Received: 30 November 2016 | Revised: 15 May 2017 | Accepted: 17 May 2017

DOI: 10.1111/eth.12636

RESEARCH PAPER

WILEY ethology international journal of behavioural biology

Feel good, do good? Disentangling reciprocity from unconditional prosociality

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Funding information
Swiss National Science Foundation

Editor: M. Herberstein

Abstract

Direct and generalised reciprocity can establish evolutionarily stable levels of cooperation among unrelated individuals, with animals reciprocating help based on whether they have been helped by a social partner before. It has been argued that the actual cooperative act by a social partner may be of minor importance for seemingly reciprocal cooperation and that a mere positive experience might suffice to enhance helpful behaviour towards a conspecific ('feel good, do good'). However, this effect could easily be exploited by defectors free-riding on an individual's enhanced propensity to cooperate after an unspecific positive experience, without investing in reciprocity themselves. Here, we use female Norway rats (*Rattus norvegicus*) to test if a positive experience that was not provided by a helping partner increases the propensity to subsequently help a social partner. We manipulated the experience of test subjects by providing them with treats, either in the presence or absence of a conspecific. Thereafter, we assessed whether they produce treats and if so, how many, for an unfamiliar social partner compared to a situation in which they had not received treats before. As the treats the test subject received had not been provided by a social partner even if the partner was present, we predicted that the rats should not be more cooperative after they had received treats than if they had not. Indeed, the helping behaviour of rats was apparently not influenced by prior experience made either in a social or non-social context. Rats have been shown previously to perform both direct and generalised reciprocity in the same variant of the iterated prisoner's dilemma game. Our results suggest that this behaviour cannot be explained by an unspecific positive experience. The decision to help a social partner seems to be contingent on previously receiving help from a social partner (reciprocity), not on any positive experience (unconditional prosociality).

KEYWORDS

affective state, cooperation, decision-making, experience, mood, prosocial behaviour, reciprocal altruism

1 | INTRODUCTION

When animals repeatedly interact with each other, cooperation may ensue from reciprocity, even if they are unrelated (Trivers, 1971; Taborsky, Frommen, & Riehl, 2016). In an iterated prisoner's dilemma game, individuals base their decision to provide help to a partner or not on the latter's previous help provided to them (direct reciprocity; Axelrod & Hamilton, 1981) or to others (indirect reciprocity; Nowak & Sigmund, 1998). Alternatively, an individual may help someone if it had previously received help from somebody else (generalised reciprocity;

Hamilton & Taborsky, 2005; Pfeiffer, Rutte, Killingback, Taborsky, & Bonhoeffer, 2005), which is a simple mechanism that can generate evolutionarily stable levels of cooperation even in large populations (Rankin & Taborsky, 2009; Barta, McNamara, Huszár, & Taborsky, 2011; van Doorn & Taborsky, 2012). Direct and generalised reciprocity depend solely on previously received help from a social partner, while indirect reciprocity is based on a 'reputation' mechanism and thus requires more advanced cognitive abilities (Nowak & Sigmund, 2005). Therefore, whereas direct and generalised reciprocity have been observed in many animals including vampire bats (*Desmodus rotundus*; Wilkinson, 1984; Carter & Wilkinson, 2013), chimpanzees (*Pan troglodytes*; de Waal, 1997), impalas (*Aepyceros melampus*; Hart & Hart, 1992), cotton-top tamarins (*Saguinus oedipus*; Hauser, Chen, Chen, & Chuang, 2003), capuchin monkeys (*Cebus apella*; de Waal, 2000; Leimgruber et al., 2014) and Norway rats (*Rattus norvegicus*; Rutte & Taborsky, 2007, 2008; see Taborsky et al., 2016 for general review), indirect reciprocity has so far been demonstrated only in humans (Wedekind & Milinski, 2000; Milinski, 2016).

A potential cause of this bias may be that the helping propensity could be based solely on the neuroendocrine effect of a previous positive experience. Such 'feel good, do good' effects have been studied intensively in human psychology (reviewed by Carlson, Charlin, & Miller, 1988; Salovey, Mayer, & Rosenhan, 1991; George & Brief, 1992). The probably earliest study of this phenomenon has shown that people who have found a coin in a public cell phone were more likely to help a stranger picking up dropped papers from the ground than control subjects were (Isen & Levin, 1972). Likewise, Strohmetz, Rind, Fisher, and Lynn (2002) observed an increase in restaurant tipping when waiters provided a candy along with the bill. However, both these experiments cannot be interpreted independently from a social context, as helping a stranger after finding coins (left by a third individual) may conform to generalised reciprocity, while increased tipping of a waiter after receiving candy from her or him is compatible with direct reciprocity. Indeed, experiments where the affective state (hereafter called 'mood') of test subjects has been enhanced in a non-social context (e.g., through nice weather, music or movies), the results are inconsistent and have been discussed controversially (e.g., Cunningham, 1979; Fried & Berkowitz, 1979; Rosenhan, Salovey, & Hargis, 1981; North, Tarrant, & Hargreaves, 2004; Kirchsteiger, Rigotti, & Rustichini, 2006). From an evolutionary perspective, if the emotional state of individuals changes their propensity to help others independently from a social context, individuals could exploit this tendency easily by accepting help readily from cheerful companions but never providing help themselves. Hence, in order for cooperative behaviour to evolve, positive experiences that are not associated with helping by a social partner should have no effect on the future cooperative propensity of an individual (Rutte & Taborsky, 2008). However, this hypothesis has not yet been tested in non-human animals.

Norway rats are highly social animals showing allogrooming, joint aggression towards intruders, communal food storing with sharing of hoarded food, and assemblage formation in winter (Calhoun, 1964). In a variant of the iterated prisoner's dilemma (IPD) game, rats show both direct and generalised reciprocity (Rutte & Taborsky, 2007, 2008), with their decision being based on the costs of the helping task, the benefit to the receiver (Schneeberger, Dietz, & Taborsky, 2012) and the value of the received help (Dolivo & Taborsky, 2015). These experiments used an apparatus by which focal subjects could produce food for a social partner. Generally, rats provided more help to partners that have previously produced food for them (direct reciprocity; Rutte & Taborsky, 2008), or simply if they have received food from another rat (generalised reciprocity; Rutte & Taborsky, 2007), as compared to if they had not been helped before.

Here, we ask if Norway rats distinguish between receiving an altruistic act by a partner and the simple receipt of a treat. First, we test if the focal rats reciprocate help after having received help by a partner (i.e., if they perform direct reciprocity and thus remember both the identity and helpfulness of a conspecific). We then test four different scenarios in which the focal rat either does or does not receive a treat in the presence or absence of a social partner in a full factorial design. In none of these cases does the social partner perform a helping act; that is, the treats are delivered to the focal subject by a different mechanism. After each of these four experiences, the focal rats are given the opportunity to produce food for a new, unfamiliar partner. If receiving a treat is a sufficient stimulus to increase the propensity to provide food for a social partner, we predicted that in the test the focal rat would preferably donate food to a partner after receiving a treat when a partner was present compared to after receiving no treat or after receiving a treat when no partner was present. If, however, focal test rats are able to distinguish between a positive experience that was not caused by a social partner, and a similar experience caused by a social partner, we predicted that the focal rats would produce similar amounts of food for an unknown partner after receiving treats or not, regardless of the presence of a partner in the experience phase of the experiment.

2 | METHODS

2.1 | Housing of experimental subjects

The procedures described in this study conform to the legal requirements of Switzerland (licence no. 02/04, Veterinary Service of the Canton Bern, Switzerland) and the guidelines of the University of Bern, where the work was carried out.

We used 36 female wild-type Norway rats (*Rattus norvegicus*) bred at the Animal Physiology Department at the University of Groningen, Netherlands, and housed at the Ethologische Station Hasli of the University of Bern. The rats were kept in groups of three to six individuals per cage (80×50x37.5 cm LxWxH) with environmental enrichment in a climate room with standardised conditions (on average 21°C temperature and 60% humidity) and a reversed dark–light cycle. Training and experiments were performed during the dark phase when rats were active, and all rats were habituated to human presence and handling.

2.2 | Training and reciprocity test

All rats were trained to produce food for each other in an operant cooperative task as applied in previous studies (Rutte & Taborsky, 2007,

2008; Schneeberger et al., 2012). For this, a testing cage was divided by a wire mesh (preventing the rats from direct physical contact), with a movable tray being installed in front of the cage. The rat in one compartment could pull the tray towards the cage with the help of a stick attached to the device. Once the rat pulled the tray towards the cage, the partner rat in the other compartment could reach a treat. The pulling rat did not receive a reward. After seven minutes, the roles were switched so that the rat that previously received the treat could reciprocate the help for the partner rat. We trained 36 focal rats to use this task to reciprocally produce food for each other and tested whether they indeed behaved according to direct reciprocity rules before entering the 'feel good, do good' experiment.

2.3 | Feel good, do good experiment

For this experiment, we manipulated the experience of the focal rat with and without a partner rat being present in the neighbouring compartment (Figure 1): with the partner being present, eight halves of raisins were sequentially presented, either only to the focal rat (positive experience, partner present), or only to the partner rat (control, partner present). When the partner was not present, in a similar way either the focal rat received eight raisin halves (positive experience, partner not present), or they were presented to the empty neighbouring compartment without the focal rat receiving something (control, partner not present). If a social partner was present, the focal rat could easily witness that this partner does not pull the tray and hence did not produce the treats. The raisins were provided by a remotely controlled food dispenser attached to the tray (Fig. S1) in order to exclude that the rats connect the provision of a food reward with the action of a human observer. The quantity of food provided was equivalent to what a partner would have produced in the same period of time. The focal rat was assigned to the four treatments in random sequence. First, the focal subject received one of the four experiences on five consecutive days. On the subsequent day (day six), the rat was then exposed to an unfamiliar partner that they had never met before, for which she could pull food during seven minutes. We chose 24 hr between the last experience and the test session to make sure that our experiment can serve as a proper control for previous studies on reciprocity in Norway rats using the same set-up (Rutte & Taborsky, 2007, 2008; Schneeberger et al., 2012; Dolivo & Taborsky, 2015). The behaviour of the focal rat was video-recorded and observed from a neighbouring room, with the refilling of the tray being remotely controlled like in the experience phase. For each focal rat, we recorded the pulling frequency and the latency between pulls. We changed the stick after each session and cleaned the cage after each day to avoid that the rats could use odour cues from former social partners. Additionally, we recorded the age and body weight of the rats, as the helping propensity may depend on the status of a partner (Smith, Berdoy, & Smith, 1994; Schneeberger et al., 2012). Due to observational problems, the number of pulls and the latencies were not available for all 36 rats, which was why we excluded missing values from the data set.

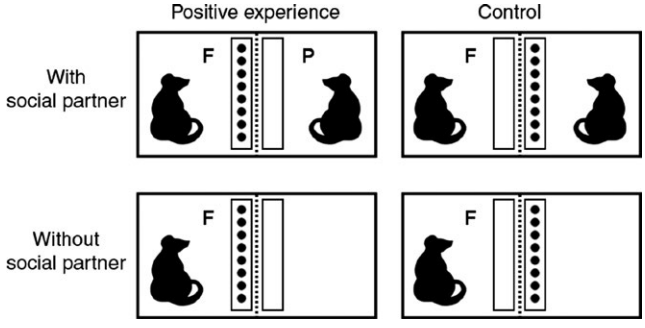

FIGURE 1 Experience treatments. The focal test rat (F) received eight raisin halves (black dots) by a remotely controlled food dispenser in the 'positive experience' treatments (left column) either with a social partner (P) present in the neighbouring compartment (upper row), or without (lower row). In the 'control' situation (right column), the raisin halves were presented in the neighbouring compartment, where either a social partner was present (upper row), or not (lower row)

2.4 | Statistical analyses

First, we compared the focal rats' pulling behaviour for their training partners from which they had previously received food with their pulling frequency for the partners that did not provide food for them while being present when the test subjects received treats by a different mechanism. Using a Friedman one-way ANOVA, we thus tested for direct reciprocity. We then used bootstrapping (package 'boot' of R, 5000 repetitions) to calculate the 95% confidence interval (BCa method) of the difference in the number and latency of pulls of individuals across treatments during the feel good, do good test and applied a paired nonparametric permutation t-test (package 'broman' of R, 5000 permutations) to test for differences between treatments (positive experience or control; partner present or absent). We analysed the data with R statistical software (version 3.1.3; http://www.r-project.org).

3 | RESULTS

The focal rats pulled significantly more often for partners that had pulled for them before (i.e., during the training sessions), than for partners that had not pulled for them while food was still delivered in a similar way but by a different mechanism (i.e., during the experience phase of the test). This indicates that the rats performed direct reciprocity (X^2 = 50.222, N = 35, p < .001). This was consistent over all 4 test days, but the difference declined from day 1 to day 4 (Fig. S2).

In contrast, during the 'feel good, do good' tests the number of pulls by the focal rats for their partners was not influenced by their previous experience; neither with regard to whether they received a treat, nor with regard to whether a partner had been present during the experience phase (Table 1; Figure 2; see Figure 3 for comparison of all four treatments and Appendix for ratios). Generally, the number of pulls did not differ between trials in which the positive experience

TABLE 1 Number of pulls

Treatment	Mean difference (pulls/min)	*CI*	*p*
Positive experience > control, partner present	0.182	−0.546, 0.849	.682
Positive experience > control, partner absent	0.528	−0.333, 1.25	.235
Partner present < absent, positive experience	−0.470	−1.37, 0.118	.255
Partner present < absent, control	−0.176	−0.912, 0.588	.704
Positive experience, partner present > control, partner absent	0.118	−0.588, 0.736	.802
Positive experience, partner absent < control, partner present	−0.735	−1.44, −0.118	.053

Pairwise comparison between treatments using bootstrapping. Mean difference, 95% confidence intervals (BCa method) and *p*-values are given. '>' and '<' indicate the directions of trends and differences.

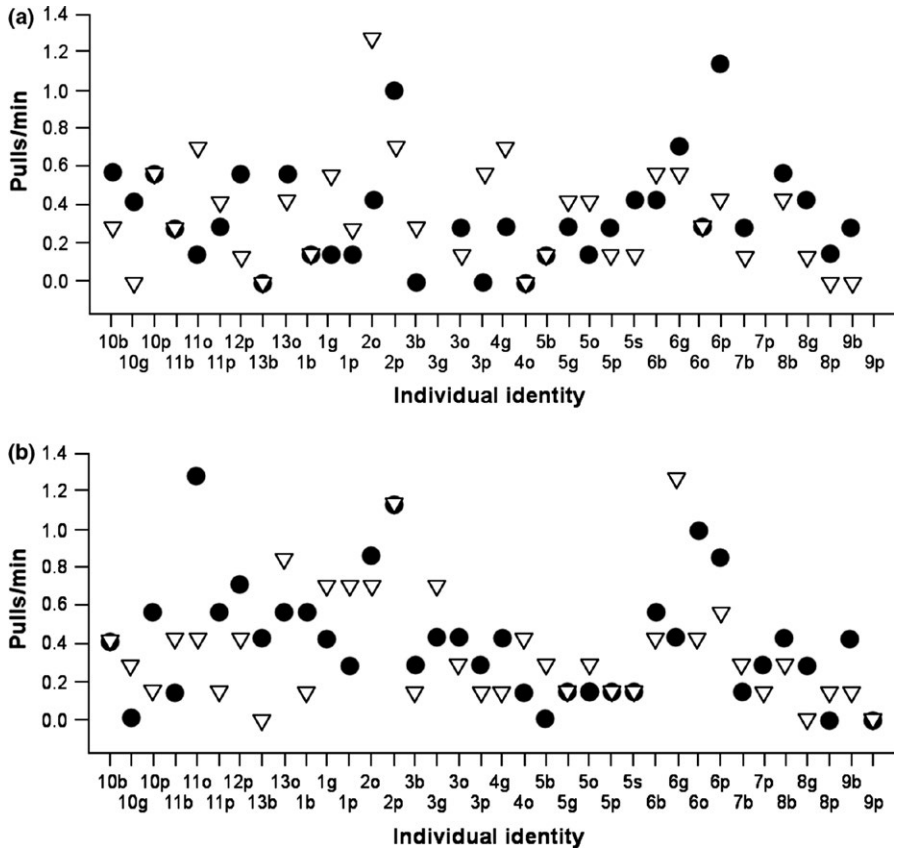

FIGURE 2 Individual pulling frequencies. Rats did not pull more often for a partner rat after receiving food that was not delivered by that partner (dots) than after receiving no food (triangles), both in a social context (a) and in a non-social context (b)

had occurred in a social or in a non-social context (mean difference = 0.324 pulls/min; *CI* = *−1.382*, *0.088*; *N* = 72, *p* = .248).

Like with pulling frequencies, the median intervals between pulls did not differ between trials involving rewarded or unrewarded experiences, neither with a social partner present nor without (Table 2; Fig. S3 and S4). Also, the median pulling intervals in the test phase did generally not differ between trials in which the positive experience had occurred in a social or a non-social context (mean difference = 17.31 sec; *CI* = *−11.37*, *44.41*; *N* = 72, *p* = .232).

The same holds for the latencies until the first pull, which did not differ between the trials involving receipt of treats or not in the experience phase, neither with a partner present nor without (Table 3; Fig. S5 and S6). Also, there was no significant difference in the latency to the first pull between the social and non-social contexts in general (mean difference = 6.54 sec; *CI* = *−28.59*, *11.14*; *N* = 72, *p* = .518).

Overall, the number of pulls performed by the focal rats did not correlate with the age or body mass of their social partners (age:

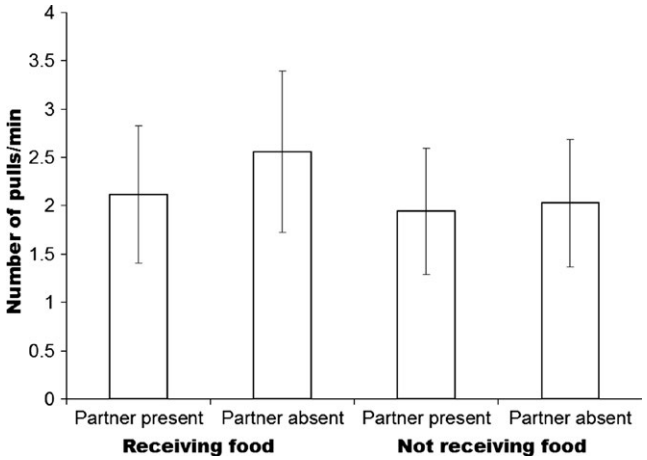

FIGURE 3 Number of pulls by the focal rats after each experienced treatment (mean ± 95% confidence interval)

$Z = -0.913$, $N = 23$, $p = .361$; body mass: $Z = -0.393$, $N = 36$, $p = .695$; Fig. S7). Furthermore, there was neither a sequence effect nor any overall effect of treatments during the test phase (for details, Fig. S8).

4 | DISCUSSION

As expected, the rats showed direct reciprocity by rewarding individuals that had previously produced food for them during the training phase, whereas their food provisioning to social partners in the 'feel good, do good' test was not found to be influenced by receiving food before through a different mechanism. This confirms that the rats perform direct reciprocity memorising previous helpfulness of social partners, as had been shown in previous studies (Rutte & Taborsky, 2008; Schneeberger et al., 2012; Dolivo & Taborsky, 2015; Wood, Kim, & Li, 2016). Remarkably, we did not find an effect of a previous positive experience (i.e., receiving food by a different mechanism) on the focal rats' propensity to provide help to an unknown conspecific in the 'feel good, do good' test, regardless of whether a social partner had been present or not during food delivery in the experience phase. This is in contrast to results of an experiment where a different partner rat had provided food to the focal subject during the experience phase of the experiment (Rutte & Taborsky, 2007), that is in a test of generalised reciprocity. Combined with this previous study, our results suggest that helping an unfamiliar individual is not merely the effect of any previous positive experience (e.g., receiving a treat), but instead reflects reciprocal altruism, that is, help that is contingent on previously experienced help by a social partner. Thus, positive experience, even in the presence of a partner, seems not to induce cooperative behaviour towards a conspecific, unless this positive experience has resulted from the helpful behaviour of the previous partner. This may facilitate the establishment of an evolutionarily stable level of cooperation in a population by reducing the risk that defectors would free-ride on a 'feel good, do good' effect without engaging in helping themselves (Rankin & Taborsky, 2009; Barta et al., 2011; Taborsky, 2013).

Previous experiments have shown that in general, Norway rats pull the tray more often if a conspecific is present compared to if they are alone in the test cage. This might imply that their pulling behaviour reflects some form of prosocial helping behaviour (Rutte & Taborsky, 2007, 2008; Schneeberger et al., 2012). In contrast, our results did not reveal an influence of a social partner's presence during the experience phase of this experiment, which did not involve any helping behaviour of the social partner. If the focal subject had interpreted the receipt of treats in the presence of the social partner as a cooperative act by the latter, they should have provided more help to an unfamiliar partner after receiving treats in the presence of a social partner during the experience phase, compared to when no other rat had been present. However, we did not find a difference in the help provided by the focal rat to an unfamiliar partner after she had made a positive experience either with or without a social partner present. Our results therefore suggest that rats are able to associate received gains with a specific behaviour provided by a social partner (i.e., pulling the tray towards the cage using the provided stick; Rutte & Taborsky, 2007, 2008). If the social partner does not show this behaviour, received

TABLE 2 Mean delay between pulls

Treatment	Mean difference(s)	*CI*	*p*
Positive experience < control, partner present	−0.20	−37.84, 28.90	.993
Positive experience > control, partner absent	29.2	−3.73, 74.07	.155
Partner present > absent, positive experience	12.32	−39.00, 57.83	.626
Partner present > absent, control	21.77	−1.75, 59.04	.188
Positive experience, partner present > control, partner absent	28.93	4.39, 54.72	**.033**
Positive experience, partner absent < control, partner present	−4.25	−50.77, 44.12	.574

Pairwise comparison between treatments using bootstrapping. Mean difference, 95% confidence intervals (BCa method) and *p*-values are given. '>' and '<' indicate the directions of trends and differences. A significant difference is marked in bold; it's direction is opposite to prediction.

TABLE 3 Latency to first pull

Treatment	Mean difference(s)	*CI*	*p*
Positive experience < control, partner present	−0.154	−48.69, 35.17	.995
Positive experience > control, partner absent	26.21	−13.11, 76.68	.283
Partner present < absent, positive experience	11.58	−30.38, 49.87	.592
Partner present > absent, control	15.96	−13.81, 65.08	.434
Positive experience, partner present < control, partner absent	14.52	−11.00, 43.69	.323
Positive experience, partner absent < control, partner present	−2.85	−54.41, 43.90	.904

Pairwise comparison between treatments using bootstrapping. Mean difference, 95% confidence intervals (BCa method) and *p*-values are given. '>' and '<' indicate the directions of trends and differences.

gains apparently do not change the propensity of rats to be helpful towards social partners. Thus, the decision of an individual to help a conspecific to obtain food seems to be based solely on the previously experienced helpfulness of a social partner, and not on unconditional prosociality.

The mean pulling frequencies of the focal subjects amounted to 0.29–0.43 pulls/min, depending on treatment. This is within the range of previous studies on Norway rats using the same set-up (Schneeberger, 2009; Schneeberger et al., 2012), even if it was higher in others (Rutte & Taborsky, 2007, 2008). Interestingly, there was a significant treatment effect in a previous study of reciprocity with the same set-up (albeit smaller sample size) and similar pulling frequencies (mean = 0.43 pulls/min, *N* = 14; Schneeberger, 2009; Schneeberger et al., 2012).

Our findings contrast with results from experiments with humans, where the propensity to help others has been shown to increase with a variety of previous positive experiences (Isen & Levin, 1972; Cunningham, 1979; Strohmetz et al., 2002; North et al., 2004; but see Feldt, Jagodzinski, & McKinley, 1997; Kirchsteiger et al., 2006). For example, persons listening to up-cheering music were more willing to distribute leaflets right thereafter than contestants listening to 'annoying' music, while the willingness to sign a petition did not differ between these experimental groups (North et al., 2004). Our study suggests that on the contrary, the helping propensity of Norway rats is enhanced only by help previously received from a social partner, at least if experience and test occur on different days. Notably, rats seem to not be influenced in their helping decision by the potential connection between positive experience and the presence of a partner, if the partner is not truly helping. Previous experiments showed that also the costs of pulling food for a partner affect the rats' helping propensity and, especially, their discrimination between previous cooperators and defectors (Schneeberger et al., 2012). Thus, the number and latency of pulls reflect measures of the rats' investment into an altruistic act that is returned to a social partner after receiving help from it (direct reciprocity; Rutte & Taborsky, 2008) or from a different individual (generalised reciprocity; Rutte & Taborsky, 2007). Our study suggests that rats merely transferred into 'good mood' by previous food donations will not become more helpful, which seems to be in contrast to humans.

Positive experience might influence the 'mood' of individuals, however, for a short period of time. In our experiment, the experience of test subjects was obtained one day before the test to make the experiment comparable to previous studies testing for generalised reciprocity (Rutte & Taborsky, 2007, 2008). Importantly, the comparison between our results with these previous studies revealed that only positive experiences connected to a helpful act received from a social partner influence the helping propensity of rats, and not the mere receipt of treats. As previous experiments had shown, the rats do memorise received help over the same time period as used in this study (Rutte & Taborsky, 2007). Future studies may use shorter time delays between experience and test phases to test for potential short-term effects of a 'good mood'.

Our study provides an important control for a potential non-social influence of positive experience on reciprocity in rats. The comparison of the results of this and previous studies prompts the conclusion that in Norway rats, only information about previously experienced help from a conspecific may trigger the decision to provide help to a social partner, and not any experienced gain.

ACKNOWLEDGEMENTS

We are grateful to Cornelia Spahni for her help during the experiment, the Swiss National Science Foundation for financial support, and two anonymous referees for helpful comments on the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Schmid R, Schneeberger K, Taborsky M. Feel good, do good? Disentangling reciprocity from unconditional prosociality. *Ethology*. 2017;00:1–8. https://doi.org/10.1111/eth.12636

APPENDIX

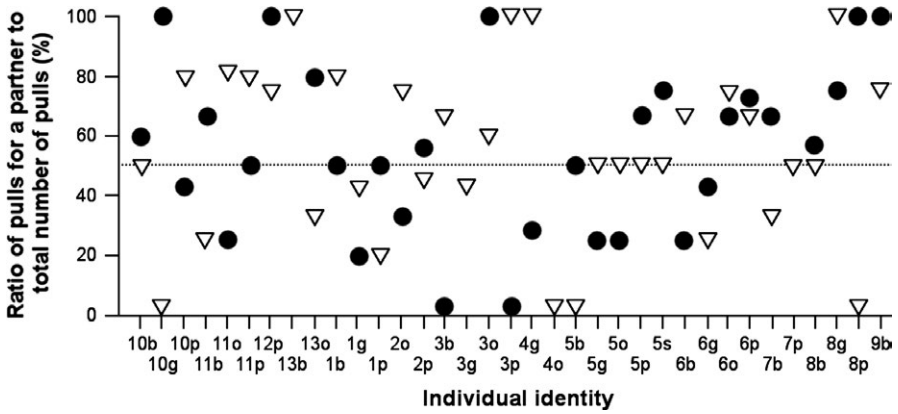

FIGURE A1 Ratio of pulls for a partner to the total number of pulls. Dots: after receiving food; triangles: after receiving no food