RESEARCH ARTICLE

Cooperative intentions and their implications on reciprocal cooperation in Norway rats

Manon K. Schweinfurth[1,2] iD

[1]School of Psychology and Neuroscience, University of St Andrews, St Andrews, Scotland

[2]Department of Behavioural Ecology, University of Bern, Hinterkappelen, Switzerland

Correspondence
Manon K. Schweinfurth, School of Psychology and Neuroscience, University of St Andrews, KY16 9JP St Andrews, Scotland.
Email: ms397@st-andrews.ac.uk

Abstract

One way to cooperate with others and avoid exploitation is reciprocal cooperation. Reciprocity is the selective helping of those who were cooperative before, which is commonly based on outcomes. Yet, outcomes may not reflect intentions, that is if an individual is unable but willing to help. Humans, including children, show such intention-based reciprocity. However, it is unclear whether other animals consider intentions in reciprocal settings. Here, I tested whether Norway rats (*Rattus norvegicus*) reciprocate help based on intentions by manipulating the outcome while keeping the partner's cooperative intentions the same. Subjects experienced a partner that was able to help by providing food via a movable platform. In another condition, the same partner was unable to help because the platform was blocked. When the roles were exchanged afterwards, subjects provided food more often to "able" than "unable" partners, even though the latter attempted to help. I compared these findings to data using "willing" and "unwilling" partners that were able to help. Again, rats based their cooperative behaviour on outcomes rather than the intention to help. This suggests that rats reciprocate primarily based on outcomes and seem to not consider cooperative intentions. Although subjects provided consistently less food to partners that did not help, they provided them with some help. Potentially, rats use a cognitively less demanding strategy by helping defectors a bit to maintain cooperation. Thereby, cooperation might be resistant to situations in which an apparent defector was actually unable to help, but had cooperative intentions and might be a good cooperation partner in the future.

KEYWORDS
ability, cooperation, intention, Norway rats, outcome, reciprocity

1 | INTRODUCTION

Human adults perceive others as intentional agents and attribute thoughts, beliefs and intentions to them, which helps to explain and predict the behaviour of others (Gummerum & Chu, 2014). Understanding others' intentions is fundamental for legal systems, sport competitions and many other of our daily interactions. Furthermore, reading intentions might be especially important in the context of reciprocal cooperation, where individuals help those that are cooperative (Trivers, 1971). Reciprocity is a strong determining factor for human behaviour; we reciprocate with familiar and unfamiliar partners on an almost daily basis (Bowles & Gintis, 2011). In order to only cooperate with helpful

partners, and avoid exploitative ones, we usually evaluate the kindness of an action and not only its outcome—based on intentions (Falk & Fischbacher, 2006). Indeed in economic games, participants always reward and almost never punish those with good intentions in contrast to those with bad intentions, even if the outcomes do not differ between those with different intentions (Charness & Levine, 2003; Falk et al., 2003). This motivation to reciprocate based on intentions extends from monetary to non-monetary favours (Chao, 2018) and from direct to generalised reciprocity, which is a general motivation, after being helped, to help not only your helper but anyone (Sun et al., 2020). Intention-based reciprocity can also explain why we are less likely to trust and reward people, who only help because they strategically plan to receive a favour in return compared with those who give because of kindness (Orhun, 2018).

Intention-based reciprocity might also exist in non-human animals. Many animals show reciprocal cooperation (Díaz-Muñoz et al., 2014; Schino & Aureli, 2010; Schweinfurth & Call, 2019; Taborsky, 1994; Taborsky et al., 2016). However, outcome-based reciprocity, that is help based on the consequence of an action, might be too rigid for cooperation to evolve. For example, if an individual is hungry and begging for food, but their partner has no food, it might be important to realise that this partner is not generally unwilling to cooperate, but simply unable at this occasion. In the future, this partner might be able and willing to help and thus might be a good cooperation partner. Hence, making predictions about future interactions with a partner based on intentions might be better than on outcomes, which can be determined by external factors that are out of control of the partner. Intention-based reciprocity has been shown to be evolutionary stable in theory because it enables individuals to engage in enduring mutual cooperation (Fishman, 2006).

While such a strategy based on intentions provides benefits, it might also involve costs, for example in terms of greater cognitive demands. In order to read the intention of another agent, one must understand (i) that the partner has a goal towards which she is acting, (ii) the partner's ability to act according to the goal and (iii) the end state of an action, that is whether the partner has reached that goal (Tomasello et al., 2005). Thereby, intention reading enables understanding the motivation to help based on the ability to ascribe mental states to others, that is theory of mind (Premack & Woodruff, 1978). For example, the same outcome of an action could be interpreted as getting rid of, moving, returning, trading, sharing or giving a piece of food (cf. Tomasello et al., 2005).

In line with this, only a handful of animals have been suggested to respond to intentions of human experimenters, which may comprise the reading of behaviours and minds. These include primates (reviewed in Krupenye, 2021) such as great apes (Kano & Call, 2014), capuchin monkeys (Phillips et al., 2009) and Tonkean macaques (Canteloup & Meunier, 2017). There is also evidence in other species, for example in grey parrots (Péron et al., 2010) and horses (Trösch et al., 2020). That intention reading is a complex trait is also highlighted by the fact that children gradually increase this skill (Behne et al., 2005; Hamlin, 2013; Liu et al., 2019). Interestingly, although children can read intentions relatively early in their ontogeny, they cooperate mostly based on

outcomes compared with teenagers and adults, who cooperate more based on intentions (Sutter, 2007). Still, even though they mostly respond to outcomes, children can consider intentions. Under some circumstances, they help unable more than unwilling partners (Dunfield & Kuhlmeier, 2010) and avoid helping partners with harmful intentions (Vaish et al., 2010). The enhancing effect of complex cognitive skills, including intention reading, on the evolution of cooperation and *vice versa*, has been recognised repeatedly (Hill & Dunbar, 2003; Moll & Tomasello, 2007). Given the ubiquitous occurrence of cooperation throughout the animal kingdom, it is hence not unlikely to find intention reading also in other animals during cooperation.

The only study to date on intention-based reciprocity in animals, I am aware of, investigated predator mobbing behaviour in neighbouring pied flycatchers (*Ficedula hypoleuca*). These birds were more likely to help neighbours that were unable to help on a previous instance, because they were caught by the experimenters, than seemingly unwilling neighbours that were also caught but alarm calls were played back (Krams et al., 2013). This shows that the birds seem to interpret and excuse their neighbour's defection, either based on ability or intentions. At present, both possibilities can, however, not be disentangled.

Thus, this study asked whether individuals base their reciprocal decisions on outcomes, intentions or abilities to help. Norway rats (*Rattus norvegicus*) are the ideal candidate to test this idea. Rats are highly social and show complex social cognitive skills (Schweinfurth, 2020), including emotional contagion (Atsak et al., 2011) and emotion reading (Nakashima et al., 2015). In recent years, they have also turned into an important model organism for cooperation. Rats have a high propensity to cooperate (Oberliessen et al., 2016) and reciprocally exchange, for instance food (Rutte & Taborsky, 2007) and allogrooming (Schweinfurth et al., 2017) with their conspecifics. Over 20 studies using various paradigms showed that rats provide more help to partners that helped them compared with partners that did not help them in the past (reviewed in Schweinfurth, 2021). As previous studies used specially trained partners, it remains unclear, however, whether rats understand the intentions and abilities of their partners or whether they respond purely to the outcomes of their partner's action.

Here, I aim at separating outcomes from intentions or abilities by testing whether rats differ in their responses towards able versus unable conspecifics, both of whom exhibited cooperative intentions. If rats' decisions are guided predominantly by others' intentions, rats should help both partners equally often. If guided predominantly by the outcomes, rats should help "able" partners more often than

TABLE 1 Overview of the subjects' experience before they could return favours

Ability	Intention	Outcome
Able	Willing	Help received
Unable	Willing	No help received
Able	Unwilling	No help received

Note: Partners were either able or unable to help and willing or unwilling to help.

"unable" partners. Furthermore, I compared this to earlier results on partners that were able but unwilling in order to separate outcomes from abilities. If rats evaluate partners primarily based on their ability to help, they should help able and unwilling partners more often than unable and willing partners, although both showed no help. However, if rats help based primarily on outcomes, they should make no difference between those partners as the outcome is the same (Table 1).

2 | METHODS

2.1 | Experimental subjects

This study investigates helping behaviour in outbred Norway rats that were descendants of wild-caught individuals (source: Animal Physiology Department, University of Groningen, the Netherlands). The subjects of this study were adult (563–571 days old) females, weighing between 256 and 408 g. The rats were housed in same-sex groups of five individuals. Twelve groups were housed in one room, and the groups had limited visual but acoustic contact with rats of other cages. The cages (80 × 50 cm and 37.5 cm high) were enriched with a (non-monopolisable) wooden house, sitting board, salt block, hiding tunnel and a piece of wood to nibble. They were provided with litter and hay as bedding material. The cages were cleaned, and the bedding exchanged once a week. Food (conventional rat pellets) and water were provided *ad libitum*, and the rats were never food-deprived. In addition, the rats received a snack, which was a grain mix, in the afternoon four times a week and fresh fruits or vegetables twice a week. All rats were carefully accustomed to handling right after weaning and arrival at the facility and thus showed no signs of stress when being picked up or transported. Testing took place in a separate room. The ambient temperature of the housing and testing room was $20 \pm 1°C$, with a relative humidity of 50%–60%. The light:dark cycle was set to 12:12h with lights on at 8p.m. and 30 min of dawn and dusk. The study was conducted during the day under red light. The subjects were not selected but were all available animals at that time, and the rats were randomly assigned to their role (i.e. subject or partner). In addition, the test order of the subjects was randomly chosen, but the order was kept the same in both conditions, so that rats were tested at the same time of the day.

2.2 | Pre-experimental training

In order to participate in this study, the rats were trained to use the food exchange apparatus that was established by Rutte and Taborsky (2007). The apparatus consisted of a movable platform (grey PVC) on a wooden table. The platform was connected to a stick. By pulling the stick (about 0.14N), the platform moved into the experimental cage (80 × 50 cm and 37.5 cm high) that was divided into two equally

sized compartments by mesh. The training followed an established training protocol (for more detail, see the comprehensive description of Dolivo and Taborsky (2015)). In summary, the training was divided into two phases. In the first phase, all rats learned to use the platform by pulling food (here an oat flake) towards themselves (all rats received 11 sessions). Thereafter, the rats entered the second phase of the training, receiving 18 sessions. Here, every rat was paired with a cage mate. Pulling the platform provided food only to their training partner but never to the active rat anymore. The roles were exchanged, and the delays between role reversals were gradually increased, that is from role reversals directly after one donation to role reversal after seven minutes, that is the experimental time.

2.3 | Experimental procedure

Every subject rat ($n = 27$) experienced the same familiar partner ($n = 25$, two partners used twice) in two conditions on two different days, consisting of one experience and one test phase, respectively, following a within-subject design. In the "able" condition, every subject rat experienced a partner that was able to help by providing food via the movable platform for seven minutes, which the subject and partner rats were familiar with from the pre-experimental training. In the "unable" condition, the partner was unable to help the subject rat for seven minutes because the experimenter blocked the platform with a piece of rope that was visible. Thus, the platform could not be moved and could not deliver food to the subject rat, although the food was visible. Every experience phase was followed by a test phase (seven minutes) in which subject rats could provide food to their partner. I noted down how often subject rats provided food to their partner. As a measure for the unable partner's intention to help, I also recorded whether partners tried to help by pulling the stick that was fixed to the immobile platform. I had to exclude eight rat dyads as the partner did not attempt to provide food in the unable condition, and it was thus unclear whether the partner was perceived as "unable" ($n = 19$). Note that including those dyads did not change the results.

To investigate whether subjects respond to the ability to help or the outcome, that is help received or not, I compared the data to archival data, using the same rat cohort (Schweinfurth & Taborsky, 2020). Here, subjects ($n = 21$) experienced trained cooperators ($n = 6$) that were "willing" and trained defectors ($n = 6$) that were "unwilling" to help, respectively. Importantly, cooperators and defectors were able to help, that is the platform was not blocked. The experimental protocol was the same as above.

2.4 | Statistical analyses

All tests were done in R (version 3.6.0) with RStudio, using the package "lme4." To test whether rats differentiated between partners that were able or unable to help, I calculated a generalised linear mixed model (command: glmer) for the donation rate, assuming a
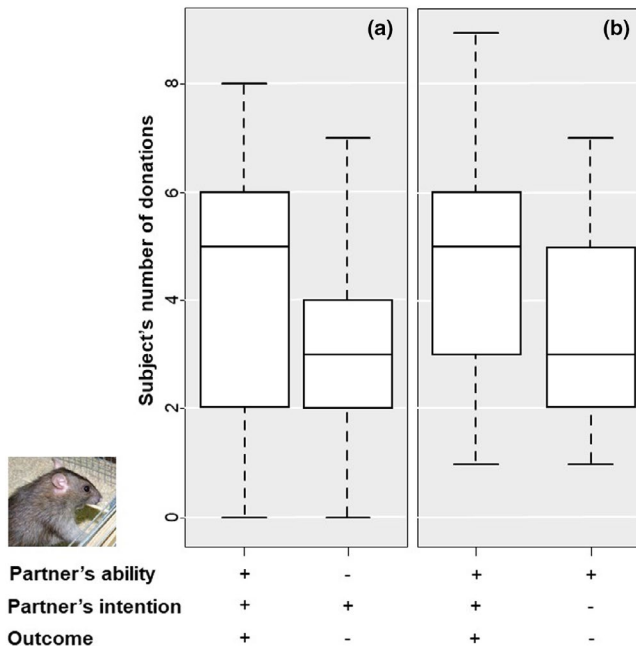
FIGURE 1 Donation rate of subject rats towards partners that differ in ability and intention Subject rats provided food by pulling a stick (see picture) more often to partners that helped them previously compared to partners that did not help. Thereby the outcome of actions explained their donations best in comparison to the partner's ability (+ indicates being able to help, - being unable to help) or intention to help (+ being willing to help, - being unwilling to help). Panel (a) shows the donations of subjects towards partners that were generally willing to help but differed in whether they were able or unable to help. Panel (b) shows the donations of subjects towards partners that were able to help but differed in whether they were willing or unwilling to help. The boxplots depict the median and interquartile range as box and the lower and upper quartile as whiskers

Poisson distribution. Experimental condition, that is able and unable, was included as fixed factor. Some rats were used as partner and as subject, but never twice as a subject rat. To correct for multiple testing, the identities of the subject (nested with their cage) and partner identity was included in the models as random effects. The model fit was assessed visually with the help of Q-Q plots and the residuals were normally distributed (Shapiro–Wilk normality test: $W = 0.98$, $p = .69$), suggesting a good model fit. To disentangle ability from outcomes, I conducted pairwise comparisons, using the Wilcoxon signed-rank tests for paired (able and willing versus able and unwilling) and the Mann–Whitney U tests for unpaired data (able and unwilling versus unable and willing).

3 | RESULTS

Subject rats distinguished between both conditions and provided more food to "able" food-providing partners compared to "unable" partners, which could not provide food as the device was blocked (Generalised linear mixed model: $\beta = -0.48 \pm 0.17$, $n = 19$, $p = .004$, Figure 1a). Subjects helped able and willing partners more often than

able and unwilling partners (Wilcoxon signed-rank test: $V = 128.0$, $p = .015$, Figure 1b). No difference could be detected between able but unwilling and unable but willing partners (Mann–Whitney U test: $U = 222.0$, $p = .58$, Figure 1a,b).

4 | DISCUSSION

Rats distinguished between a partner that was able to help in one and unable to help in another condition by providing food more often to the able partner. Importantly, the unable partners attempted to help by pulling the stick that was connected to the blocked platform, suggesting that they had cooperative intentions. Thus, rats seem to not consider their partner's intention to help but base their decision on outcomes or abilities to help. The responses reflect those of rats who encountered specially trained partners that were willing or unwilling to help. Those trained partners differed in their intention, but not in their ability to help. Again, subjects provided more help to those that helped them in the past, suggesting that ability to help cannot explain their response either. In a direct comparison, the subjects showed no difference in helping an unable, but willing compared with an able, but unwilling partner. Taken together, this suggests that rats evaluate their partner's cooperativeness predominantly based on outcomes and not on their partner's intention or ability to help.

If rats base their decisions predominately on outcomes, how do they make sure to not categorise an unable partner with cooperative intentions as a defector, which can have dramatic effects on future co-operation. When potential cooperators are not recognised as cooperators, reciprocity can lead to the loss of cooperation over evolutionary time frames (Stevens et al., 2011). This is mainly because reciprocal strategies, such as tit for tat, are not overly forgiving or flexible. If a partner has failed to cooperate once or was incorrectly memorised as a defector, the other individual stops cooperating with this partner. Consequently, this partner is lost as a future cooperation partner. To mitigate this problem, rats might use a different strategy that is helping defectors a bit, but less than cooperators. Thereby, their strategy is more flexible and less prone to losing future cooperation partners that have cooperative intentions, but that are unable to help on a specific occasion. In fact, in all published studies on cooperation in rats, they rarely showed zero help towards unwilling defectors, but help cooperators significantly more often than defectors that receive a bit of help. This effect was found in female rats (Rutte & Taborsky, 2008), male rats (Schweinfurth et al., 2019), related and unrelated rats (Schweinfurth & Taborsky, 2018b) and even when they exchange grooming for received help in this task (Schweinfurth & Taborsky, 2018a). This strategy might be cognitively less demanding as only outcomes need to be assessed. A model using flexible investments showed that a continuous response can facilitate the evolution of cooperation, especially when there are few interactions, as expected for a short-lived animal, like rats (Killingback & Doebeli, 2002).

Further studies could clarify whether rats are not able to read intentions or are able but do not use them in this cooperative context. For example, the used paradigm might have been challenging

for rats to understand. Although the unable partners attempted to provide food by pulling the blocked platform, which was audible and visible, subject rats might not understand that the platform was blocked. While this is possible, I think it is rather unlikely because (i) when the platform was blocked eight partners did not even attempt to pull it and (ii) rats have been shown to have good physical cognition in similar tasks. For example, rats use and manipulate pulling tools and understand which tools are functional (Nagano, 2019; Nagano & Aoyama, 2016). Still, conceptual replications, which are testing the same concept by using different means (cf. Nosek & Errington, 2020), could clarify whether the finding that rats predominantly use outcomes for their cooperative decisions is due to the here used task or due to the cooperative context.

There are two additional paradigms that have been commonly used to assess intention reading in other species. One paradigm requires subjects to copy a demonstrator who performs an unusual action that in one condition can be explained by an external factor or not in another condition, like switching off a lamp with the forehead when the hands are tied or free. Children copy the action more often, if the experimenter's hands are free, suggesting some goal understanding (Gergely et al., 2002). Rats are highly sensitive to the actions of conspecifics and are known to copy others (Galef & Laland, 2005). Hence, a version of this task might be possible. However, such copying tasks require the identification of causally irrelevant components and a lack of over-imitation, which might come with challenges in itself (cf. Whiten, 2019). Another paradigm compares the subjects' response to an intentional or accidental situation, like placing or dropping a marker on a food container to indicate the food location (Call & Tomasello, 1998). This might be a more promising next step. In the current study, rats might have been able to understand their partner's intention, but they did not use intentions in cooperative contexts. The intentional/accidental paradigm yields direct benefits to the acting individual, and hence, subjects might be more motivated to use their knowledge about intentions. Developing several paradigms for rats might clarify whether rats generally cannot read intentions or might not use them for cooperative decisions.

In conclusion, this study suggests that rats base their decision to reciprocate predominantly on cooperation outcomes rather than on their partner's intentions or abilities. By using a buffering system of helping defectors a bit, but considerably less than cooperators, rats might use a cognitively less demanding strategy to reciprocate help. Whether rats are unable or unwilling to use intentions in cooperative decisions should be subject to future studies.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

The author declares no conflict of interest.

AUTHOR CONTRIBUTIONS

MKS conceived and conducted the study, analysed the data and wrote the manuscript.

ETHICAL NOTE

All procedures were non-invasive and conducted in accordance with the Swiss Animal Welfare Legislation, approved by the Swiss Federal Veterinary Office under licence BE25/14. Rats remained in stock after the study.

DEDICATION

This paper is dedicated to Prof. Michael Taborsky, who supervised my doctoral work. He taught me a lot about animal behaviour, evolutionary theory and conducting science in general. I am extremely grateful that we have shared highly inspiring years together at the Hasli, which have greatly shaped my scientific thinking. Michael has always had cooperative intentions.

ORCID

Manon K. Schweinfurth https://orcid.org/0000-0003-2066-7892

REFERENCES

Atsak, P., Orre, M., Bakker, P., Cerliani, L., Roozendaal, B., Gazzola, V., Moita, M., & Keysers, C. (2011). Experience modulates vicarious freezing in rats: A model for empathy. *PLoS One*, *6*(7), e21855. https://doi.org/10.1371/journal.pone.0021855

Behne, T., Carpenter, M., Call, J., & Tomasello, M. (2005). Unwilling versus unable: Infants' understanding of intentional action. *Developmental Psychology*, *41*(2), 328–337. https://doi.org/10.1037/0012-1649.41.2.328

Bowles, S., & Gintis, H. (2011). *A cooperative species - human reciprocity and its evolution*. Princeton. https://doi.org/10.1007/s00712-011-0237-5

Call, J., & Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and human children (*Homo sapiens*). *Journal of Comparative Psychology*, *112*(2), 192–206. https://doi.org/10.1037/0735-7036.112.2.192

Canteloup, C., & Meunier, H. (2017). "Unwilling" versus "unable": Tonkean macaques' understanding of human goal-directed actions. *PeerJ*, *2017*(5), 3227. https://doi.org/10.7717/peerj.3227

Chao, M. (2018). Intentions-based reciprocity to monetary and non-monetary gifts. *Games*, *9*, 74. https://doi.org/10.3390/g9040074

Charness, G., & Levine, D. I. (2003). *The road to hell: An experimental study of intentions*. In UC Santa Barbara: Department of Economics - Repository. https://doi.org/10.2139/ssrn.437870

Díaz-Muñoz, S. L., DuVal, E. H., Krakauer, A. H., & Lacey, E. A. (2014). Cooperating to compete: Altruism, sexual selection and causes of male reproductive cooperation. *Animal Behaviour*, *88*, 67–78. https://doi.org/10.1016/j.anbehav.2013.11.008

Dolivo, V., & Taborsky, M. (2015). Cooperation among Norway rats: The importance of visual cues for reciprocal cooperation, and the role of coercion. *Ethology*, *121*, 1071–1080. https://doi.org/10.1111/eth.12421

Dunfield, K. A., & Kuhlmeier, V. A. (2010). Intention-mediated selective helping in infancy. *Psychological Science*, *21*(4), 523–527. https://doi.org/10.1177/0956797610364119

Falk, A., Fehr, E., & Fischbacher, U. (2003). On the nature of fair behavior. *Economic Inquiry*, *41*(1), 20–26. https://doi.org/10.1017/CBO9781107415324.004

Falk, A., & Fischbacher, U. (2006). A theory of reciprocity. *Games and Economic Behavior*, *54*(2), 293–315. https://doi.org/10.1016/j.geb.2005.03.001

Fishman, M. A. (2006). Involuntary defection and the evolutionary origins of empathy. *Journal of Theoretical Biology*, *242*(4), 873–879. https://doi.org/10.1016/j.jtbi.2006.05.004

Galef, B. G., & Laland, K. L. (2005). Social learning in animals: Empirical studies and theoretical models. *BioScience*, *55*(6), 489–499.

Gergely, G., Bekkering, H., & Király, I. (2002). Rational imitation in preverbal infants. *Nature*, *415*(6873), 755. https://doi.org/10.1038/415755a

Gummerum, M., & Chu, M. T. (2014). Outcomes and intentions in children's, adolescents', and adults' second- and third-party punishment behavior. *Cognition*, *133*(1), 97–103. https://doi.org/10.1016/j.cognition.2014.06.001

Hamlin, J. K. (2013). Failed attempts to help and harm: Intention versus outcome in preverbal infants' social evaluations. *Cognition*, *128*(3), 451–474. https://doi.org/10.1016/j.cognition.2013.04.004

Hill, R. A., & Dunbar, R. I. M. (2003). Social network size in humans. *Human Nature*, *14*(1), 53–72. https://doi.org/10.1007/s12110-003-1016-y

Kano, F., & Call, J. (2014). Great apes generate goal-based action predictions: An eye-tracking study. *Psychological Science*, *25*(9), 1691–1698. https://doi.org/10.1177/0956797614536402

Killingback, T., & Doebeli, M. (2002). The continuous Prisoner's Dilemma and the evolution of cooperation through reciprocal altruism with variable investment. *American Naturalist*, *160*(4), 421–438. https://doi.org/10.1086/342070

Krams, I., Kokko, H., Vrublevska, J., Aboliņš-Abols, M., Krama, T., & Rantala, M. J. (2013). The excuse principle can maintain cooperation through forgivable defection in the Prisoner's Dilemma game. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20131475. https://doi.org/10.1098/rspb.2013.1475

Krupenye, C. (2021). The evolution of mentalizing in humans and other primates. In M. Gilead, & K. Ochsner (Eds.). *The neural basis of mentalizing: A social-cognitive and affective neuroscience perspective*. Springer.

Liu, S., Brooks, N. B., & Spelke, E. S. (2019). Origins of the concepts cause, cost, and goal in prereaching infants. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(36), 17747–17752. https://doi.org/10.1073/pnas.1904410116

Moll, H., & Tomasello, M. (2007). Cooperation and human cognition: The Vygotskian intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 639–648. https://doi.org/10.1098/rstb.2006.2000

Nagano, A. (2019). Rats' (*Rattus norvegicus*) tool manipulation ability exceeds simple patterned behavior. *PLoS One*, *14*(12), e0226569. https://doi.org/10.1371/journal.pone.0226569

Nagano, A., & Aoyama, K. (2016). Tool-use by rats (*Rattus norvegicus*): Tool-choice based on tool features. *Animal Cognition*, *20*(2), 199–213. https://doi.org/10.1007/s10071-016-1039-5

Nakashima, S. F., Ukezono, M., Nishida, H., Sudo, R., & Takano, Y. (2015). Receiving of emotional signal of pain from conspecifics in laboratory rats. *Royal Society Open Science*, *2*, 140381. https://doi.org/10.1098/rsos.140381

Nosek, B. A., & Errington, T. M. (2020). What is replication? *PLoS Biology*, *18*(3), e3000691. https://doi.org/10.1371/journal.pbio.3000691

Oberliessen, L., Hernandez-Lallement, J., Schäble, S., van Wingerden, M., Seinstra, M., & Kalenscher, T. (2016). Inequity aversion in rats, *Rattus norvegicus*. *Animal Behaviour*, *115*, 157–166. https://doi.org/10.1016/j.anbehav.2016.03.007

Orhun, A. Y. (2018). Perceived motives and reciprocity. *Games and Economic Behavior*, *109*, 436–451. https://doi.org/10.1016/j.geb.2018.01.002

Péron, F., Rat-Fischer, L., Nagle, L., & Bovet, D. (2010). 'Unwilling' versus 'unable': Do grey parrots understand human intentional actions? *Interaction Studies*, *11*(3), 428–441. https://doi.org/10.1075/is.11.3.06per

Phillips, W., Barnes, J. L., Mahajan, N., Yamaguchi, M., & Santos, L. R. (2009). "Unwilling" versus "unable": Capuchin monkeys' (*Cebus apella*) understanding of human intentional action. *Developmental Science*, *12*(6), 938–945. https://doi.org/10.1111/j.1467-7687.2009.00840.x

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *The Behavioral and Brain Sciences*, *4*, 515–526. https://doi.org/10.1017/S0140525X00076512

Rutte, C., & Taborsky, M. (2007). Generalized reciprocity in rats. *PLoS Biology*, *5*(7), 1421–1425. https://doi.org/10.1371/journal.pbio.0050196

Rutte, C., & Taborsky, M. (2008). The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): Direct vs generalised reciprocity. *Behavioral Ecology and Sociobiology*, *62*(4), 499–505. https://doi.org/10.1007/s00265-007-0474-3

Schino, G., & Aureli, F. (2010). A few misunderstandings about reciprocal altruism. *Communicative and Integrative Biology*, *3*(6), 561–563. https://doi.org/10.4161/cib.3.6.12977

Schweinfurth, M. K. (2020). The social life of Norway rats (*Rattus norvegicus*). *eLife*, *9*, 54020., https://doi.org/10.7554/eLife.54020

Schweinfurth, M. K. (2021). Reciprocity in Norway rats (*Rattus norvegicus*). In A. Kaufman, J. Call, & J. Kaufman (Eds.), *Cambridge Handbook of Animal Cognition*. Cambridge University Press.

Schweinfurth, M. K., Aeschbacher, J., Santi, M., & Taborsky, M. (2019). Male Norway rats cooperate according to direct but not generalized reciprocity rules. *Animal Behaviour*, *152*, 93–101. https://doi.org/10.1016/j.anbehav.2019.03.015

Schweinfurth, M. K., & Call, J. (2019). Revisiting the possibility of reciprocal help in non-human primates. *Neuroscience and Biobehavioral Reviews*, *104*, 73–86. https://doi.org/10.1016/j.neubiorev.2019.06.026

Schweinfurth, M. K., Stieger, B., & Taborsky, M. (2017). Experimental evidence for reciprocity in allogrooming among wild-type Norway rats. *Scientific Reports*, *7*(1), 4010. https://doi.org/10.1038/s41598-017-03841-3

Schweinfurth, M. K., & Taborsky, M. (2018a). Reciprocal trading of different commodities in Norway rats. *Current Biology*, *28*, 594–599. https://doi.org/10.1016/j.cub.2017.12.058

Schweinfurth, M. K., & Taborsky, M. (2018b). Relatedness decreases and reciprocity increases cooperation in Norway rats. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 20180035. https://doi.org/10.1098/rspb.2018.0035

Schweinfurth, M. K., & Taborsky, M. (2020). Rats play tit-for-tat instead of integrating social experience over multiple interactions. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1918), 20192423.– https://doi.org/10.1098/rspb.2019.2423

Stevens, J. R., Volstorf, J., Schooler, L. J., & Rieskamp, J. (2011). Forgetting constrains the emergence of cooperative decision strategies. *Frontiers in Psychology*, *1*, 235. https://doi.org/10.3389/fpsyg.2010.00235

Sun, Z., Ye, C., He, Z., & Yu, W. (2020). Behavioral intention promotes generalized reciprocity: Evidence from the Dictator Game. *Frontiers in Psychology*, *11*, 772. https://doi.org/10.3389/fpsyg.2020.00772

Sutter, M. (2007). Outcomes versus intentions: On the nature of fair behavior and its development with age. *Journal of Economic Psychology*, *28*(1), 69–78. https://doi.org/10.1016/j.joep.2006.09.001

Taborsky, M. (1994). Sneakers, satellites, and helpers: Parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior, 23*, 1–100. https://doi.org/10.1016/S0065-3454(08)60351-4

Taborsky, M., Frommen, J. G., & Riehl, C. (2016). Correlated pay-offs are key to cooperation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150084.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *The Behavioral and Brain Sciences*, *28*(5), 691–735. https://doi.org/10.1017/S0140525X05000129

Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, *46*(1), 35–57. https://doi.org/10.1086/406755

Trösch, M., Bertin, E., Calandreau, L., Nowak, R., & Lansade, L. (2020). Unwilling or willing but unable: Can horses interpret human actions as goal directed? *Animal Cognition*, *23*, 1035–1040. https://doi.org/10.1007/s10071-020-01396-x

Vaish, A., Carpenter, M., & Tomasello, M. (2010). Young children selectively avoid helping people with harmful intentions. *Child Development*, *81*(6), 1661–1669. https://doi.org/10.1111/j.1467-8624.2010.01500.x

Whiten, A. (2019). Conformity and over-imitation: An integrative review of variant forms of hyper-reliance on social learning. *Advances in the Study of Behavior*, *51*, 31–75. https://doi.org/10.1016/bs.asb.2018.12.003

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.