Failure to find altruistic food sharing in rats

Haoran Wan, Cyrus Kirkman, & Timothy D. Hackenberg

Reed College

**Abstract**

Prior research has found that one rat will release a second rat from restraint in the presence of food, thereby allowing that second rat access to food. Such behavior, clearly beneficial to the second rat and costly to the first, has been interpreted as altruistic. Because clear demonstrations of altruism in rats are rare, such findings deserve a careful look. The present study aimed to replicate this finding, but with more detailed methods to examine more systematically if, and under what conditions, a rat might share food with its cagemate partner. Rats were given repeated choices between high-valued food (sucrose pellets) and 30-s social access to a familiar rat, with the (a) food size (number of food pellets per response), and (b) food motivation (extra-session access to food) varied systematically across conditions. Rats responded consistently for both food and social interaction, but at different levels and with different sensitivity to the food-access manipulations. Food production and consumption was high when food motivation was also high (food restriction) but substantially lower when food motivation was low (unlimited food access). Social release occurred at moderate levels, unaffected by the food-based manipulations. When food was abundant and food motivation low, the rats chose food and social options about equally often, but sharing occurred at extremely low levels across sessions and conditions (mean < 1%, across subjects and conditions). The results are therefore inconsistent with claims in the literature that rats are altruistically motivated to share food with other rats.

Pro-social behavior can be defined as behavior that produces benefits for another, sometimes even at a cost to the individual (Fehr et al. 2002; West et al., 2007). One type of pro-social behavior gaining currency in recent years is *social release*, in which one animal releases another from a trap or restraint. In an experiment by Ben-Ami Bartal, Decety, and Mason (2011), for example, one rat was restrained in a plastic tube restraint, one end of which could be opened by a second rat. This permitted the restrained animal to leave the tube for the remainder of the 60-min session in the presence of the other rat. Most of the rats learned eventually to open the restraint, and generally did so only when the restraint contained another rat and opening permitted social release. Subsequent studies have verified that rats will, under a variety of conditions, respond in ways that similarly release a rat from a restraint (Ben-Ami-Bartal et al., 2014; Blystead et al., 2019; Hachiga et al., 2018; Hiura, Tan, & Hackenberg, 2018; Sato et al., 2015; Schwartz et al., 2017; Silberberg et al., 2014). The basic effect is thus reliable, replicated across different procedures and laboratories, but its core mechanisms remain a matter of debate.

According to some authors (e.g., Ben-Ami Bartal et al., 2011, 2014; Sato et al., 2015), social release arises from altruistic motives: the free rat senses distress on the part of the trapped rat, and acts altruistically out of empathic concern for its social partner. An alternative explanation is based on social contact: social release is motivated by opportunities for social interaction (Hachiga et al., 2018; Hiura et al., 2014; Schwartz et al., 2017; Vanderhooft et al., in press). In other words, social release is a type *operant* (or *instrumental*) behavior, established and maintained by contingent social contact as a form of reinforcement. The competing theoretical accounts have been difficult to disentangle experimentally, owing to the fact that under many conditions in the standard procedure, releasing the other rat from a restraint can be viewed in terms consistent with either a social contact view (opportunities for social interaction) or an altruistic view (releasing a distressed rat, at a cost to the individual). Therefore, unless special conditions are arranged to disentangle the two interpretations (cf. Hachiga et al., 2018; Sato et al., 2015; Schwartz et al. 2017), the mere fact of social release may not necessarily support either view.

Although most of the work to date on social-release procedures has focused on the main procedure, a later set of conditions in the Ben-Ami Bartal et al. (2011) study is especially relevant to the question of underlying mechanisms, yet has received far less empirical attention. In these conditions, rats were given a choice between two restrainers, one of which contained high-value food rewards (5 chocolate chips), the other of which was contained a restrained rat. These conditions permitted social release, as in the standard procedure, but here, was pitted against a known and powerful food reward as a means of assessing the relative value of social release. On average, the rats learned to approach and open the tube containing food more quickly (earlier in testing) than the tube containing another rat, though the latencies to access both tubes became low and roughly comparable (< 10 s) by the end of the 12-session experiment. And on slightly more than half of the trials, the trapped rat was released before the food was completely consumed, enabling the trapped rat access to the food rewards. This resulted in lower levels of food intake (70% of maximum, on average) than in a control condition in which the alternative restraint was empty (in which the free rats ate 96% of the food).

These two patterns of findings led the authors to the following conclusions: (a) the reward value of releasing a restrained rat is comparable to that of high-valued food (similar latencies to food and social release doors), and (b) social release in some cases comes at the expense of food intake (lower levels of food intake in a social context). In other words, rats not only value social contact equally with food, but engage in altruistic food sharing, taking less for themselves in favor of their distressed social partner. On its face, these findings appear to lend strong support to accounts appealing to some type of altruism, and simultaneously pose serious theoretical challenges to strict cost-benefit models. If not for altruistic motives, why would a rat sacrifice its own food for the good of another? While there is ample evidence of food sharing in rats, it is usually of the reciprocal exchange (tit-for-tat) variety, in which animals alternate roles as donors and receivers (Taborsky et al. 2016). Far less common is the type of unreciprocated food sharing reported by Ben-Ami Bartal et al. (2011), in which a rat sacrifices its own highly-valued food for another with nothing obvious in return. Given both the novelty and theoretical significance of the findings, these food-sharing conditions warrant closer examination.

The main objective of the present study was to replicate and extend the food-sharing conditions from Ben-Ami Bartal et al. (2011), using more robust methods for (a) assessing reward value and preference, and (b) for defining food sharing. The methods were patterned after Hiura et al. (2018), in which rats were given repeated choices between high-valued food rewards (sucrose pellets) and social release (10-s social contact). Unlike the findings reported by Ben-Ami Bartal et al. (2011), however, Hiura et al. found that rats showed a consistently strong preference for food over social release, even in the face of large increases in food cost (number of responses to produce food), while the costs of social release remained low. Costs were manipulated via a progressive ratio (PR) schedule, in which the number of responses per reward was low at the beginning of the session, but increased with each reward earned. Social release typically only occurred in the latter parts of the session, when food costs were high and after many food rewards had been earned and consumed. The overall session-wide preference for food generally exceeded 90%.

This strong preference for the food over the social release option is at odds with the equal value of social release and food reported by Ben-Ami Bartal et al. (2011). There are several procedural differences between the experiments, however, that may account for the different findings. First, and perhaps importantly, there were differences in motivation. In the Ben-Ami Bartal et al. experiment, there were no restrictions placed on social or food access outside the session: rats had free access to food and social contact in their homecages. In the Hiura et al. experiment, on the other hand, food or social access (or both) were restricted outside the session. Responding for both rewards was higher when access was restricted outside of the session than when it was freely available, showing sensitivity to motivational variables. When food was freely available outside the session, the rats still preferred food over social contact, but substantially less so than when it was restricted, more closely resembling the patterns reported by Ben-Ami Bartal et al. (2011). In the present experiment, we included conditions that both restricted and did not restrict access to food and social contact outside the sessions to assess the impact of motivational variables on the relative value of food and social rewards. If the higher levels of food versus social responding reported by Hiura are due primarily to motivational variables (restricted post-session access to rewards), then providing free access to those rewards would be expected to reduce the reward value of food, reducing or eliminating food preferences, more akin to findings of Ben-Ami Bartal et al. (2011).

We also included conditions that permit a more direct measure of food sharing, the second important claim put forth by Ben-Ami Bartal et al. (2011). In the Hiura et al. (2018) procedure, food and social release were concurrently available only at the start of a choice trial; the first response on either option disabled the other. As a result, either food or social release occurred on a given trial, but they did not occur together. Unlike the Ben-Ami Bartal (2011) procedure, then, food sharing was not possible. The present procedures were therefore modified in such a way that food rewards did not preclude social access. Of particular interest was a particular behavior sequence involving (a) food production, followed by (b) social release, given that (c) food was still remaining, permitting (d) the formerly restrained rat access to food. This sequence constituted our operational definition of *sharing*.

Finally, we arranged opportunities for food and social access to occur repeatedly each session rather than just once per session, as in the Ben-Ami Bartal et al. (2011) experiment. In that procedure, there was only a single choice opportunity per session; the duration of social contact therefore depended on when in the session the door opening occurred. Instead, we used a consistent (30 s) duration of social contact throughout the present experiment, while manipulating food amount (number of pellets delivered per reward) systematically across blocks of sessions. In some conditions, designed to match even more closely the Ben-Ami Bartal (2011) procedures, rats chose between 30-s social contact and 5 sucrose pellets each trial, and had free access to food outside the session. Collectively, the methods permit a rigorous test of Ben-Ami Bartal’s two main predictions, namely, that (1) reward value of food and social release are roughly comparable, and (2) a rat will share food with another rat, even at the expense of food for itself.

**Method**

**Subjects**

Six female Sprague-Dawley rats (*Rattus norvegicus*) were used in this experiment. The rats were experimentally naïve, and were pair-housed in a temperature-controlled colony room, with a 12-hr light/dark cycle. One rat from each pair designated the unrestrained (focal) rat and the other the restrained rat. In the homecages, both rats had continuous access to water; food (Purina rat chow) and social contact with the other rat was sometimes freely available and was sometimes limited to 60-120 min access shortly after experimental sessions.

**Apparatus**

The apparatus consisted of two adjacent chambers, each with a wire grid floor. The left chambers measured 31 cm × 25 cm × 22 cm, and the right chamber measured 62 cm×25 cm×22 cm. The right chamber contained two levers (5 cm × 1.5 cm × 1.5 cm), small light (2 cm diameter) mounted above each lever, and one pellet receptacle. Both chambers contained a Plexiglas rodent restrainer (25 by 8.75 by 7.5 cm, Harvard Apparatus, Holliston, MA), separated by a mechanical metal door that opened into the center chamber. Experimental events were controlled and data recorded via a PC computer programmed in MedState Notation language and MED-PC software.

**Training**

**Food reinforcement training.** Focal rats were trained to press the right lever by reinforcing successive approximations with food, delivered into the pellet receptacle (see Fig 1). Only the right lever was active in these sessions, denoted by the illumination of the right cue light.

**Escape training.** To minimize the delay between lever pressing and social interaction, restrained rats were trained to leave the restraint soon after the door was opened. During the escape training session, the restraint door was lifted response-independently. Escape was defined as the entire body of the rat (except the tail) outside the restrainer. Once the rat escaped the restrained and in the left chamber, rats were allowed to explore for 30 s before being returned to the restrainer for the next trail. Sessions lasted for 30 min.

**Social reinforcement training.** After food training was complete, all rats received social reinforcement training. In these sessions, the restrained rat began each trial in the restrainer in the left chamber, with the focal rat in the center (choice) chamber. Only the left lever was active in these sessions, denoted by the left cue light. A left lever press opened the door to the restraint, and produced a xxx tone. When the restrained rat left the restrainer and entered the center chamber, the door was closed, beginning the 30-s social interaction period. This also extinguished the light and deactivated the lever. After 30 s, the restrained rat was returned to the restraint for the next trial. One unrestrained rat was inactive during the social reinforcement session and did not have any response for social reinforcement, so that pair of rats was excluded from the following sessions.

**Procedure**

Sessions were conducted five days per week and lasted for 30 min. In a concurrent choice procedure, rats were given repeated choices between social release and food. Choice trials began with both left and right cue lights illuminated. A press on the left (social release) lever turned off the left cue light and opened the door on the left for a 30-s social interaction period. A press on the right (food) lever produced food. A within-subject experimental design was employed, wherein each subject was exposed to a series of conditions in which the main independent variables (food amount, food deprivation, food location) were systematically manipulated across blocks of sessions. Table 1 shows the sequence of conditions and the number of sessions conducted in each condition. *Food quantity* (number of food pellets per lever press) was varied systematically across conditions (Conditions 1, 2, and 3, with food quantities of 1, 2, and 4 pellets, respectively) with food motivation and location held constant. *Food motivation* (restricted vs. unrestricted access to food in the homecage outside the sessions) was manipulated across Conditions 4 and 5, with food amount and food location held constant. *Food location* (food cup vs. tube) was manipulated across blocks of conditions. In Conditions 1-4, presses on the food lever produced food pellets dispensed into the tray to the left of the food lever; in Conditions 5-7, lever presses opened a door to a restraint to the right of the food lever, behind which food pellets were available. The number of food pellets per response (5) and the motivational conditions (free homecage access to food and social contact) were held constant across these final three conditions. Condition 5 served as a food control, in which only the right (food) lever was active, denoted by the right cue light; the restrained rat was not present, and responses on the social lever had no programmed consequences. In Conditions 6 and 7, both food (5 pellets in the tube) and social contact (30 s access) were concurrently available, with both cue lights illuminated at the beginning of each trial. In Condition 6, trials continued until all of the food pellets were consumed; in Condition 7, trials lasted for a fixed 30 s (timed from door opening), equal to the trial duration following a social choice.

**Results**

Table 2. mean social and food responses and SR+

Fig 1. Relative preference across 6 choice conditions (mean and individual, box-whisker?)

Fig 2. Food produced and shared (and left?) across conditions (mean and individual, box-whisker?)

Fig 3. Within-session data?

Rats selected both social and food outcomes in every session across all conditions. Table 2 shows the mean number of social and food choices per condition for each rat. These data are expressed in relative terms (mean choices for food as a percentage of total choices), averaged across rats (individual data shown as unconnected circles) (or box-whisker plots?) in Figure 2. Relative food preference varied inversely with food amount (pellets per response), ranging from a mean of xx in the 1-pellet condition to a mean of xx in the 4-pellet condition (Compare 1 v 3? Or all 3 in a repeated measures?). These changes in preference were driven largely by decreases in food choices, as the frequency of social choices per session remained relatively constant across these conditions (ranging from xx to xx; see Table 2). Removing the restriction on post-session access to food in Condition 4 reduced yet further the number of food choices (or did it? Compare 3 v 4?). Maintaining free access to food outside sessions but delivering food to the tube rather than the food cup (Conditions 6-7) did not appreciably alter preference: food and social options were selected about equally often in these conditions, and did not differ significantly from Condition 4 (Compare 4 v 7 or 4 v 6-7?).

Figure 2 shows the number of food pellets produced and the number of food pellets shared across conditions. High numbers of food pellets were produced (an average of xx per session), when food was restricted outside the sessions (Conditions 1-3) but these numbers decreased appreciably (average of xx per session) in later conditions with free access to food outside the session (Compare Conditions 1-2-3 v 4-6-7?). The number of earned food pellets that met the operational definition of *sharing* was low across conditions for all rats (mean = xx, across subjects and conditions. (Not obvious what the comparison here should be. I seem to remember that we collected data on food left in the cup. Did we have this for all conditions – or just for the conditions 6-7? This would provide a better measure against which to assess sharing than some arbitrary value)

Figure 3 shows within-session data…?