

Norway Rats (*Rattus norvegicus*) Communicate Need, Which Elicits Donation of Food

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Reciprocal cooperation has been observed in a wide range of taxa, but the proximate mechanisms underlying the exchange of help are yet unclear. Norway rats reciprocate help received from partners in an iterated Prisoner's Dilemma game. For donors, this involves accepting own costs to the benefit of a partner, without obtaining immediate benefits in return. We studied whether such altruistic acts are conditional on the communication of the recipient's need. Our results show that in a 2-player mutual food-provisioning task, prospective recipients show a behavioral cascade reflecting increasing intensity. First, prospective receivers reach out for the food themselves, then they emit ultrasonic calls toward their partner, before finally showing noisy attention-grabbing behaviors. Food-deprived individuals communicate need more intensively than satiated ones. In return, donors provide help corresponding to the intensity of the recipients' communication. This indicates that rats communicate their need, which changes the helping propensity of potential donors. Communication of need and corresponding adjustment of cooperation may be a widespread proximate mechanism explaining the mutual exchange of services between animals.

Keywords: reciprocity, cooperation, communication, altruism, iterated Prisoner's Dilemma

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One crucial difference between human cooperation and that among other animals is their differential ability to communicate mutual need (Bullinger, Melis, & Tomasello, 2014; Call, 2009; Melis & Semmann, 2010). Nevertheless, cooperation based on the communication of goals (de Waal, 2008) has recently been described in chimpanzees and orangutans (Dufour, Pelé, Neumann, Thierry, & Call, 2009; Pelé, Dufour, Thierry, & Call, 2009; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Yamamoto & Tanaka, 2009; Yamamoto, Humle, & Tanaka, 2012; but see Horner, Carter, Suchak, & de Waal, 2011). Chimpanzees, for instance, can direct the attention of others to a certain goal, and partners can respond appropriately to such signals (Yamamoto et al., 2012). In addition, animals ranging from invertebrates to primates respond to more intensive begging behaviors of their offspring by increased help (Bee & Miller, 2016). Need might be communicated passively as cues or actively as signals (Maynard Smith & Harper, 2003) to which partners can respond (reviewed in

Laidre & Johnstone, 2013). This fine-tuning of helpful behavior to a partner's specific situation implies that the observer obeys the help request, which seems puzzling if the social partners are unrelated.

Cooperation among conspecifics, such as one individual helping another, is common in animals (Bourke, 2011; Taborsky, Frommen, & Riehl, 2016). If interacting partners are unrelated to each other, potential evolutionary mechanisms underlying such behavior include coercion, mutual benefits, and reciprocity (Clutton-Brock, 2009; Lehmann & Keller, 2006; Taborsky et al., 2016). If service and commodities are reciprocally exchanged, it is largely unclear how individuals negotiate about mutual help (Bräuer, 2015; Noë, 2006). Negotiation about mutual help might be an important mechanism responsible for the evolution of cooperation, because it can generate greater fitness rewards and lead to higher levels of cooperation than kin selection (Quiñones, van Doorn, Pen, Weissing, & Taborsky, 2016). The efficiency of reciprocal cooperation will greatly increase if social partners respond to each other's desires (Schneeberger, Dietz, & Taborsky, 2012; Yamamoto et al., 2012). This would be facilitated if prospective recipients communicate their need to potential donors to request help.

In iterated cooperative interactions, donors should provide more help to recipients in greater need, as the value of received help may influence the future helping propensity of social partners (Brosnan & de Waal, 2004; Carter & Wilkinson, 2013; Dolivo & Taborsky, 2015b; Kilner & Johnstone, 1997; Noë & Hammerstein, 1995). Iterated cooperative interactions imply that players share interests about the outcome, because they are mutually dependent on each other (Axelrod & Hamilton, 1981; Taborsky et al., 2016; Trivers, 1971). This is different from parent-offspring interactions, where

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it is in the interest of the offspring to receive more care than the parents are selected to provide (Trivers, 1974); hence, the latter should only respond to honest signals (Bee & Miller, 2016; Hinde, Johnstone, & Kilner, 2010; Kilner & Johnstone, 1997; Royle, Hartley, & Parker, 2002). Because of the turn-taking in reciprocal relationships, it is in the interest of the signal producer to communicate need only if it is honestly in need, because later the roles will be exchanged. Hence, the signal intensity of potential recipients, where increased intensity could be the repetition of one signal or a switch to different signals (Genty, Neumann, & Zuberbühler, 2015), should honestly represent need (Kilner & Johnstone, 1997) and, at the same time, positively correlate with the conflict of interests between players. If there is a conflict of interests between the social partners, for instance, because the occurrence of future interactions is not fully predictable in an iterated Prisoner's Dilemma situation, the signal intensity should be enhanced to provide a stronger sign of need. In other words, if two players fully share interests, even weak signals of indigent recipients would suffice to trigger the help of donors. With increasing conflict of interests, signal intensity should rise to enhance the helping propensity of potential donors (Figure 1). In an iterated reciprocity game, in which the roles (donor/recipient) are regularly switched between social partners, there is little conflict of interest, as donors act in their own interest when helping their partner, because returns by the latter can be well predicted.

Presently, it is not known whether outside of primates, unrelated animals communicate need and whether they help each other upon such communication. Here, we investigate whether female Norway rats communicate their need to get food and whether their partners respond with increased helping levels in a variant of the

iterated Prisoner's Dilemma game involving reciprocal food exchange (Rutte & Taborsky, 2008). Rats form social groups of various sizes (McGuire, Pizzuto, Bemis, & Getz, 2006) and show a high propensity to cooperate (Schuster, 2002) and to share food (Barnett & Spencer, 1951). Their propensity to provide food to a social partner depends on their previous cooperative experience (Rutte & Taborsky, 2007, 2008). Experimental manipulations of the recipients' need in wild-type Norway rats showed that donors adjust their help to the recipients' need: When producing food for a social partner, rats consider their own costs and the benefits to the recipient by adjusting help levels to the hunger state of their recipient (Schneeberger et al., 2012). Furthermore, they return help in dependence of the quality of received help (Dolivo & Taborsky, 2015b): The better the quality of help they received, the more they pay back to their previous donors. It is yet unknown, however, whether this adjustment of help is due to a communication of need by recipients, and how a possible communication may reflect different levels of need.

We used an established experimental paradigm in which rats can provide food to a social partner by pulling a movable platform toward the latter (Rutte & Taborsky, 2007, 2008). Prospective recipients were either satiated or hungry to experimentally manipulate their level of need for help. Norway rats use various means of communication, including the production of ultrasonic signals (Brudzynski, 2009). They were shown to cooperate better if acoustic contact was enabled (Łopuch & Popik, 2011). Therefore, we investigated both visual and acoustic communication to identify potential signals of need. We predicted that if rats show interest in the reward and request help from a social partner, prospective recipients should communicate their need more intensely when hungry than when satiated. Furthermore, we predicted that if potential donors understand the recipient's goal, namely, to get access to the desired food, they should adjust helping levels to the latter's signaling intensity.

Method

Experimental Subjects and Holding Conditions

We used 50 outbred wild-type adult (2-year-old) female Norway rats (source: Animal Physiology Department, University of Groningen, the Netherlands) weighing on average 300 g. The rats were habituated to handling right after weaning. They were individually marked with standard hair tinting lotion with a hydrogen peroxide base, and they were housed with littermates in groups of three to five sisters. The cages (80 × 50 × 37.5 cm) were separated from each other through opaque dividers to exclude visual and physical interactions between the groups. The ambient temperature was 20°C ± 1°C, with a relative humidity of 50–60% and a 12:12 hr light/dark cycle with lights on at 20:00 hr, and 30 min of dawn and dusk. As Norway rats are primarily nocturnal (Norton, Culver, & Mullenix, 1975), all trainings and experiments were conducted during the dark phase of the daily cycle. We used red light for behavioral observations to minimize disturbance, as rats lack red light receptors (Yokoyama & Radlwimmer, 1998).

In accordance with animal welfare legislation of Switzerland (Tierschutzverordnung Schweiz 04/2008), we provided the rats (weight category 300–400 g) with cages (80 × 50 × 37.5 cm) enriched with various materials (a wooden house and board, a

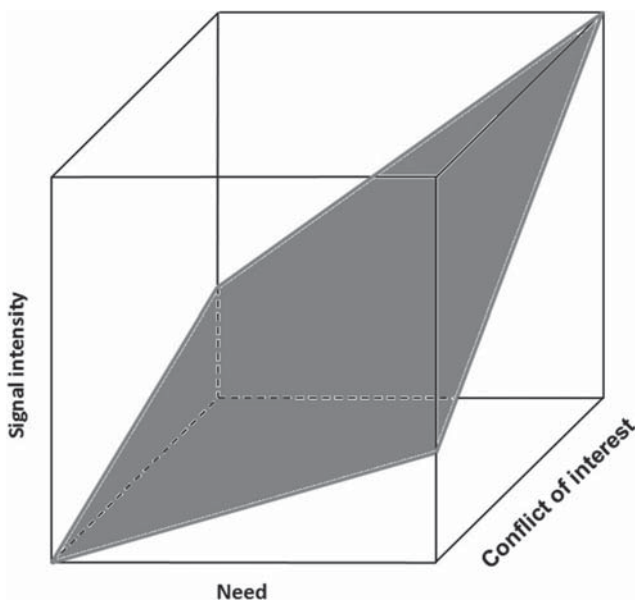


Figure 1. Hypothetical relationship between need, conflict of interests, and signal intensity in an iterated Prisoner's Dilemma paradigm. If there is a conflict of interests between social partners, the signal intensity, which correlates with the level of need, should be enhanced to receive help. However, if the conflict of interests is low, even weak signals of recipients in need should suffice to trigger the help of donors.

tube, a piece of wood to nibble, a loo roll to play, digging material [wood shavings], nest-building material [shredded and crumbled paper], and a salt block; Forbes, Blom, Kostmitsopoulos, Moore, & Perretta, 2007). Food (conventional rat pellets and corn mix) and water were provided ad libitum, if rats were not food deprived for the experiment as described later in the text. We established small groups with a maximum of five rats per cage (Sharp, Zammit, Azar, & Lawson, 2003). In our experiments, there was no possibility of physical contact between the test individuals due to a wire mesh separating the experimental compartments, and no injuries occurred. Animal housing and experimentation were approved by and conducted in accordance with the guidelines set by the Swiss Federal Veterinary Office under license BE98/11.

Preexperimental Training

The experimental setup (Rutte & Taborsky, 2007, 2008) was based on a two-player sequential food-exchange task (de Waal & Berger, 2000). Experimental cages ($80 \times 50 \times 37.5$ cm) were divided into two chambers by a wire mesh. We used the same rats as stated in Dolivo and Taborsky's (2015a) work, which also describes a detailed plan of the previously established training scheme. The training was divided into two parts: First, every single rat was trained to pull rewards for itself. To get a reward, it learned to pull a fixed stick on a movable platform into the experimental cage. Every time the rat pulled the platform into the cage, it received a food reward. Therefore, the number of rewards received depended on the rats' pulling frequency and was not fixed by the experimenter. We considered that rats had reached the learning criterion if they pulled food eight times or more for themselves, according to Dolivo and Taborsky (2015a). Once the rats had learned to pull the platform toward the cage, they never got a reward for pulling the platform any more. Instead, the rats were paired with a cage mate as training partner, and they learned over 18 sessions to provide several food items to their cage mate. By pulling alternatively for each other, the rats experienced that only

their social partner received a treat if they pulled the platform. The roles (donor and recipient) were exchanged, and the intervals between these switches were increased gradually from switching after every food item provided to switching after series of provided items, which lasted up to 7 min (i.e., the length of the subsequently used experimental period, because previous studies have successfully used the same interval). Rats were only trained once before three experiments were performed (Dolivo & Taborsky, 2015a, 2015b; Schweinfurth & Taborsky, 2016), and the rats were not retrained for this study.

Test Procedure

The experimental design and procedure used a modified version of the iterated Prisoner's Dilemma paradigm following Rutte and Taborsky (2008), in which rats pulled a tray with a treat toward a partner rat without receiving a reward for themselves. During the experience phase, focal individuals ($n = 25$) provided food (i.e., piece of a highly preferred banana; Dolivo & Taborsky, 2015b) to an unknown partner, which they had never met before. Rats that were unfamiliar to each other were used, to avoid confounding effects of previous social experience. Each focal rat could decide how many food items to provide sequentially to its partner during the 7-min experimental period; that is, this number was not determined by the experimenter. Thereafter, the roles were exchanged by changing the position of the stick on the platform, and the partner rats could produce food to the focal individuals during the test phase of the experiment to pay back experienced favors. Again, the number of food items sequentially provided during the 7-min experimental period was determined by the rat and not by the experimenter (Figure 2). Each focal rat was tested twice with its partner in a random sequence, once being satiated and once being hungry (food deprived for 10 hr, but water access ad libitum). Partner rats (i.e., recipients in the experience phase and potential donors in the test phase; $n = 25$) were always fed ad libitum before the experiment (i.e., no experimental variation of

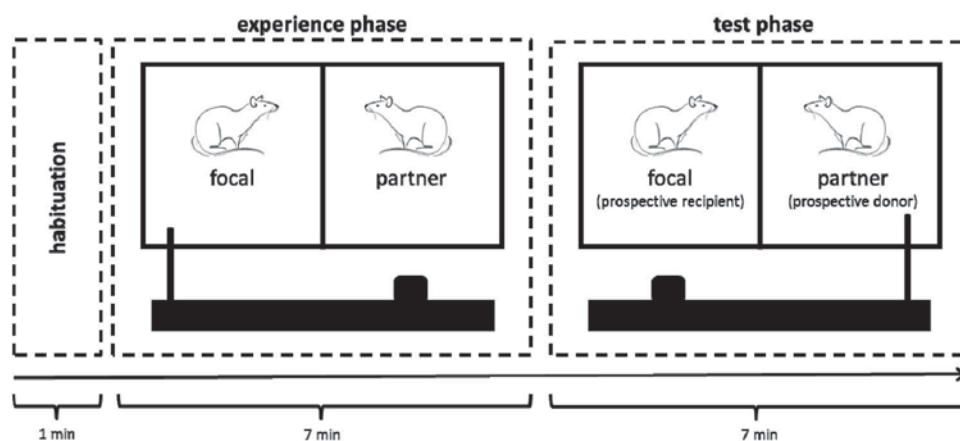


Figure 2. Experimental setup. After 1 min of habituation, focal rats ($N = 25$) could pull food toward the cage for a partner for a period of 7 min. The number of food items sequentially provided to the partner was determined by the rat and not by the experimenter. Immediately thereafter, the roles were exchanged; now partners (i.e., donor) could sequentially pull food items toward the cage for focal rats (i.e., recipient), again for a period of 7 min. Focal rats were tested in both conditions, hungry and satiated, and were always paired with the same partner. A timeline of the experiment is given on the x-axis.

their hunger state). Focal individuals and their partners had never met before this experiment, and they were unrelated. Before this experiment, experimental rats had participated in a maximum of three tests with different partners, in which they had performed both the donor and the recipient roles. To check whether rats consider the social context to pull for a partner, in a nonsocial control situation, rats could pull the platform when the neighboring compartment of the experimental cage was empty, for the same period of 7 min like in the experiment with the partner, and again when being either hungry or satiated.

Behavioral Data

In the test phase, all food-directed behaviors (i.e., reaching behaviors: stretching the paw(s) toward or sniffing in the direction of the treat) of focal rats and pulling behavior (total number of pulls, latency to first pull, and median interval between pulls) of partner rats were recorded. In addition, the short 50-kHz ultrasonic calls of focal rats (prospective recipients) were detected with the help of a bat detector with a resolution of 1 kHz (CDB 103 R3-bat detector, Ciel Electronique, Saint-André-de-la-Roche, France) attached to head phones. Ultrasonic calls can be detected sometimes by a contraction of the flanks of the calling rat. It is not possible to observe this every time under the red-light conditions used in these experiments, but all flank contractions we detected were shown by the prospective receivers; that is, we did not observe such flank contractions in the donating rats. This implies that the recorded calls were uttered by the prospective receivers and not by the donors of food. The total number of 50-kHz calls, which are characterized by a narrow bandwidth (Brudzynski, 2005), and the latency to the first 50-kHz call were noted. These short calls are known to have an affiliative function in the communication of Norway rats (Brudzynski, 2009; Burgdorf & Panksepp, 2006).

Further, the duration and the latency of attention-grabbing behaviors of focal recipients were recorded. Attention grabbing included a combination of jumping onto the mesh, nibbling of the dividing wire mesh, clattering the mesh with the teeth, and running up and down in front of the mesh. These behaviors were shown exclusively by focal rats during the test phase (in their role as prospective recipients) when partner rats did not pull food for them. In addition, these behaviors were exclusively directed toward the potential donor; that is, they were not performed in another direction of the cage, and they were only performed in the described context.

The experimental period was 420 s for all rats; however, depending on how many times the rats pulled, the time for which the stick was present varied slightly due to the time required to reload the platform. During reloading the platform with a new piece of banana, the stick was removed, which led to some variation in experimental durations. The experimenter, who was present at all times to reload food and collect the data, therefore noted down when the stick was not available to the rats. All data (except of latencies) were therefore corrected for experimental durations, which corresponded to 420 s subtracted by the time the stick was out of reach for the rat.

Statistical Analyses

All statistical analyses were performed using R (Version 2.15.2; <http://www.r-project.org>; packages “lme4,” “car,” “survival,” and “nortest”). The use of parametric or nonparametric statistics depended on the distribution of residuals or on the distribution of raw data, which we tested with the Shapiro–Wilk test. The α level was set to 0.05 in all tests.

Do hungry and satiated rats differ in their donation rates?

We tested whether focal rats provide food more often and earlier to their partners during the experience phase when they were themselves hungry. We used Wilcoxon’s matched-pairs signed-ranks tests or paired *t* tests, depending on data distributions. We used the same tests to check whether the results can be explained by a mere increase in motivation by comparing their food provisioning behavior between pulling for an empty cage and for a social partner.

Does communicating need follow a standard sequence?

To identify the sequence of all three forms of communication (reaching, 50-kHz calls, and attention grabbing) of focal rats during the test phase, we conducted a sequence analysis following Bakeman and Gottman (1997). We first tested whether the sequence of the three forms of communication differs between satiated and hungry rats using a χ^2 test of independence, which was not the case ($\chi^2 = 5.23$, $df = 4$, $p = .26$). We thus pooled the data for satiated and hungry rats. We had to exclude nine out of 50 data points because these rats only showed one of the three forms of communication. We then tested whether the possible six sequence combinations (e.g., 1,2,3; 1,3,2; 2,3,1; 2,1,3; 3,1,2; 3,1,2) of the three forms of communication differ from a random expectation using a Pearson χ^2 test. In addition, we tested whether reaching was significantly more often the first of the three behaviors shown, and whether reaching was significantly more often followed by 50-kHz calls than by attention grabbing, by using Pearson χ^2 test.

Do hungry rats communicate need more intensively?

We tested whether focal rats showed all three forms of communication earlier and more often if they were hungry. For nonnormally distributed data, Wilcoxon’s matched-pairs signed-ranks tests were used to compare experimental rats in satiated and hungry states. For normally distributed data, we used paired *t* tests. For rats that have not shown a certain behavior during the experimental period, the maximum time was considered (420 s).

To check whether the probability of focal rats (prospective recipients) to emit 50-kHz calls depends on the response of partner rats to the focal rats’ reaching behaviors, we used a “time to event analysis” for the time interval between a focal rat’s reaching behavior and a partner’s subsequent pull. This was censored by whether a 50-kHz call was uttered by focal rats or not. First, we investigated whether hungry rats call earlier after reaching behavior was shown than when they were satiated, by using the R-command “coxph.” Then we assessed whether the probability to call increased with the course of time passed from showing reaching behavior. We used a nonlinear regression model for this with the R-command “survreg,” which controls for the mere time course.

Do donors and recipients respond to each other’s behavior?

We tested whether partner rats provided food earlier to focal rats that communicated their need (i.e., reaching behaviors, 50-kHz ultrasonic calls, and attention-grabbing behav-

iors) by using a generalized linear mixed model: We included as dependent variable the latencies to the partner's first pull, and as explanatory variables the focal rats' latencies to show reaching behaviors, 50-kHz calls, and attention-grabbing behaviors, as well as the focal rats' hunger state. After logarithmic transformation ($\log(\text{variable} + 1)$) of latencies, residuals did not differ from normal distributions. As random factors, we included the identity of focal rats to account for testing each individual once hungry and once satiated. Some rats (seven focal and three partner rats of the test phase) nibbled at least once on the stick that served to pull rewards for the conspecific. As nibbling is known to influence pulling behavior (Schweinfurth & Taborsky, 2016), we included nibbling on the stick by both focal and partner rats as further random effects. In addition, we tested whether partners decrease the time between their pulls in dependence of the frequency of each of the three forms of communicating need using Spearman rank correlation analyses.

Results

Do Hungry and Satiated Rats Differ in Their Donation Rates?

In the experience phase, hungry rats (prospective donors during the experience phase) pulled more often for their social partner (prospective recipients during the experience phase) than satiated ones (Wilcoxon signed-ranks test: $V = 165$, $N = 25$, $p = .024$) and started earlier to do so (Wilcoxon signed-ranks test: $V = 56.5$, $N = 25$, $p = .008$; Figure 3). Regardless of whether focal rats were hungry or satiated, their pulling rates were always lower for an empty cage than when accompanied with social partners (Wilcoxon signed-ranks test for hungry rats: $V = 0$, $N = 25$, $p < .001$; for satiated rats: $V = 0$, $N = 25$, $p < .001$), and the latency to start pulling was much shorter for a partner than for an empty cage (Wilcoxon signed-ranks test for hungry rats: $V = 12$, $N = 25$, $p = .002$; for satiated rats: $V = 16$, $N = 25$, $p = .005$; Figure 4).

Does Communicating Need Follow a Standard Sequence?

We identified three distinct behaviors indicating different levels of need for help (Figure 5). First, focal rats (prospective recipients during the test phase) showed food-directed reaching behaviors such as stretching the paws toward the reward or sniffing through the mesh in the direction of the reward. Second, rats vocalized in the 50-kHz frequency range. Finally, 13 of the 25 rats showed behaviors that appeared to serve "attention grabbing," which refers to a combination of noisy behaviors directed toward the potential donor. Both satiated and hungry rats showed the same specific sequence of these three communication forms, which was significantly different from a randomly expected sequence of these behaviors (Pearson χ^2 test: $\chi^2 = 82.85$, $df = 5$, $p < .0001$). Reaching was more often the first behavior of the cascade than any other behavior (Pearson χ^2 test: $\chi^2 = 49.95$, $df = 1$, $p < .0001$), and it was followed by calling more often than by the last behavior in the sequence, which is attention grabbing (Pearson χ^2 test: $\chi^2 = 12.60$, $df = 1$, $p = .0004$).

Do Hungry Rats Communicate Need More Intensively?

Hungry focal rats showed more reaching behaviors, paired t test: $t(24) = 3.795$, $p = .001$, and there was a nonsignificant trend to start showing this behavior earlier (Wilcoxon signed-ranks test: $V = 230$, $N = 25$, $p = .071$) than satiated rats. When they were hungry, the rats called more often than when satiated (Wilcoxon signed-ranks test: $V = 210$, $N = 25$, $p = .030$), and there was a nonsignificant trend to emit calls earlier (Wilcoxon signed-ranks test: $V = 91$, $N = 25$, $p = .095$). Hungry rats did not show more attention-grabbing behaviors than satiated ones (Wilcoxon signed-ranks test: $V = 135$, $N = 25$, $p = .27$). There was a nonsignificant trend that hungry rats started earlier to show attention grabbing to their potential donors (Wilcoxon signed-ranks test: $V = 60$, $N =$

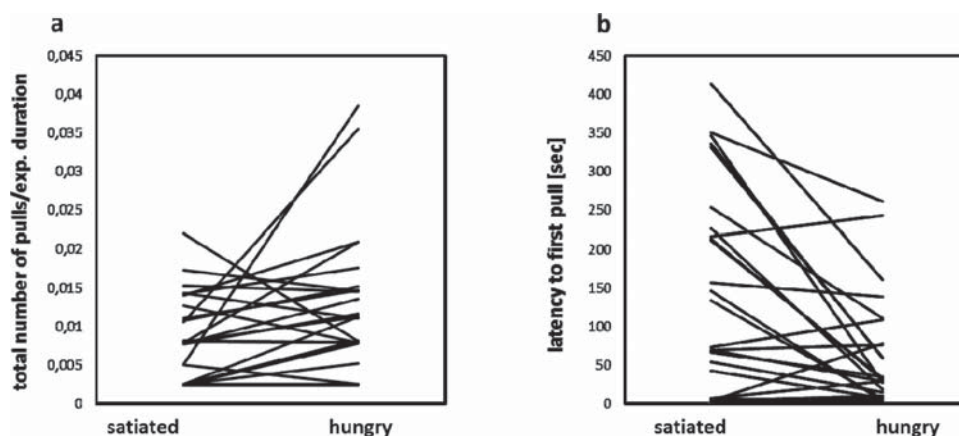


Figure 3. Total number of pulls and latencies to the first pull of hungry and satiated rats. In the experience phase of the experiment (Figure 1), focal individuals (a) pulled significantly more often for their partner when they were hungry than when they were satiated, and (b) started earlier to pull for them. The y-axis shows total numbers of pulls (standardized for the exact duration of the experiment in seconds) and latency to the first pull. The x-axis shows whether focal rats were hungry or satiated. Each line indicates the behavior of one individual once being hungry and once being satiated.

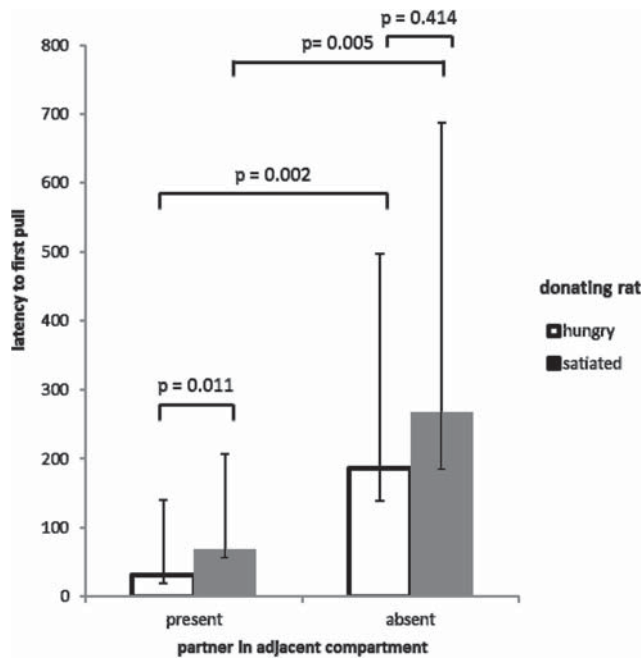


Figure 4. Comparisons between experiment (pulling for a partner) and control (pulling for an empty cage). Hungry (open bars) and satiated (gray bars) rats pulled later for an empty cage (i.e., control) than when a social partner was present. The latency to pull for a social partner was shorter in hungry rats than in satiated ones, but hunger level did not influence pulling delays in the control treatment. Medians and interquartile ranges are shown.

25, $p = .097$). Rats that were hungry started calling more readily after they had shown reaching compared with satiated rats (Cox proportional hazard rate model: $\beta = -1.2011 \pm 0.4053$, $p = .003$).

Do Donors and Recipients Respond to Each Other's Behavior?

The longer a partner (potential donor) waited with pulling food after the focal rat had shown reaching behaviors, the higher was the probability that the focal rat would utter 50-kHz calls (parametric time to event regression model for hungry rats: $\beta = -0.85 \pm 0.21$, $N = 25$, $p < .0001$; and for satiated rats: $\beta = -0.81 \pm 0.30$, $N = 25$, $p = .007$; Table 1 and Figure 6). The latency until focal rats started to emit 50-kHz vocalizations toward their partner predicted the start of the latter's helpful pulling in dependence of the focal rat's hunger state (generalized linear mixed model: $\beta = -4.004 \pm 1.647$, $N = 25$, $p = .012$; Table 2): If hungry rats started to call early, their donor pulled for them after a shorter time interval than if satiated rats called early. In addition, the more hungry and satiated focal rats showed reaching behaviors, the shorter was the time interval between pulls of partner rats (satiated focal rats: Spearman rank correlation: $r_s = -0.551$, $p = .028$; hungry focal rats: Spearman rank correlation $r_s = -0.447$, $p = .004$). A higher number of 50-kHz calls by hungry focal rats also reduced the delay between the partners' pulls, which was not the case when focal rats were satiated (hungry

focal rats: Spearman rank correlation: $r_s = -0.629$, $p = .009$; satiated focal rats: Spearman rank correlation: $r_s = -0.178$, $p = .42$; Table 3).

Discussion

Our results indicate that female Norway rats exposed to a variant of the iterated Prisoner's Dilemma game show signs of need by a regular sequence of behaviors. This cascade follows a specific chronology, which reflects increasing intensity. First, rats reach toward the food, then they emit 50-kHz ultrasonic calls, and finally, they show noisy, attention-grabbing behaviors directed toward the potential donor. Hungry rats show reaching and 50-kHz calls more often than satiated ones, indicating that these behaviors may depend on their level of need. Only few animals showed attention-grabbing behaviors; thus, the sample size is small. This last behavior was not shown more often, but there was a trend that it was performed earlier. In addition to this regularity in behavioral sequence, our data revealed that prospective recipients that had to wait long for a food reward donated by their partner after they showed interest by reaching out for it changed to the next intensity level (50-kHz call) with greater likelihood. Importantly, partners reacted to enhanced communication of need by providing help quicker.

If a demand is communicated between partners, potential recipients may reveal their need in two principal ways, by expressing interest in a reward and by direct requests for help to a potential donor (Cronin, 2012). Interest in the reward can be transmitted, for instance, by pointing toward the desideratum, which conforms to active signaling, or by reaching out for it, which may serve either as a cue of need or as a signal of demand (Maynard Smith & Harper, 2003). Reaching, the first activity in the described chronological sequence, might be a cue to the donor indicating the partner's interest in the reward. It is yet unclear, however, whether it corresponds to an evolved, partner-directed response to the situation, that is, whether it reflects a "signal" according to Maynard Smith and Harper's (2003) definition. The other two behaviors, 50-kHz calls and attention grabbing, may be more clearly interpreted as signals, because they are not directed toward the food but oriented toward the partner, possibly serving as requests for help. The ultrasonic 50-kHz calls are associated with affiliation and positive affective states during social interactions (Burgdorf, Panksepp, Brudzynski, Kroes, & Moskal, 2005). The attention-grabbing behaviors were directly pointed toward the partner.

To better understand this behavioral cascade, future studies should investigate whether the three forms of communication are only shown when partners are present or also when the neighboring compartment is empty, to clarify the motives for these behaviors and whether they reflect signals or cues. Further, it might be worth comparing the cascade when shown in the presence of a potential donor known to be cooperative or defective, to investigate the flexibility of the cascade. Moreover, the importance and motives of each of the three behaviors might be disentangled by carefully manipulating each of them and measuring the response of potential donors. Future studies could also clarify how rats acquire these forms of communication, which may be learned. If rats behave according to their need and this elicits an appropriate response by their partners, this could in turn reinforce the original behavior.

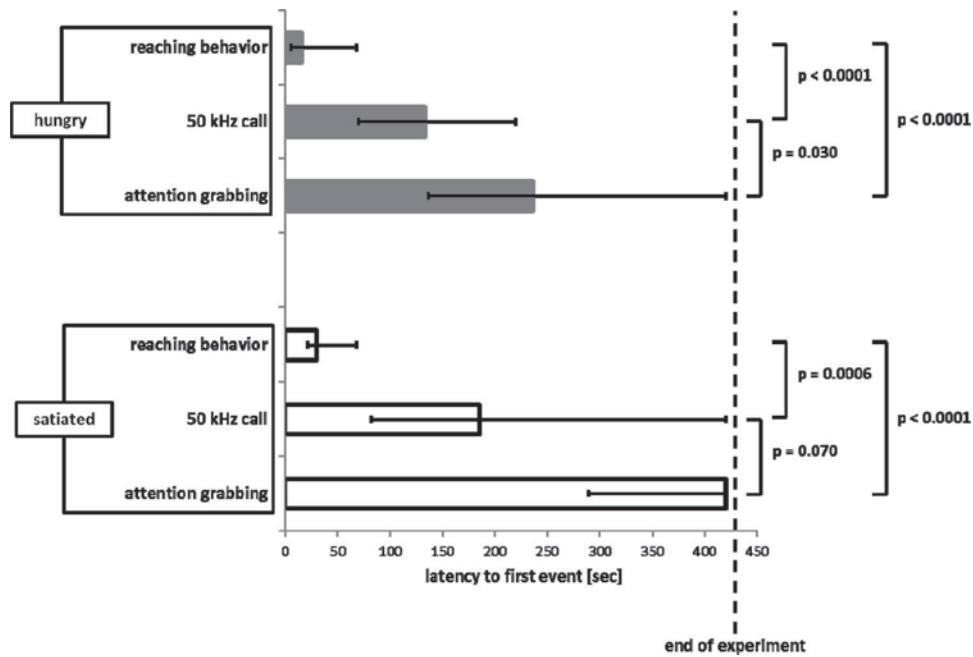


Figure 5. Sequence of behaviors shown by hungry (above) and satiated (below) prospective receivers to communicate need. Both hungry and satiated focal rats showed a systematic chronology of the three forms of communication (y-axis). The x-axis depicts median time points of the first occurrence of the respective behaviors, with interquartile ranges.

The three forms of communication shown by the focal rats do not indicate harassment. The ultrasonic 50-kHz sound is typically emitted in prosocial contexts (Brudzynski, 2005), and the reaching behaviors can hardly transmit a threat toward potential donors. The third stage of the sequence, which corresponds to a collection of behaviors referred to as “attention-grabbing behaviors,” might reflect an attempt to physically interact with the partner, which could indicate coercion. However, we did not observe any physical aggression, such as biting attempts toward partners. This conforms with the observation that rats decrease their helping propensity when attacked by previously cooperative partners (Dolivo & Taborsky, 2015a).

The regular sequence of these three forms of communication seems to reflect a referential signaling cascade, which in accor-

dance with referential gestures can be defined by five attributes: goal directedness, mechanical ineffectiveness, directedness toward a potential recipient, release of a voluntary response, and demonstration of hallmarks of intentionality (Pika & Bugnyar, 2011; Vail, Manica, & Bshary, 2014). Whereas “reaching” was directed

Table 1

Relationship Between the Probability to Switch to the Next Step of the Behavioral Cascade, Namely, Ultrasonic Calling, Dependent on the Time Between Reaching Behavior and the Partner’s Food Provisioning

Factors	Estimate ± SE	z value	p value
State (hungry vs. satiated)	-1.20 ± .40	-2.96	.003
Probability per time unit (hungry rats)	-.85 ± .21	-3.98	<.0001
Probability per time unit (satiated rats)	-.81 ± .30	-2.71	.0006

Note. Focal rats started calling earlier when being hungry, and the probability to call increased with an increasing time interval between reaching behavior and the partner’s pulling behavior. “Time to event analysis” with focal rats that were either hungry or satiated is indicated (i.e., treatment; N = 25).

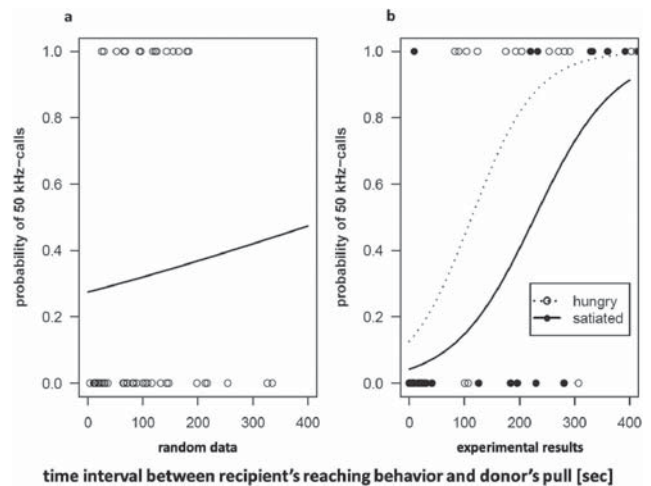


Figure 6. Influence of the donor’s pulling delay after the recipient’s reaching behavior on the recipient’s probability to emit 50-kHz calls. The longer the time interval was between a prospective recipient’s reaching behavior and the donor’s pulling response (x-axis), the higher was the recipient’s probability to emit a 50-kHz call (y-axis), with hungry recipients (dashed line) calling earlier than satiated ones (solid line).

Table 2
Relationship Between the Donors' Latency to Start Pulling Food and the Prospective Recipients' Timing of Communicating Its Need

Focal rat (prospective recipient)	Estimate \pm SE	<i>t</i> value	<i>p</i> value
Intercept	2.946 \pm .914	3.222	
Latency to show reaching behavior	-.262 \pm 2.708	-.097	.913
Latency to emit 50-kHz call	.948 \pm 1.145	.829	.370
Latency to perform attention grabbing	-.547 \pm 1.198	-.457	.622
State (hungry vs. satiated)	1.497 \pm .769	1.947	.040
Latency to Emit 50-kHz Call \times Treatment	-4.004 \pm 1.647	-2.431	.012

Note. Donating partner rats pulled earlier for hungry focal rats (recipients) that called early compared with satiated recipients calling early. This effect was reversed in individuals that were calling late. Overall, donors pulled earlier for hungry than for satiated individuals. General linear mixed model with recipients that were hungry or satiated (i.e., treatment; $N = 25$) is indicated; *p* values $< .05$ are highlighted in bold.

toward the food item, the other two behaviors were clearly directed toward the potential donor. In addition, the last two behaviors are also inherently mechanically ineffective, as they are not directed to the food. To all three signs of need, partners can respond voluntarily with an increase in help. Hallmarks of intentionality have been defined as persistence until the goal is reached, elaboration of the communication if it does not initially achieve its goal, and means–ends disassociation by using two signals for the same goal (Vail et al., 2014). All this applies to the described signaling cascade. If rats did not reach their goal (receiving food) and had to wait longer for a response from their partner, they showed the next solicitation form of the cascade with increasing probability, thereby showing persistence, elaboration, and disassociation by using three different forms of communication.

An important component of this reciprocal exchange of services is the fact that rats respond mutually to each other's behavior: Partner rats help prospective recipients based on their signs of need, and the latter in turn adjust their communication to the partners' help. The more time elapsed between the focal rat's reaching behavior and the partner's pulling response, the higher was the focal rat's probability to emit 50-kHz calls. In addition, partners pulled earlier for hungry rats than for satiated ones, depending on the point of time when these prospective recipients started calling. This interaction effect indicates a rather low conflict of interest in this negotiation process about costly help, because donors apparently respond to the focal rats' latency to call in dependence of the latter's need. Rats can smell whether partners are hungry or satiated and donate food more readily to partners that

are hungry than to satiated ones (Schneeberger & Taborsky, 2012). Our results corroborate previous observations showing that rats help others in correspondence to the latter's need (Schneeberger et al., 2012). Apparently, rats take a set of communicative components (here olfactory, acoustic, and visual) as a basis for their decision to help their partner. Thus, the observed cascade can be described as multimodal communication (reviewed by Partan & Marler, 2005). By using different modalities, detection may be enhanced or one sensory modality might be used to gain attention, whereas other channels convey the message.

Importantly, partners react to enhanced communication of need by providing help quicker. This result cannot be explained by state-matching, because rats responded to the hunger state of their partner independently of their own state (Burkett et al., 2016). Besides in humans, evidence for the fine-tuning of help according to the level of need of social partners is hitherto rare (Duguid, Wyman, Bullinger, Herfurth-Majstorovic, & Tomasello, 2014). Outside the context of reciprocal cooperation, however, nonhuman animals are known to respond to the communication of need, in particular, in the context of brood care (Bell, 2008; Kilner & Johnstone, 1997). Furthermore, such referential signaling has been shown in animals performing cooperative tasks with human experimenters (Hirata & Fuwa, 2007; Povinelli, Nelson, & Boysen, 1992), or between conspecifics to reach selfish goals in chimpanzees (Pika & Mitani, 2006) and ravens (Pika & Bugnyar, 2011). In an interspecific context, predatory fishes have been shown to coordinate their hunting strategies with referential signals (Vail et al., 2014). These studies suggested that animals frequently communicate and respond to the need of others and that referential signals are not restricted to large brained animals; why humans are particularly good in fine-tuning help according to another's need remains unexplained (Tomasello, 2010). Our results are the first to show that the use of a sequence of solicitation behaviors can be a successful mechanism generating reciprocal cooperation.

Empathy is one possible explanation for why donors increase their help in response to the hunger state of their partner. However, it may not be necessary to imply this concept for explaining our results. Empathy is the ability to recognize and care about the emotional state of others (Hecht, Patterson, & Barbey, 2012). Empathy had been suggested to be important when rats liberate a social partner from a trap (Bartal, Decety, & Mason, 2011; Sato, Tan, Tate, & Okada, 2015), but the described behavior can also be explained differently (Vasconcelos, Hollis, Nowbahari, & Kacel-

Table 3
Relationship Between a Recipient's Solicitations and the Donor's Intervals Between Its Pulls

Focal rat (prospective recipient)	Influence on partner rat's interval between the pulls	
	Correlation	<i>p</i> value
Reaching behavior	$r_S = -.551$ (Spearman)	.028
Reaching behavior ^a	$r_S = -.447$ (Spearman)	.004
50-kHz call	$r_S = -.178$ (Spearman)	.42
50-kHz call ^a	$r_S = -.629$ (Spearman)	.009
Attention grabbing	$r = -.181$ (Pearson)	.57
Attention grabbing ^a	$r_S = -.330$ (Spearman)	.20

^a Hungry focal rats.

nik, 2012; Silberberg et al., 2014). In our experiment, donating rats used the recipient's behaviors to adjust their cooperation levels, but this does not inevitably require recognition of their emotional state. Rather, rats seem to influence their partners' behavior by communicating their need according to their hunger state, which may also explain that rats have been found to help trapped conspecifics (Bartal et al., 2014). Rats are known to react to ultrasonic calls by conspecifics also in other contexts, such as in fearful situations (Atsak et al., 2011).

Furthermore, individuals with enhanced need (hunger) increase their helping rates when they are in the donor's position. This seems appropriate given the experimental paradigm involving a regular exchange of roles, as partners in turn adjust their help to the quality of help they previously received (Dolivo & Taborsky, 2015b). This increased pulling propensity of hungry rats cannot be explained by a misled expectation to obtain food for themselves, because rats pulling with the same hunger state showed reduced pulling rates when pulling the platform toward an empty cage. Hence, their increased pulling rate for a partner when being hungry reflects neither a self-directed immediate feeding demand nor an undirected change in motivation (Dolivo, Rutte, & Taborsky, 2016). All rats participating in the experiment had experienced this variant of the iterated Prisoner's Dilemma paradigm before. Therefore, they had learned that the roles are always switched between rounds. Previous studies showed that rats base their decision to help on previously received help from a partner (Rutte & Taborsky, 2007, 2008; Schneeberger et al., 2012; Wood, Kim, & Li, 2016). This study is the first to show that rats not only react to the amount of perceived help from a particular partner (i.e., direct reciprocity) but also adjust their social provisioning rate to their own need. This might indicate that rats can understand the different roles of subjects in this experimental paradigm, similar to apes (Dufour et al., 2009; Melis, Hare, & Tomasello, 2006; Pelé et al., 2009).

In conclusion, rats in need show a chronology of three different forms of communication reflecting an increase in intensity. This communication of need elicits helpful food donations by social partners. Communicating need is apparently beneficial, as it provides cues to partners whom and when to help. Potential conflicts of interest are low in iterated reciprocal settings, because help is likely to be returned if previous donors are in need themselves.

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