decision to help a social partner is based on help received from someone else. And indirect reciprocity (Alexander, 1987; Nowak & Sigmund, 2005), where the decision to help a partner is dependent on the helpfulness of this partner towards others. Whereas animals seem to apply the rather simple decision rules characterising direct and generalized reciprocity in a wide range of taxa (Taborsky, Frommen, & Riehl, 2016) the application of the decision rule underlying indirect reciprocity is cognitively more demanding and seems to be largely confined to humans (Milinski, 2016).

Cooperation through indirect reciprocity can evolve if it is based on a reputation system, which implies consideration of social information beyond direct interaction partners (Nowak & Sigmund, 1998, 2005; Zahavi, 1991). Reputation can be built either through image scoring (Nowak & Sigmund, 1998) or a "standing" strategy (Leimar & Hammerstein 2001; Milinski et al. 2001; Sugden 1986). Image scoring means that the reputation of an individual increases by every helpful act towards others, whereas reputation decreases by every selfish act. The standing strategy assumes that everyone initially has good standing, which can be lost if failing to help someone in good standing or cooperating with someone in bad standing. The image scoring model has been experimentally supported by a number of games played between human subjects (Milinski, 2016). A theoretical comparison of the two strategies suggests that standing is more robust and should more effectively promote indirect reciprocity than image scoring in a population (Leimar & Hammerstein, 2001). However, memorizing the standing of each group member is more complex and therefore may constrain the application of this superior mechanism because of limited memory capacity (Milinski & Wedekind 1998; Milinski et al. 2001).

If individuals can benefit from a reputation to be helpful, they should adjust their behaviour in the presence of witnesses. An "audience effect" describes that passive observers collect information about interactions between third parties, which in turn can change the behaviour of the actors (Earley & Dugatkin, 2010; McGregor, 2005). Humans are known to cooperate more in the presence of an audience (economic game model: Haley and Fessler 2005; experimental data: Bateson, Nettle, & Roberts, 2006). So far only one experiment with fish found evidence for the role of audience effects on cooperative behaviour. In cleaner wrasses, the presence of another fish increases pro-social behaviour (Pinto, Oates, & Grutter, 2011), and there is evidence for image scoring in this interspecific interaction (Bshary & Grutter, 2006).

Rats show a preference for cooperating in learning tasks (Schuster, 2002). They share food (Barnett & Spencer, 1951) and their propensity to provide food to a social partner depends on previous helping. Norway rats have been shown to cooperate according to generalized reciprocity (Rutte & Taborsky, 2007), direct reciprocity (Rutte & Taborsky, 2008), and indirect reciprocity (Spahni, 2005). In the latter study, rats provided more help to social partners that had been observed to help a third rat than to those that refrained to help a third rat. Therefore, focal individuals base their decision to help on observed interactions that did not provide any direct benefits to them. In addition, rats use information about a conspecific's presence: when a hungry rat was released in a cage with available food, the latency of the rat's approach to the food was significantly shorter in the presence of a conspecific (Narikiyo et al., 2010). Hence, rats apparently evaluate their social partners' behaviour through observation and they are aware of the presence of an observer. Under free-ranging conditions Norway rats live in burrows and form social groups (colonies) with dominance hierarchies (Seward, 1944) that contain up to 200 individuals (Telle, 1966). It seems that under such conditions, a reputation system may be beneficial, if the costs of monitoring and memorizing are not too high.

Here we used individually trained rats performing a two-player sequential food-exchange task following Rutte and Taborsky (2008). Focal animals were first exposed to a cooperating (providing food) or a defecting partner (providing no help to get food). After this experience they could provide food for their previous partners. Both phases, experience and test phase, were conducted with and without an audience (a conspecific present behind a mesh). We predicted that if rats had evolved a reputation mechanism based on image scoring, focal rats would in general provide more help when an audience is present, irrespective of whether the partner had previously cooperated or defected. If rats had evolved a reputation mechanism based on standing, we predicted them to distinguish stronger between cooperators and defectors in the presence of an observer. We therefore expected to find a difference according to the two alternative mechanisms in particular regarding help provided to defectors, because helping defectors would increase the subjects' image score but decrease their standing.

Methods

Experimental subjects and housing conditions

We used adult female outbred wild-type Norway rats (source: Animal Physiology Department, University of Groningen, Netherlands) weighing on average 300g. All rats were experienced with handling from an early age, so they were well habituated and not stressed when being transported to the experimental cage and by the presence of an observer. The rats were individually marked with standard hair tinting lotion on a hydrogen peroxide basis, and they were housed with littermates in groups of three to five sisters. The cages (80 x 50 x 37,5 cm) were separated from each other through opaque walls to exclude interactions between the groups, whereas rats could smell and hear other rats. The ambient temperature was 20°C ± 1°C, with a relative humidity of 50 - 60% and a 12:12 h light/dark cycle, with lights on at 20:00 hours after 30 minutes of dawn and with a respective dusk period in the morning. All trainings and experiments were conducted during the dark phase of the cycle, because rats are primarily nocturnal (Norton, Culver, & Mullenix, 1975).

Pre-experimental training

The experimental setup (Rutte & Taborsky, 2007, 2008) was based on a two-player sequential food-exchange task (de Waal & Berger, 2000). Test cages (80 x 50 x 37. 5 cm) were divided into two chambers by a wire mesh. Rats were trained individually and the training was divided into two parts: First, every single rat was trained to pull a reward for itself. To get the reward the rat learned to pull a stick fixed on a movable platform, which thereby slid into the test cage. In the second training phase, rats were paired with a training partner and learned over 18 sessions to provide food for their partner and vice versa. Roles were exchanged and the intervals between these switches were increased gradually from one single pull to a pulling period of seven minutes. A detailed plan of this training has been described by Dolivo and Taborsky (2015a). At the end of the training, a potential donor was able to produce an oat flake to a potential receiver, again by pulling a stick attached to a movable platform. The donor did not receive a reward for this action (Fig. 1).

Five rats were trained to never pull (defectors) and five rats were trained to always pull (cooperators) for their partner. These ten rats had been chosen at random, and in the experiment described below they served as the social partners providing the respective experience to the focal test subjects. Defectors were trained by placing them several times into the training cage while the platform was blocked for seven minutes.

Test procedure

Rats (n= 48) were tested in four different situations in random order with one treatment each per day. After placing the focal subject and a social partner into the test cage and waiting one minute to acclimatize, the partner (cooperator or defector) got access to the stick and was able to pull a reward (an oat flake) for the focal individual without any direct benefits for itself (Fig. 1). At the end of seven minutes, the roles were exchanged immediately and the focal subject could move the platform into the cage, again without any direct benefit for it. After every trial both cages were cleaned with alcohol to remove potential scent marks. In half of the treatments, a sister of the focal rat was present as an audience. Sisters stayed in a directly adjacent cage allowing visual, olfactory and tactile contact with the focal individual. Focal rats and their sisters were unrelated and have never met the social partners (cooperator and defector) before the experiment. In summary, the same focal individual experienced a cooperative partner in presence and in absence of an audience, and it also experienced a defective partner in presence and in absence of an audience.

To check whether the intention of focal subjects was to pull the platform for the social partner, i. e. whether they considered the social context, we conducted a control directly after the experiment. We tested the same focal individuals from the described experiment in two treatments. Here, focal individuals experienced cooperative ("control C") and defective ("control D") partners as described above. However, after the experience phase we removed the partners. Hence, when the focal rat had access to the pulling stick it was able to pull for an empty cage instead of a social partner (see Fig. 2 for a description of the entire experimental sequence).

Behaviours

For focal subjects and cooperators, the frequency of pulling and the latency to the first pull were measured.

Statistical Analysis

We analysed the data with R (Version: 3.1.0.) using the packages: lme4, car and survival. All recorded behaviours of focal rats and cooperators were not normally distributed, therefore non-parametric tests were used.

A generalized linear mixed model was used to account for the repeated measures design with focal rat's identity as a random factor. We compared the four treatments by including audience (present / absent) and cooperation level (cooperator / defector) as fixed factors, and the focal rats' pulling frequency as dependent variables. We tested the model for overdispersion, which was not the case, and simplified it by taking out the non-significant interaction between cooperation level and audience.

To test for differences in the time to the first pull according to the treatments, we conducted a survival analysis with the latencies to first pull by focal rats during the test phase as the dependent variable, cooperation level and audience as fixed factors and rat identity as a random factor. Like in the previous model we simplified the model by taking out the non-significant interaction between treatment and audience.

To compare the control situation (pulling for an empty cage) with the test situation (pulling for a cooperator or defector), we used Wilcoxon matched-pairs signed-ranks tests for the focal rats' pulling frequency and latency to the first pull. To check for a possible audience effect in cooperators during the experience phase, their pulling rate was compared between the treatments in the presence and absence of an audience also with the Wilcoxon matched-pairs signed-ranks tests.

Eleven out of 48 focal rats nibbled the stick (until it broke). These rats pulled randomly and did not direct their pulls towards their partner. This nibbling behaviour significantly affected the pulling. "Nibblers" pulled more often than "non-nibblers" (GLMM: $z= -6.797$, $p< 0.0001$) and the latency to the first pull was shorter in "nibblers" (GLMM: $z= 3.425$, $p< 0.001$). This indicates that these rats pulled the stick for different motivations than to produce food for their partners; hence these individuals were excluded from all analyses.

Ethical Note

In accordance with the animal welfare regulations of Switzerland (Tierschutzverordnung Schweiz 04/2008) rats (weight category 300 - 400g) were housed in enriched cages of 80 x 50 x 37. 5 cm. Enrichment included a wooden house and board, a channel, a piece of wood to nibble, a loo roll to play, digging-material (shavings), nest-building material (shreds and crumbled papers), and a salt block. Food (conventional rat pellets and corn mix) and water were provided *ad libitum* according to recommendations of the Federation of Laboratory Animal Science Associations (Forbes et al. 2007). We established small groups with a maximum of five individuals per cage (Sharp et al. 2003). All rats experienced a handling procedure from early age onwards, so they were well habituated to humans and not stressed while being transported to the experimental cage or by the presence of an observer. The housing of the animals and the experimental procedure were authorized by the Swiss Federal Veterinary Office under license BE98/11. In our experiments there was no possibility of physical contact between the individuals through separating wire mesh, and 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 experiment could have been stopped immediately.

Results

Influence of cooperation level and audience on pulling behaviour

Rats distinguished between pulling for a cooperator and pulling for a defector; they pulled significantly less often for the latter (GLMM: β= -0.33 ± 0.11, X^2= 8.80, *N*= 37, *p*= 0.003, Fig. 3), and started to pull for defectors significantly later than for cooperators (Proportional Hazards Regression Model: ß= -0.62 ± 0.19, X^2= 10.70, *N*= 37, *p*= 0.001; see Fig. 2 of the Appendix).

There was no measurable audience effect, neither regarding the pulling frequency (GLMM: β= -0.90 ± 0.11, X^2= 0.70, *N*= 37, *p*= 0.40, Fig. 3) nor the latency to the first pull (Proportional Hazards Regression Model: ß= -0.14 ± 0.18, X^2= 0.55, *N*= 37, *p*= 0.46).

Similar to focal subjects, the cooperators did not show an audience effect either: their helping behaviour did not differ when pulling for a focal rat in the presence or absence of a third rat (sister of focal rat), neither regarding the total number of pulls (Wilcoxon-Test: V= 332.0, *N*= 5, *p*= 0.418) nor the latency to the first pull (Wilcoxon signed-ranks test: V= 479.5, *N*= 5, *p*= 0.942).

Non-social control

Focal rats pulled more often and earlier for cooperative partners than for an empty cage (Wilcoxon signed-ranks test: frequency: V= 308.0, *N*= 37, *p*= 0.004; latency: V= 65.0, *N*= 37, *p*= 0.049, Fig. 4). However, focal rats did not provide more food to defective partners or pulled for them earlier than for an empty cage (Wilcoxon signed-ranks test: frequency: V= 188.5, *N*= 37, *p*= 0.13; latency: V= 145.0, *N*= 37, *p*= 0.12). Further, focal rats showed similar pulling frequencies and latencies when pulling for an empty cage after they had experienced a cooperator and defector (Wilcoxon signed-ranks tests: frequency: V= 112, *N*= 37, *p*= 0.27; latency: V= 229.0, *N*= 37, *p*= 0.81).

Discussion

In contrast to our predictions, the presence or absence of an audience did not influence the helping behaviour of focal rats. There was no interaction effect between the audience (sister present or absent) and the cooperation experienced from the partner (cooperator or defector) on the focal subject's pulling rate and timing. However, irrespective of the presence of an audience, focal rats differed in their cooperative behaviour between situations with cooperators and defectors in both the frequency and timing of providing food for them. They pulled more for cooperators and started earlier to pull for them in contrast to their pulling behaviour for defectors. In addition, the rats clearly discriminated between pulling for a cooperative partner and pulling for an empty cage: they pulled much less often when the neighbouring compartment was empty. Because rats provided more food to cooperative partners, we conclude that rats base their decision to help on direct reciprocity and help social partners that have helped them before. These results confirm previous studies showing direct reciprocity in female rats (Dolivo & Taborsky, 2015a, 2015b; Rutte & Taborsky, 2008; Schneeberger, Dietz, & Taborsky, 2012). Our study shows in addition that the reciprocal help is independent of an audience.

The absence of an audience effect might imply that focal subjects did not perceive their sister's presence in the adjacent cage. However, the directly adjacent cages enabled acoustic, visual, and chemosensory contact, and we did observe behavioural interactions between focal subjects and their respective audience rats. In addition, previous studies showed that rats are able to use observed social information in a similar cooperation setup (Spahni, 2005). Therefore, this probability seems unlikely.

Why do rats not change their helping behaviour when they are observed by others? Animals are known to respond to the presence of others, particularly during competitive interactions. For example, male Siamese fighting fish (*Betta splendens*) changed their display behaviour in intrasexual contests when a female audience was present (Doutrelant, Mcgregor, & Oliveira, 2001), as did male zebrafish (*Danio rerio*) exposed to a mixed-sex shoal audience (Cruz & Oliveira, 2015). Food calls in capuchin monkeys (*Cebus apella*) were shown to depend on hierarchical structures in the audience and on food scarcity (di Bitetti, 2005; Pollick, Gouzoules, & de Waal, 2005), and ravens (*Corvus corax*) hide food caches in the presence of informed observers (Bugnyar & Heinrich, 2005). Alarm calls in vervet monkeys (*Chlorocebus pygerythrus*) vary in accordance with the relatedness to the audience (Cheney & Seyfarth, 1985). Investment in reputation due to the presence of an audience has so far been shown in cleaner wrasses (*Labroides dimidiatus*; Pinto et al., 2011) and in human children (Engelmann, Herrmann, & Tomasello, 2012). In contrast, helpers of cooperatively breeding Arabian babblers and bell miners were not found to be more cooperative towards the offspring of breeders when being watched by the latter (McDonald, te Marvelde, Kazem, & Wright, 2008; Wright, 1997, Wright & McDonald, 2016), which does not indicate strategic investment in reputation, contrary to earlier suggestions (Zahavi, 1991).

The study of cleaner fish (Pinto, Oate & Grutter, 2011) suggested that investment in reputation might not be limited by cognitive demands, but its occurrence may rather depend on ecological and social circumstances. In Norway rats, mark-recapture studies showed that natural local population size can fluctuate between 2 and 100 individuals within one year (McGuire, Pizzuto, Bemis, & Getz, 2006). In contrast to the predictable interactions with local clients at the cleaning stations of wrasses (Pinto, Oate & Grutter, 2011), rat colonies in comparison may reflect less stable social situations. Hence, while it may be beneficial for a cleaner to invest in its reputation when a potential client is near that will likely reappear over and over again at the same cleaning station, in the highly dynamic rat colonies meeting well-known social partners repeatedly may be less predictable, thereby reducing potential benefits of adjusting to an audience.

Potential audience effects in our study might have been overridden by the propensity of rats to apply direct reciprocity rules, i.e. to help a helpful partner and to refrain helping an unhelpful partner, irrespective of an audience. However, if this were the reason for the absence of an audience effect, we should have expected to find such effect in the "cooperators" used to provide helping experience to our focal subjects. Our results reveal no indication for an audience effect in these individuals as well.

To conclude, we did not find evidence for the existence of audience effects in reciprocally cooperating rats. Although rats use social information gathered by observation, they do not adjust their cooperation level to the presence of observers. This suggests that rats do not strategically invest in reputation, which might be explained by their highly dynamic social system. This study contributes to a better understanding of mechanisms underlying indirect reciprocity and reputation building in animals. If no reputation system is involved when animals cooperate by indirect reciprocity, alternative mechanisms should be investigated by future studies, such as a potential role of reputation in starting cooperative interactions.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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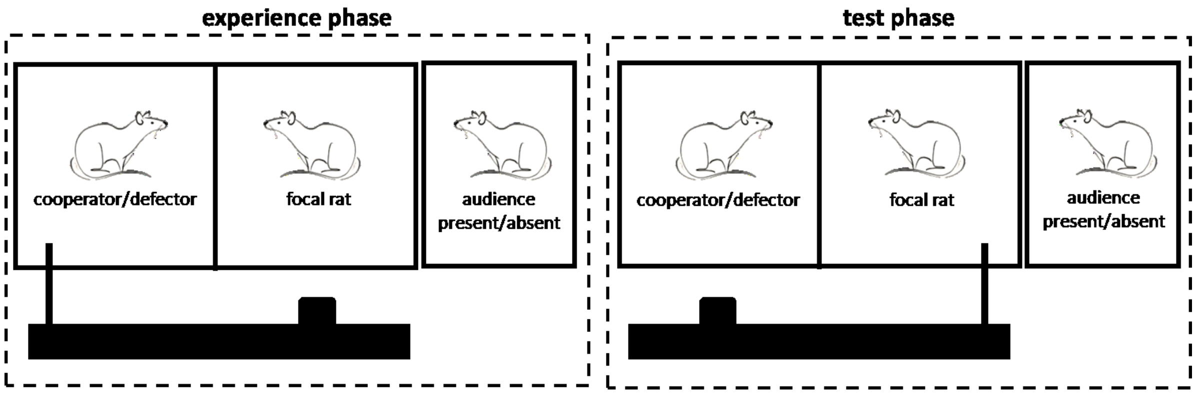

Fig. 1: Experimental setup

After a 1 min habituation phase for all individuals in the cages, a focal subject (n= 48) was exposed to a cooperator or a defector that either pulled or did not pull food for the focal rat during seven minutes. Immediately, the focal rat was able to pull for its partner for the next seven minutes. During the entire trial including experience and test phases, either a sister of the focal subject was present in an adjacent cage (audience +, indicated by eyes) or not (audience -). Every focal subject experienced all four situations (cooperator+, cooperator -, defector+, defector-).

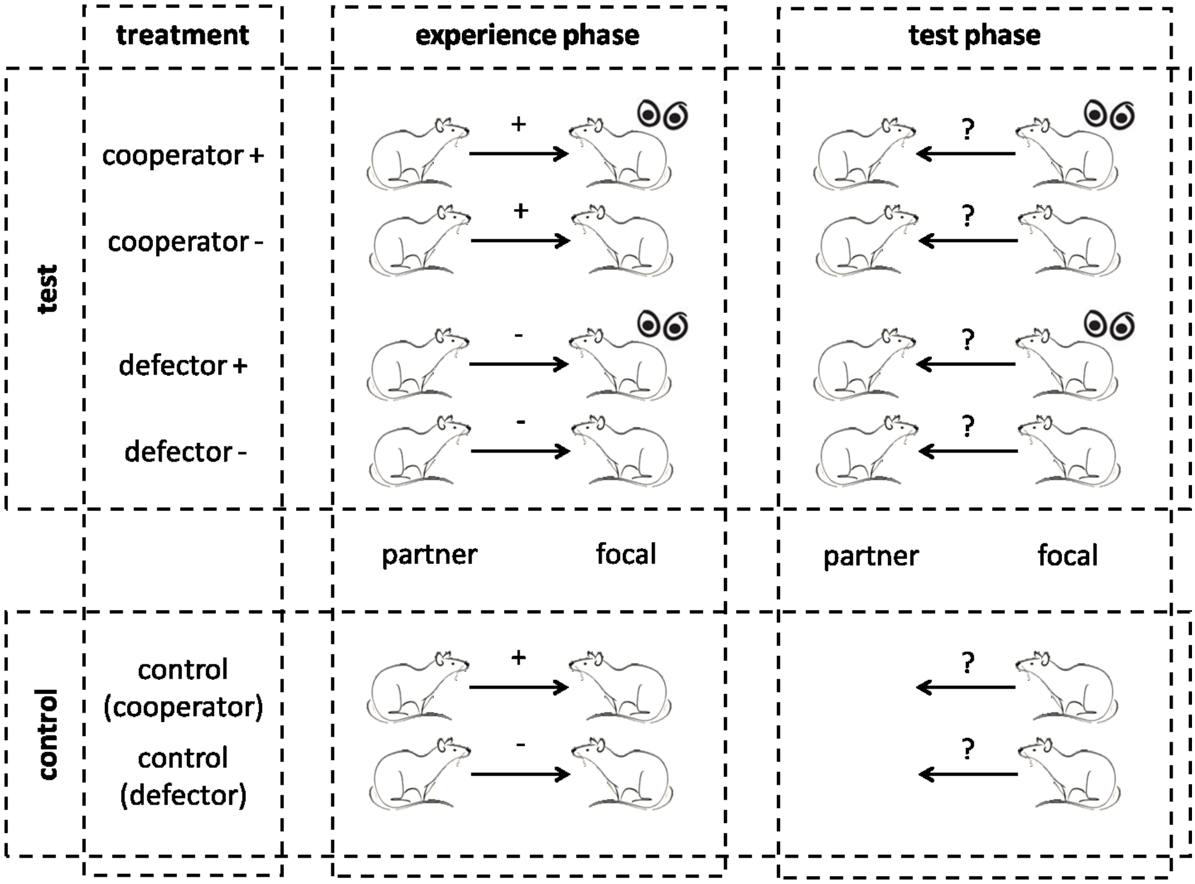

Fig. 2: Experimental procedure including four treatments and controls of both experience and test phases (the order was randomized)

cooperator (+): focal rat is exposed to a cooperator in presence of an audience

cooperator (-): focal rat is exposed to a cooperator in absence of an audience

defector (+): focal rat is exposed to a defector in presence of an audience

defector (-): focal rat is exposed to a defector in absence of an audience

control (cooperator): focal rat experienced a cooperator and can afterwards pull for an empty cage

control (defector): focal rat experienced a defector and can afterwards pull for an empty cage

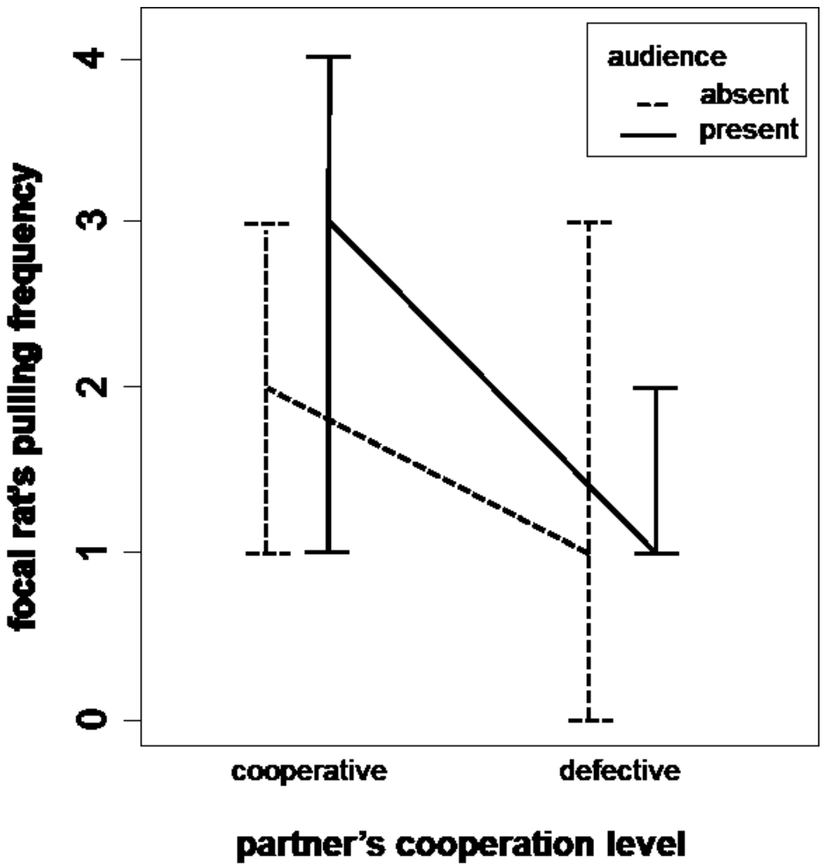

Fig. 3: Comparison between help performed towards cooperative or defective partners with or without **audience**

Rats (*N*= 37) pulled more often for previously experienced cooperative than defective partners. Whether rats were observed (solid line) or not (dashed line) by an audience did not significantly influence their decision to pull food for their partner. Medians ± interquartile ranges are shown.

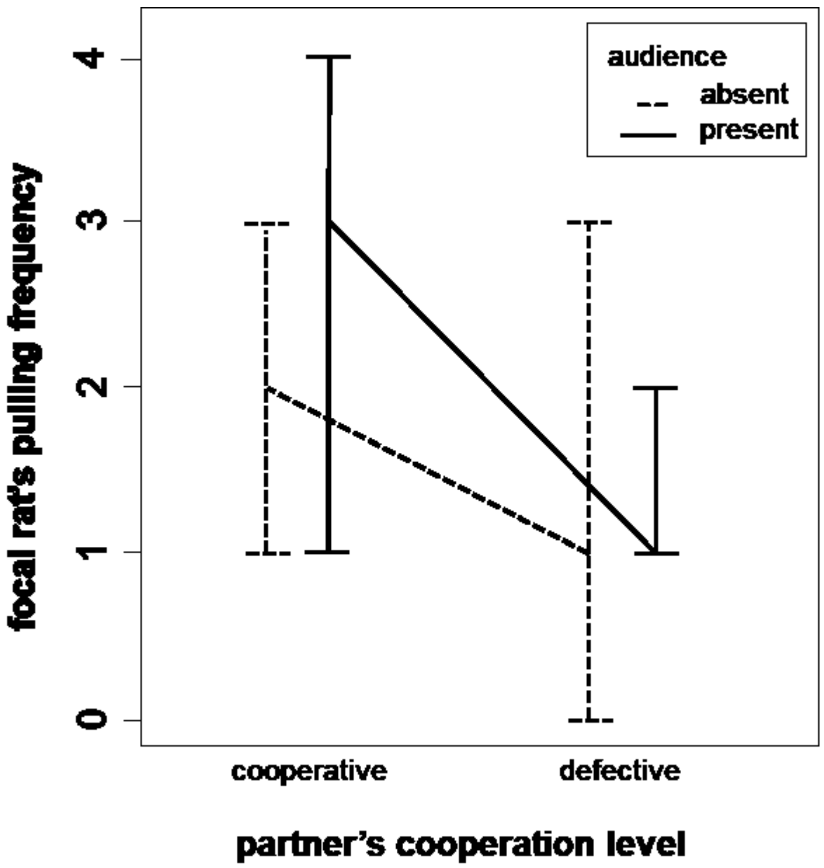

Fig. 4: Comparison between test and control situations to test for the influence of the social context on the pulling behaviour of focal subjects

Rats (*N*= 37) pulled more frequently for cooperative partners (test situation, solid line) than for an empty cage (control situation, dashed line). They did not pull more often for partners that had been defective than for an empty cage. Medians ± interquartile ranges are shown.

Appendix

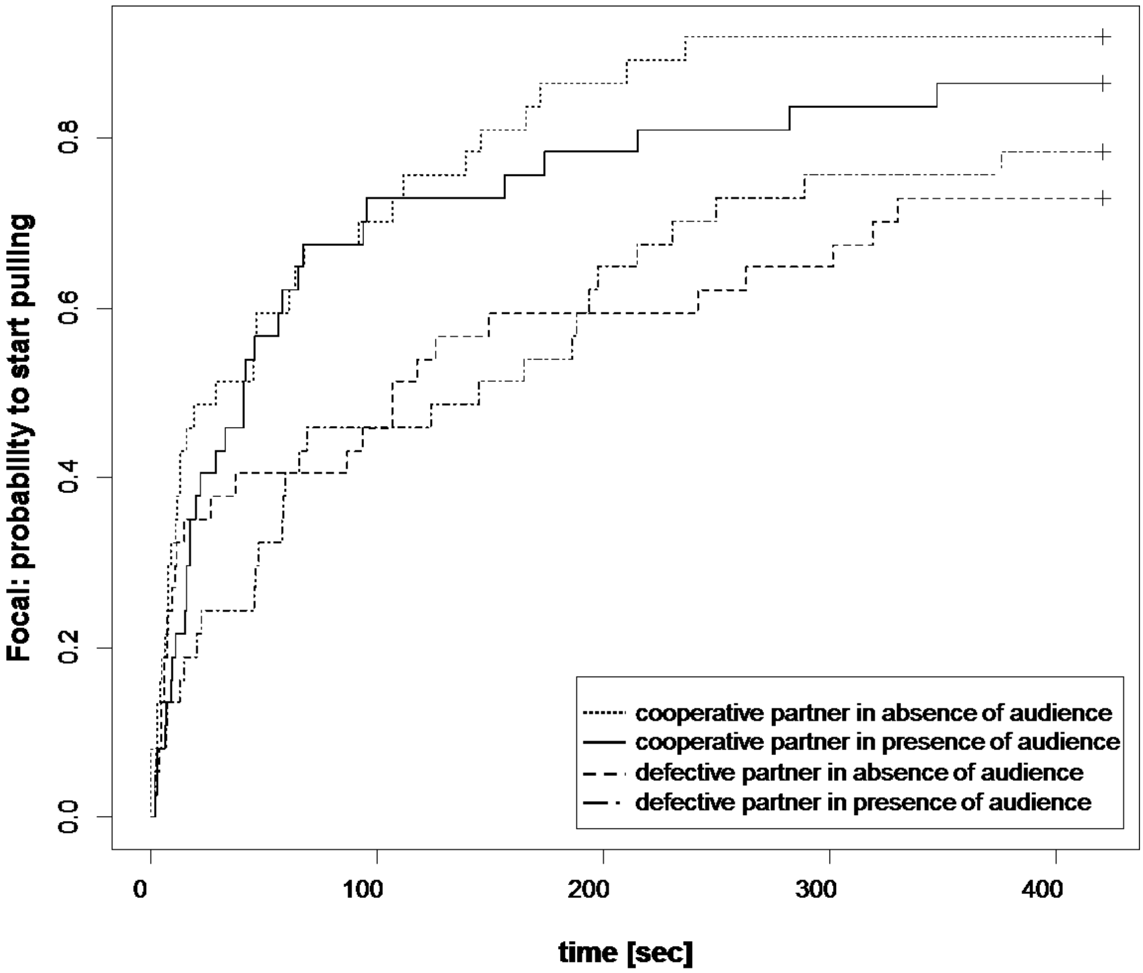

Fig. 1: Comparison between the latencies to start helping cooperative and defective partners in dependence of an audience

Rats pulled earlier for cooperators than for defectors, independently of the presence of an audience. Kaplan Meier estimates are shown (Jahn-Eimermacher et al. 2012).

Jahn-Eimermacher, A., Lasarzik, I., Raber, J. 2012: Statistical analysis of latency outcomes in behavioral experiments. Behav. Brain. Res. **221**, 271–275.