



## RESEARCH PAPER

# Cooperation among Norway Rats: The Importance of Visual Cues for Reciprocal Cooperation, and the Role of Coercion

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**Abstract**

Some animals reciprocate help, but the underlying proximate mechanisms are largely unclear. Norway rats (*Rattus norvegicus*) have been shown to cooperate in a variant of the iterated prisoner's dilemma paradigm, yet it is unknown which sensory modalities they use. Visual information is often implicitly assumed to play a major role in social interactions, but primarily nocturnal species such as Norway rats may rely on different cues when deciding to reciprocate received help. We used an instrumental cooperative task to compare the test rats' propensity to reciprocate received help between two experimental conditions, with and without visual information exchange between social partners. Our results show that visual information is not required for reciprocal cooperation among social partners because even when it was lacking, test rats provided food significantly earlier to partners that had helped them to obtain food before than to those that had not done so. The mean decision speed did not differ between the two experimental conditions, with or without visual information. Social partners sometimes showed aggressive behaviour towards focal test individuals. When including this in the analyses to assess the possible role of aggression as a trigger of cooperation, aggression received from cooperators apparently reduced the cooperation propensity, whereas aggression received from defectors increased it. Hence, in addition to reciprocity, coercion seems to provide additional means to generate altruistic help in Norway rats.

**Introduction**

Altruistic behaviour, in the sense that an individual performs a costly act that temporarily reduces its Darwinian fitness to the benefit of a social partner, is usually explained by kin selection (Hamilton 1964; West et al. 2007). Alternatively, reciprocity (Trivers 1971; Axelrod & Hamilton 1981) and coercion (Tebich et al. 1996; Fehr & Gächter 2002) can generate altruistic help as well, also among unrelated individuals (Lehmann & Keller 2006; Raihani et al. 2012; Taborsky 2013). Direct reciprocal cooperation, for instance, implies that individuals are selected to help each other in order to gain postponed benefits (Trivers 1971; Axelrod & Hamilton 1981; Taborsky 2013), whereas if altruism is triggered by coercion, individuals are selected to help others to avoid the cost of

being punished for the refusal of help (Clutton-Brock & Parker 1995; Raihani et al. 2012). Both direct reciprocity and cooperation based on coercion involve interactions among specific social partners, and if there is some delay between actions and reactions, both mechanisms imply individual recognition and rather complex social memory (Milinski & Wedekind 1998; Stevens & Hauser 2004).

Reciprocal cooperation has been observed in humans and chimpanzees (Jaeggi & Gurven 2013), vampire bats (Carter & Wilkinson 2013) and Norway rats (Rutte & Taborsky 2008). Probably, the best-known example of reciprocal cooperation is the mutual exchange of blood meals by vampire bats, which has been observed in nature (Wilkinson 1984) and experimentally verified in the laboratory (Carter & Wilkinson 2013). Reciprocal exchange of different

commodities and services has been observed in cooperative breeders, where helpers pay by raising the offspring of others to gain access to resources and to a safe territory (Taborsky 1985; Bergmüller & Taborsky 2005; Zöttl et al. 2013).

Coercion may also create helpful acts, for example in cooperative breeders, but punishment is typically hard to observe because the threat of being punished is often sufficient to create cooperation (Field & Cant 2009; Cant 2011). In cooperatively breeding cichlids, subordinates can indeed prevent punishment by increasing helping behaviour pre-emptively after periods of (experimentally) reduced help (Bergmüller & Taborsky 2005; Fischer et al. 2014). The role of punishment for promoting altruistic acts has been demonstrated in humans (Fehr & Gächter 2002; Fehr & Gintis 2007; Sigmund 2007; Raihani et al. 2012), and in keas performing an instrumental cooperative task in asymmetric hierarchical dyads (Tebbich et al. 1996). It has also been suggested to influence interspecific relations between cleaner fish and their clients (Raihani et al. 2012).

Norway rats (*Rattus norvegicus*) live in colonies of up to two hundred individuals and apply tit-for-tat-like reciprocity in laboratory experiments (Rutte & Taborsky 2007, 2008; Schneeberger et al. 2012; Dolivo & Taborsky 2015). Hitherto, the sensory modalities used while assessing the cooperative propensity of a social partner are unknown. In humans, information used to assess conspecifics is mainly visual (Barsics & Bredart 2012). Probably for this reason, even an exposure to pictures of eyes can induce cooperation (Sparks & Barclay 2013). In contrast to humans, Norway rats are nocturnal animals with a relatively low visual acuity (Prusky et al. 2000). Rats can discriminate between conspecifics solely on the basis of their olfactory signatures (Gheusi et al. 1997). They also have good auditory capacities (Rossier et al. 2000) and use acoustic signals in social interactions (Burn 2008). Rats can use visual cues in certain circumstances (Prusky et al. 2000; Cruz-Martin & Huberman 2012; Schneeberger et al. 2012; Vermaercke & Op de Beeck 2012), but whether they require visual cues for reciprocal cooperation is unclear. Thus, here we ask whether rats are able to cooperate by direct reciprocity in the absence of visual stimuli from their social partners.

To determine whether a lack of visual information affects direct reciprocity, we trained female rats in an instrumental cooperative task (Rutte & Taborsky 2008) and tested them in two experimental situations, either with or without visual contact between them. At the same time, chemical and acoustic information

exchange between the test rat and her social partner was allowed.

Even if a specific sensory cue is dispensable for accomplishing a task, its absence may be detrimental if potential benefits associated with multisensory information are missing. For example, reaction times in a non-social stimulus detection task were slower in rats exposed to cues of only one sensory modality than when auditory and visual cues were simultaneously present (Gleiss & Kayser 2012). It is not known, however, whether social responses to the behaviour of partners are affected by constrained sensory information. For this reason, we compared the decision speed of reciprocally cooperating rats in a situation allowing visual, olfactory and auditory information exchange with a situation in which visual information was suppressed.

The experimental procedure used to exclude visual information exchange has generated two unavoidable by-product effects: physical contact and the exchange of non-volatile olfactory cues were also prevented in the 'blind' test situation. The suppression of non-volatile olfactory cues may affect direct reciprocity, and the suppression of physical contact may affect social responses of rats, especially if coercion is involved. During our experiment, the social partners of the test rats sometimes behaved aggressively against them. Considering the possibility that coercion might also induce altruistic help, we included the aggressive behaviour of partners against the test rats in our analysis to assess the role of aggression as potential trigger of cooperation.

## Material and Methods

### Subjects

This study involved 43 female wild-type Norway rats (source: Animal Physiology Department, University of Groningen, Netherlands) out of a batch of 60, which were kept in 12 different cages containing five sisters each. Ten female rats unrelated to the tested individuals and placed in a separate room were used as cooperators and defectors: 5 dyads of 'cooperator-defector' were used for the experiment. Each dyad consisted of one cooperator and one defector that were unrelated to each other and housed in separate cages. Each of these dyads was combined experimentally with 7–12 focal test individuals. During an experimental session, the cooperator and the defector of a dyad were consecutively paired up with the focal test individual. Cages (80 cm × 50 cm × 40 cm) were enriched with wood and paper toys, a tunnel and a wooden shelter.

Water and rat pellets were provided *ad libitum*. In addition, the rats received special treats (seeds, fruits, vegetables, pasta or rice) in the afternoon. As rats are predominantly nocturnal, an inverted 12:12 light:dark cycle with lights on at 20:00 h allowed us to work during the rats' natural activity phase (i.e. in the day hours under artificial red light, for which rats have a weak sensitivity; Jacobs et al. 2001).

### Pre-Experimental Training

The pre-experimental training followed Rutte & Taborsky (2007). Rats were trained in a cage split in two compartments by wire mesh (Fig. 1). During the first 11 sessions, test individuals learned to pull a stick to obtain food for themselves. The rats could reach the reward when the baited platform to which the stick was attached had moved inside the cage, and during these 11 sessions, all test rats had learnt to pull for themselves. We considered that rats had reached the learning criterion if they pulled 8 times or more (sometimes up to 59 times) for themselves during at least one of the eleven 5 min sessions.

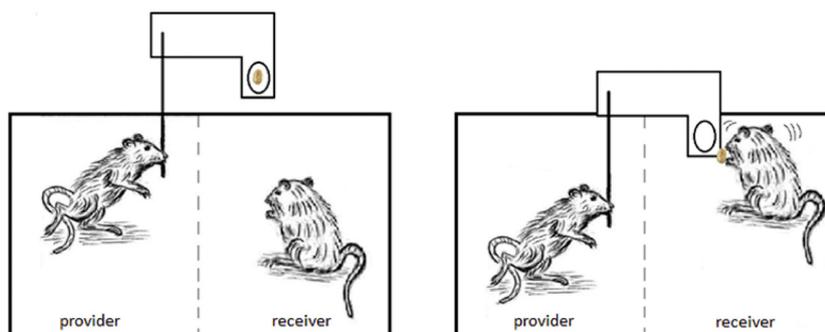
After these 11 sessions, the test rats never obtained food for themselves anymore by pulling the stick. During subsequent 18 sessions, the test rats learned to pull the stick in order to provide food to a partner positioned in the neighbouring compartment, whereby the interval between the exchange of roles was gradually increased. From sessions 1 to 14, each training lasted 8 min, and the sessions 15–18 lasted 7 min for each partner. During the first four sessions of this role exchange training, the roles of provider and receiver were

exchanged as soon as a rat had pulled once for her partner; for sessions 5–8, the roles were exchanged as soon as a rat had pulled twice for her partner; for sessions 9 and 10, the roles were exchanged as soon as a rat had pulled 4 times for her partner; during sessions 11 and 12, the roles were exchanged each 2 min; during sessions 13 and 14, the roles were exchanged once after 4 min; in sessions 15 and 16, a rat could pull during 7 min for her partner; and the roles were exchanged 30 min later. At the two last training sessions (17 and 18), this interval was increased to 1 d (cf. Rutte & Taborsky 2007).

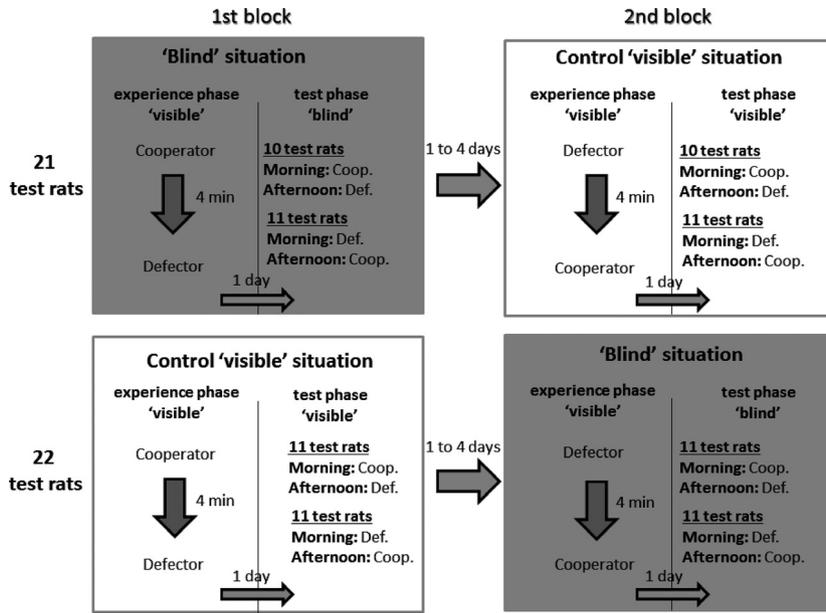
Rats assigned to the role of cooperators have had the same training as test rats, but in contrast to the latter, they have been regularly rewarded directly after pulling to enhance their pulling motivation. Rats assigned to the role of defectors were naïve individuals that had never learned how to pull.

### Experiment

The propensity of focal test rats to reciprocate received help was assessed in two different situations: one allowing visual information exchange between partners (control situation identical to the one described by Rutte & Taborsky (2008)), and another suppressing exchange of visual information with partners by the addition of opaque plastic mesh to the wire separation between the two rats. The experiment was thus split into two blocks (control 'visible' situation and 'blind' situation), each including an experience phase and a subsequent test phase. A schedule of the experimental procedure is presented in Fig. 2. Twenty-one of the 43 test rats were first tested in the 'blind situation'



**Fig. 1:** Experimental set-up used for training, the experience phase, and the test phase in the control situation. The cage was split into two compartments by a wire mesh. The provider could pull a moving tray towards the cage by an attached stick, which provided a reward to the experimental partner, but not to the provider. Left panel: before the pulling; right panel: thereafter. For the test phase in the 'blind' experimental situation, an opaque plastic mesh was added to the wire mesh separating the two compartments of the cage (dotted line) to prevent visual information transfer between the experimental partners, which also prevented any physical contact between them.



**Fig. 2:** Schedule of the experimental procedure to which the 43 test rats were exposed (21 first in the blind and then in the control condition, 22 in reverse order). During the experience phase, each test rat was first exposed to one of her assigned partners (cooperator or defector): after 1 min of acclimatization to the respective neighbour, the pulling stick was accessible to the partner during 7 min (cooperators could pull whereas defectors were prevented to pull). The test rat was then left alone in the cage for 4 min. Thereafter, she was exposed to her other assigned partner (defector or cooperator), which again had access to the pulling stick during 7 min after 1 min of acclimatization. Then the test phase followed using either the 'blind' or the 'visible' (control) condition.

and subsequently in the control situation, and for the other 22 test rats, the sequence was reversed. An interval of 2–4 d (in two cases only 1 d) separated the two blocks of the experiment. All individuals were tested in all four experimental situations, that is with cooperators and with defectors, and with and without possibility for visual information exchange, in a 2 × 2 full factorial design with balanced sequence. A similar cage as used in the training was used in the experience phase independently of the situation. This allowed visual, olfactory and acoustic information to be exchanged between experimental partners, and it enabled physical contact between them through the wire mesh separation (Fig. 1). During the first experience phase of the experiment (control 'visible' situation for half of the test rats and 'blind' treatment for the other half), each test rat was first exposed to her assigned cooperator: after 1 min of acclimatization to the respective neighbourhood, the pulling stick was put into the compartment of the cooperator and the cooperator could provide the test rat with food during 7 min. The test rat was then left alone in the cage during 4 min. Thereafter, she was exposed to her assigned defector. After 1 min of acclimatization to the defector, the pulling stick was put into the compartment of the defector, who never provided the test rat with food during 7 min. The second experience phase was similar to the first one, except for the sequence: each test rat was first exposed to her assigned defector, and then to her assigned cooperator. It is important to note that the rats could see each other during the experience phase of all experimental situations.

To motivate the 'cooperators' to pull for the focal test rat during the experience phase, they were allowed to pull four times for themselves in an isolated condition before they were presented to the test rat. In addition, we sometimes needed to motivate the cooperator rats to pull during the experience phase by rewarding them for pulling with an oat flake. As this might have influenced the test rats' perception of the cooperators' performance or motivation, we also sometimes provided the defectors with an oat flake in a similar way, so that the test rats would not perceive any difference in the way the cooperators and defectors were treated.

The test phase followed the experience phase on the subsequent day. Now the test rats were allowed to pull for the same partners as in the experience phase during 7 min. In the control 'visible' situation, a similar cage as used in the experience phase and in the training was used in the test phase: the cage was split into two compartments only by wire mesh, allowing visual, olfactory and acoustic information to be transmitted, and not preventing physical contact. In the 'blind' situation, an opaque six-layer white plastic mesh (900 holes/cm<sup>2</sup> for each layer) was added to the wire mesh, which allowed test rats to smell and hear the partner, but not to see her ('blind situation') or to interact with her physically. In both situations, half of the test rats were tested with the cooperator in the morning and with the defector in the afternoon, and for the other half, the sequence was reversed.

Among both the cooperating and the defecting partners of test rats, individuals were either peaceful

during the experience phase (in 34 cases for cooperators and in 37 cases for defectors during the experience phases preceding the control situations; in 28 cases for cooperators and in 39 cases for defectors during the experience phases preceding the 'blind' treatments), or they were aggressive against test subjects by attempting to bite their paws through the wire mesh (in 9 cases for cooperators and in 6 cases for defectors during the experience phases preceding the control situations; in 15 cases for cooperators and in 4 cases for defectors during the experience phases preceding the 'blind' treatments).

We noted the pulling rate as well as the latency before the first pull of each test rat when pulling for the cooperator or the defector, both in the control and in the 'blind' situation. In addition, we noted for each test rat and in each test phase whether or not the partner of the test rat had attempted to bite the test rat during the experience phase preceding the respective test phase.

### Statistical Analysis

Generalized linear mixed models (GLMM) with the number of pulls as the dependent variable were performed using the lme4 package of RStudio (Version 0.98.50). Focal test individual identity and partner identity were included as random factors in each model.

We compared latencies before the first pull of the test rats depending on their partners' previous role (cooperator or defector), using a one-tailed Wilcoxon matched-pairs signed-ranks test with the software package IBM SPSS and with RStudio. A one-tailed test was used as it had been established in previous studies using the same instrumental cooperative task that test rats are more helpful to cooperators than to defectors (Rutte & Taborsky 2008; Schneeberger et al. 2012); hence, the test rats were not expected to show a higher pulling motivation for defectors than for cooperators.

In addition, we used a two-tailed Wilcoxon matched-pairs signed-ranks test to determine whether the latencies before the first pull differed between the test situation providing all sensory information and the test situation in which visual information exchange was prevented. This test was meant to check for potential benefits of multimodal information transmission when reciprocating received help.

All analyses except the comparison between the decision delay between the 'blind' (absence of visual information) and the control (all sensory information

available) situations were performed separately for the two experimental situations ('blind' and control).

Medians and interquartile ranges are given for all samples compared with Wilcoxon matched-pairs signed-ranks tests. Model estimates are reported as  $\beta \pm \text{SE}$ .

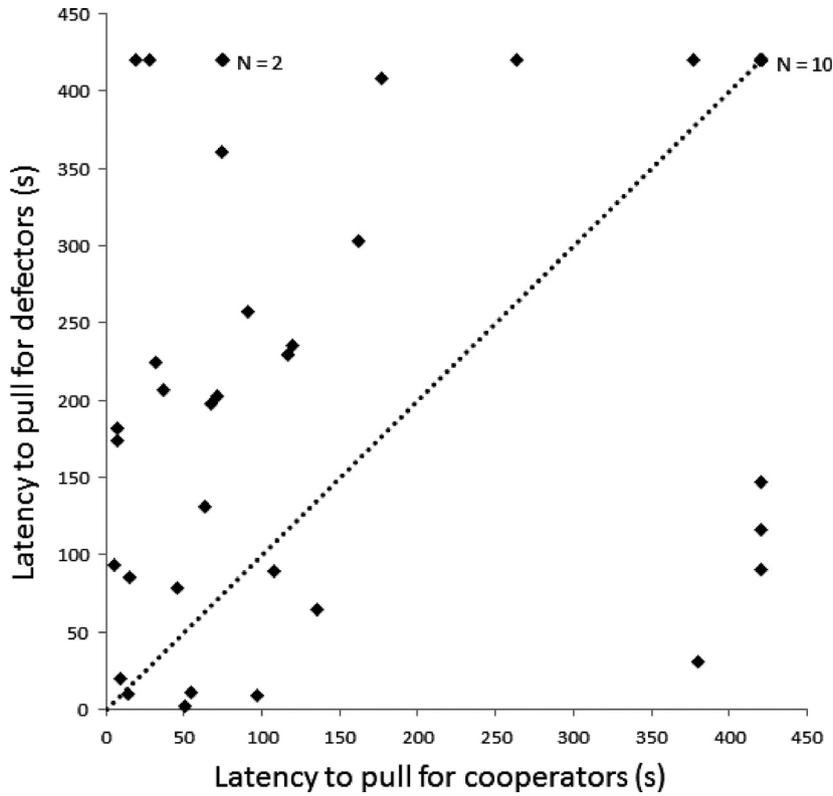
## Results

### Latency before the First Pull

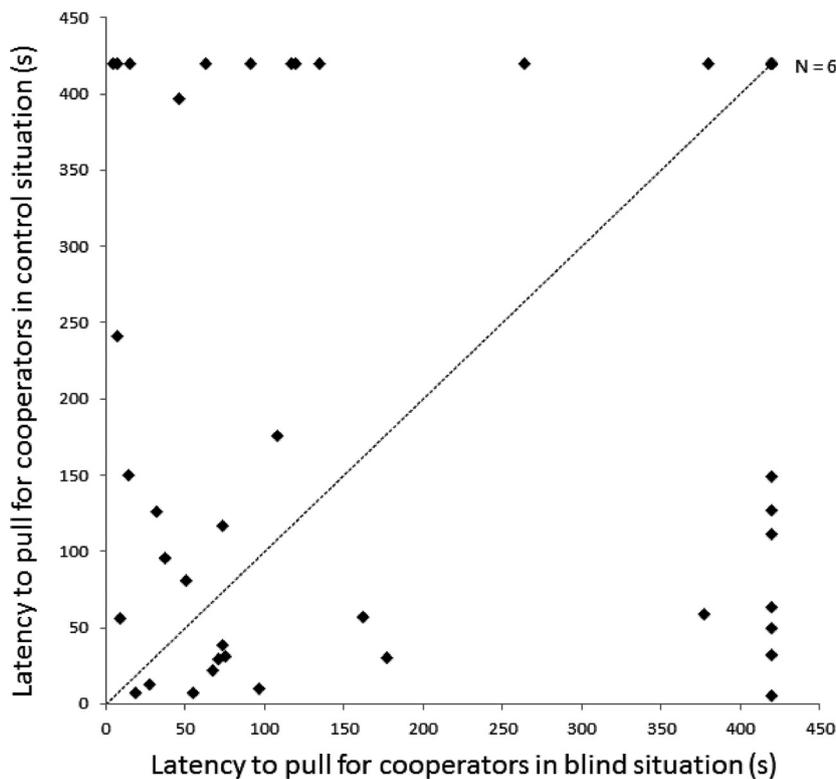
In the 'blind' test situation preventing visual information exchange and physical contact, the mean latency before the first pull was significantly longer when the test rats pulled for defectors than when they pulled for cooperators (defectors: 229 s [91.5–420], cooperators: 108 s [48.5–420]; Wilcoxon test,  $n = 43$ ,  $V = 148.5$ ,  $p = 0.009$ , Fig. 3). In the control 'visible' condition allowing visual information exchange and physical contact, the mean latency before the first pull did not differ significantly between the situations in which test rats could pull for cooperators or defectors (defectors: 129 s [51.5–420], cooperators: 127 s [44.5–420]; Wilcoxon test,  $n = 43$ ,  $V = 290.5$ ,  $p = 0.45$ ). No general difference between the 'blind' and control 'visible' situations was observed for the latency before the first pull (blind situation: 179.5 s [68–420], control situation: 128 s [50–420]; Wilcoxon test,  $n = 86$ ,  $V = 1495.5$ ,  $p = 0.56$ ). This was true also for separate comparisons of the pulling latencies for cooperators (blind situation: 108 s [48.5–420], control situation: 127 s [44.5–420]; Wilcoxon test,  $n = 43$ ,  $V = 318$ ,  $p = 0.61$ , Fig. 4) and those for defectors (blind situation: 229 s [91.5–420], control situation: 129 s [51.5–420]; Wilcoxon test,  $n = 43$ ,  $V = 437$ ,  $p = 0.2$ , Fig. 5).

### Number of Pulls

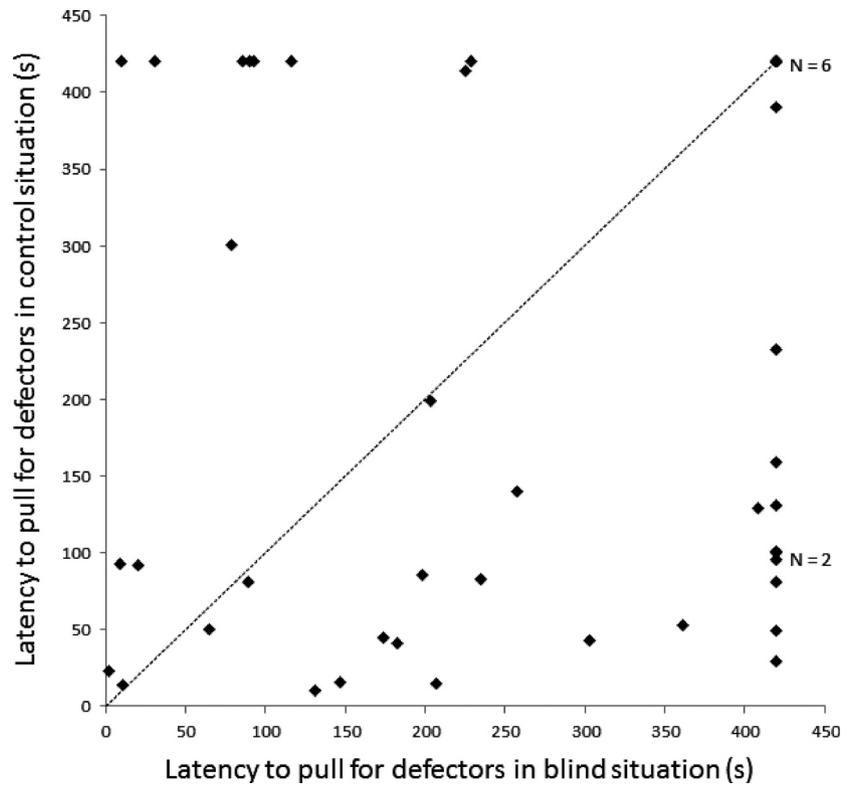
The previous role of the partner (cooperator or defector) did not influence the number of the test rats' pulls, neither in the 'blind' ( $\beta = -0.08 \pm 0.22$ ,  $\chi^2 = 0.11$ ,  $df = 1$ ,  $p = 0.74$ ) nor in the control 'visible' situations ( $\beta = -0.02 \pm 0.23$ ,  $\chi^2 = 0.009$ ,  $df = 1$ ,  $p = 0.92$ ; GLMM assuming a Poisson distribution, including the partner's previous role as a fixed effect). When adding the partner's aggressive behaviour observed during the previous experience phase ('occurrence or absence of biting attempts') in the GLMM as fixed binomial factor, there was a significant negative interaction between the treatment (cooperator or defector) and the 'biting effect' ( $\beta = 1.21 \pm 0.55$ ,  $\chi^2 = 4.76$ ,  $df = 1$ ,  $p = 0.03$ ) in the



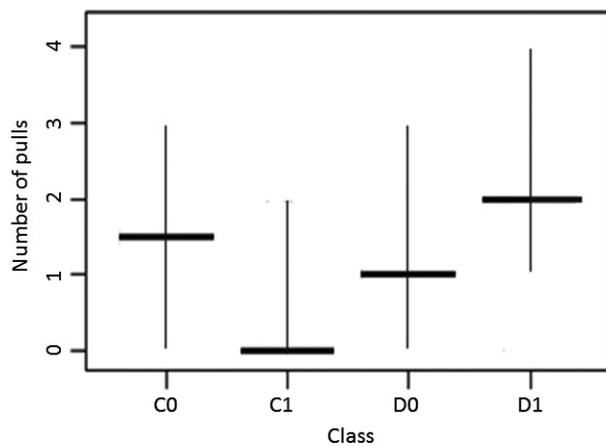
**Fig. 3:** Latency (in seconds) before the first pull of each test individual according to her previous experience with the partner (cooperator or defector) in the ‘blind’ test situation, which allows focal individuals to smell and hear their social partner, but prevents visual information exchange and physical contact. Each symbol represents one test individual except where numbers are denoted for overlapping symbols. Points above the dashed line denote individuals that pulled quicker for the cooperator than for the defector, and the opposite holds for points lying below the line. The mean latencies before the first pull differed significantly between treatments (see text for statistical results).



**Fig. 4:** Latency (in seconds) before the first pull for the cooperating partner of each test individual according to the two experimental situations, ‘blind’ or control. Each symbol represents one test individual except where numbers are denoted for overlapping symbols. Points above the dashed line denote individuals that pulled quicker in the ‘blind’ situation than in the control situation, and the opposite holds for points lying below the line. The mean latencies before the first pull did not differ between the situations (see text for statistical results).



**Fig. 5:** Latency (in seconds) before the first pull for the defecting partner of each test individual according to the two experimental situations, 'blind' or control. Each symbol represents one test individual except where numbers are denoted for overlapping symbols. Points above the dashed line denote individuals that pulled quicker in the blind situation than in the control situation, and the opposite holds for points lying below the line. The mean latencies before the first pull did not differ between the situations (see text for statistical results).



**Fig. 6:** Number of test rats' pulls depending on the partner's previous cooperation and aggression in the control situation (C0: number of pulls for a cooperator who has not attempted to bite; C1: number of pulls for a cooperator who has attempted to bite; D0: number of pulls for a defector who has not attempted to bite; D1: number of pulls for a defector who has attempted to bite). Medians and interquartile ranges are shown.

control 'visible' situation (Fig. 6). In the 'blind' situation, the interaction between both factors ( $\beta = -0.87 \pm 0.66$ ,  $\chi^2 = 1.88$ ,  $df = 1$ ,  $p = 0.17$ ) was not significant.

### Discussion

When visual information exchange with partners was prevented, test rats started to reward cooperators earlier than defectors. This supports our hypothesis that visual information exchange is not needed when rats decide about whether to reciprocate received help. Interestingly, when information could be exchanged between the social partners by all sensory modalities and when physical contact was not prevented, test individuals inverted the directionality of their trend to pull differentially for cooperators and defectors according to the partners' aggressive behaviour in the previous interaction. This suggests that cooperators reduce the help-inducing effect of their prosocial behaviour by showing aggression against their social partners, whereas non-cooperators can increase the helping propensity of their partners by attacking them. Coercion might hence be an alternative mechanism generating altruistic behaviour in Norway rats.

### Cues Used to Gain Information

The fact that visual information is not required to recognize individual social partners and to reciprocate help is not a trivial result. Despite being

predominantly nocturnal and having poor visual acuity compared to humans (Burn 2008), rats are able to solve tasks involving visual information only, and they can follow complex visual strategies (Cruz-Martin & Huberman 2012; Vermaercke & Op de Beeck 2012). In certain experimental tests of rodent behaviour, cues other than visual are efficient only when combined with visual information (Rossier et al. 2000). Furthermore, wild-type Norway rats have better visual acuity (1.5 c/d, with c/d corresponding to cycles per degree, a measure of spatial resolution accounting for stimulus size and distance; Burn 2008) than inbred strains of rats usually used for behavioural studies, as for instance Wistar rats (0.5 c/d; Burn 2008), which may suggest that wild-type Norway rats rely on visual stimuli to a greater extent than their inbred laboratory descendants. In addition to the necessity to recognize social partners individually when performing direct reciprocity, cooperating partners may communicate their intentions and thereby modify each other's propensity to cooperate in repeated interactions (Mendres & de Waal 2000; Clutton-Brock 2009; Schweinfurth 2013). In Norway rats, for instance, the propensity to reciprocate help was shown to be influenced by the hunger state and by the body condition (weight) of the social partner (Schneeberger et al. 2012), which might involve the exchange of visual information such as begging gestures (Schweinfurth 2013).

Our results showing that rats can cooperate reciprocally even when separated by an opaque plastic mesh are remarkable also because in their olfactory communication, information transfer involves both non-volatile and volatile components (Burn 2008), but our rats only had access to volatile olfactory cues in the 'blind' test situation. These results also highlight that mechanisms of cooperation based on reciprocity are not impaired by the absence of both physical contact and exchange of non-volatile chemical cues.

The simultaneous use of multiple sensory sources may enhance recognition and cognitive performance (Winters & Reid 2010), and improved task performance indeed has been observed in a multisensory experimental context in rats (Gleiss & Kayser 2012). However, in our experiment, we could not detect such benefits: the mean latency before the first pull was not shorter in the control 'visible' situation where all sensory modalities were available than in the 'blind' situation where visual information was prevented, neither in general nor when pulling specifically for cooperators.

Visual perspective taking has been considered to be a prerequisite for the ability to form concepts about others' mental state in some circumstances (Overduin-de Vries et al. 2014). Our findings suggest that visual perspective taking can be replaced by olfactory or auditory perspective taking and that the tendency to consider vision as a predominant information source for social relations does not seem generally justified.

It might be interesting to test whether visual cues may play any role in the context of direct reciprocity. Instead of preventing visual information exchange between partners like in this study, a similar experiment preventing any information exchange between partners except visual cues might be performed. Furthermore, to establish which modality plays the primary role for Norway rats cooperating in an iterated prisoner's dilemma game, test subjects could be provided with 'crossed' information. When allowed to reciprocate help for their partner, subjects could, for instance, be provided with the visual information of a partner who had previously cooperated, and at the same time, with the auditory or olfactory information of a partner who had previously defected.

#### Alternative Strategies Used to Solicit Help

Few studies have observed the effect of coercion and punishment on an individual's propensity to cooperate. In small groups of the cooperative cichlid *Neolamprologus pulcher*, for instance, punishment for refused help can explain the cooperative behaviour of subordinates: help is traded for the toleration in the territory by dominant individuals (Fischer et al. 2014).

In our study, a plausible interpretation of the bite attempts of certain partners against the paws of test rats during the experience phase of the experiment is the potential existence of a coercive attitude meant to force test rats to provide food for them. Such manipulation attempts may occur when individuals are forced to interact with a specific partner without possibility to switch to another one, especially in series of repeated interactions (Raihani et al. 2012). In our experiments, test rats could not provide partners with food during the experience phase, because reciprocity was postponed to the next day. Some partners of test rats may thus have attempted to punish the latter for not returning their help, which could induce cooperation. Norway rats were shown to benefit from being aggressive, as this may improve the efficiency of social interactions in subsequent encounters (Lehner et al. 2011).

When comparing the two mechanisms, direct reciprocity implies that test rats should be more helpful towards cooperators than towards defectors during the test phase, whereas coercion implies that test rats should be more helpful towards partners that have attempted to bite them before, but only in experimental situations where biting is possible. This was the case in the control 'visible' situation of our experiment that allowed physical contact between the experimental partners, where we observed that the tendency of partner rats to bite the test rats reversed the latter's response to cooperators and defectors (Fig. 6). Test rats acted altruistically when defectors had tried to bite them and reciprocated help voluntarily for pacific cooperators.

For partners using cooperation and aggression simultaneously, test individuals abstained from reciprocating help, whereas the previous aggression of defectors increased the likelihood of test rats to produce food for them. Cooperating and punishing at the same time does not seem to have an additive effect, but rather a mutually exclusive effect on the probability to obtain help. Contrary to the control situation where the wire mesh separating both compartments allowed further biting attempts similar to those observed during the experience phase, the plastic mesh added to the separation in the 'blind' test situation prevented any physical contact. Cooperative behaviour was indeed only determined by direct reciprocity in the 'blind' test situation, where test rats did not have to dread further aggression by their experimental partner: the rats pulled quicker for cooperators than for defectors, and previous receipt of aggression had no effect on the test individuals' propensity to pull for their partner.

Our results suggest that coercion may work as an alternative strategy to obtain altruistic help from social partners in Norway rats. Future studies will need to experimentally manipulate the aggressive behaviour of individuals to further clarify the role of coercion in the cooperation of rats.

## Conclusion

To our knowledge, this study provides the first evidence that direct reciprocity can emerge in the absence of visual and non-volatile olfactory information exchange between social partners. It emphasizes the importance of other cues in the context of cooperative behaviour exchanged between Norway rats, which is in accordance with previous hints on the importance of olfactory cues in social interactions of rats (Gheusi et al. 1997). This seems to deviate from

the context of spatial navigation in rats, where visual cues seem to be essential (Rossier et al. 2000). Even if the best spatial vectorial representation may be visual, the best social vectorial representation might be olfactory or auditory. Depending on the context, different environmental cues seem to be favoured to gain information. In addition, our results also highlight the plausible coexistence of two alternative strategies used by rats to enhance cooperation, reciprocity and coercion, which may both be successful provided that they are not applied simultaneously.

## Acknowledgements

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## Ethics Statement

The procedure described in this manuscript conforms to the legal requirements of Switzerland and the guidelines of the University of Bern, where the work was carried out (licence number BE98/11).

## Conflict of Interests

The authors have no competing interests.

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