

Failure to find altruistic food sharing in rats

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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 reinforcement 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 no tangible short-term gain. 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 assessing reward value and 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. (2018) experiment, on the other hand, food or social access (or both) were generally restricted outside the session. 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, suggesting some sensitivity to the motivational context. 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, through satiation, to reduce the reward value of food, bringing food preferences more in line with social preference, akin to findings of Ben-Ami Bartal et al. (2011).

We also sought a more detailed characterization of altruistic food sharing, the second important claim put forth by Ben-Ami Bartal et al. (2011). In their study, sharing was defined in terms of differences in food consumed when a rat was available for release and when no rat was available (empty tube), differences thought to reflect the amount of food that is consumed (hence, shared) with the other rat. While this provides a tangible measure of some important *outcomes* of sharing, it has little to say about the functional characteristics of the sharing behavior itself, or the conditions under which it occurs. In the present experiment, we adopted a functional definition of *altruistic food sharing*, focusing on a coordinated sequence of behavior :

(a) food production, followed by (b) social release, given that (c) food was still remaining, permitting (d) the formerly restrained rat access to food. Measuring such episodes of food sharing alongside preference for food and social release will provide important information on how these behavior patterns are related to each other as well as to the experimental conditions.

In addition, to ensure that the choices were well informed by their outcomes, we gave rats repeated choices each session, rather than just once per session, as in the Ben-Ami Bartal et al. (2011) experiment. In single-choice procedures, the duration of social contact depends on when in the session the door opening occurs. If the duration of social contact contributes to reward value, as some research suggests (Vanderhooft et al., in press), then the value of social release in these single-choice procedures may fluctuate across sessions; and this may, in turn, affect sharing opportunities. We sought to hold constant the value of social contact, both within and across sessions, and therefore used a consistent (30 s) duration of social contact throughout the present experiment. Against this background of constant value of social reward, we manipulated food quantity (pellets per response) and motivational context (restricted versus unrestricted food access) on a within-subject basis, including some conditions closely resembling the original Ben-Ami Bartal et al. procedure. Collectively, the methods permit a rigorous evaluation of Ben-Ami Bartal's two main conclusions bearing on their claim of altruistic food sharing, namely, that (1) reward value of food and social release are equal, 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 some conditions, the rats had continuous homecage access to water, food (Purina rat chow) and social contact; in other conditions, homecage access to was limited to 60 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 Figure 1). Only the right lever was active in these sessions, denoted by the illumination of the right cue light.

Restraint 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 these sessions, the restraint door was lifted response-independently. Leaving the restraint was defined as the entire body of the rat (except the tail) outside the restrainer. Once the rat left the restraint and entered the middle chamber, they were allowed to explore for 30 s before being returned to

the restrainer for the next trial. These sessions lasted for 30 min, and continued for 3-5 sessions, until the rats were leaving consistently within a few seconds after the door was raised.

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. Rat 8 did not readily press the left lever for social access, and so received a few sessions of supplemental training in which presses produced food. Once pressing occurred consistently, the food was withdrawn and social access was the sole consequence of left lever presses. Rats 4 and 6 did not require additional training; left lever presses only produced social access throughout the experiment.

Experimental procedure

A concurrent choice procedure was used, wherein 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, after which the choice phase was reinstated. A press on the right (food) lever produced food, and extinguished the cue light. The location of the food varied across phases, as described below. Sessions were conducted five days per week and lasted for 30 min.

In Phase 1, presses on the food lever produced food pellets dispensed into the tray to the left of the food lever, and food quantity (number of food pellets per lever press) was varied systematically across conditions. In the first three conditions (with 1, 2, or 4 pellets per press, respectively), food was restricted outside the sessions, whereas in the fourth and final condition of Phase 1, food (lab chow) was freely available in the homecage. In Phase 2, food was available in a plexiglas tube restraint to the immediate right of the food lever, presses on which opened the door and permitted access to the food (5 pellets). In the three conditions constituting Phase 2, unrestricted access to lab chow was available outside the sessions. The first condition in this phase 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 the final two conditions, both food and 30-s social 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.

Design and analysis

A within-subject experimental design was employed, wherein each subject was exposed to experimental 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. The main dependent variables were food and social choices, food and social rewards, food consumed, and food shared. The operational definition of sharing was a sequence of behavior consisting of

producing food, followed by social release with food remaining, permitting food consumption by the restrained rat.

Results

Table 2 shows the mean number of social and food choices per condition for each rat. Rats selected both social and food outcomes in every session across all conditions. Figure 2 shows mean preference data (proportion of total choices allocated to food and social options) across the four conditions of Phase 1. Both at the individual-subject level and in aggregate, relative preference for the food option varied across conditions, ranging from a mean of 90.50% in Condition 1 (1 pellet per choice) to a mean of 50xx in Condition 4 (4 pellets per choice with unrestricted food outside the sessions). The mean differences in preference for food and social were assessed statistically..

The changes in relative preference were driven largely by decreases in overall food production. Figure 3 shows mean food pellets produced across conditions in Phase 1, and whether that food was shared or unshared. Food production was relatively high in the first three conditions, when food was restricted outside the sessions, but decreased appreciably in Condition 4, with free access to food outside the session. The food earned in these conditions was nearly always unshared food, as sharing occurred at extremely low levels across all conditions across subjects and conditions. The mean differences in shared and unshared food were assessed statistically..

Figure 4 shows within-session responding on the social and food levers in 5-min blocks across the session for each rat per condition in Phase 1. Food responding decreased systematically with time in session, whereas social responding was relatively constant across the

session. Consistent with the patterns depicted in Figure 3, the absolute level of food responding and food production decreased across the four conditions in Phase 1 for each rat.

Figure 5 shows proportion of total choices allocated to food and social options in Phase 2 conditions, with 5 pellets per food lever response and unrestricted food access outside sessions. Relative preference was approximately equal (xx). the rats selected food and social release about equally often (xx). This lack of systematic preference for either option was confirmed with..

Figure 6 shows shared and unshared food in Phase 2 conditions. Similar to Phase 1 conditions, shared food was exceedingly rare, accounting for a small xx % of pellets overall. The difference between shared and unshared food was highly significant in both conditions, though Conditions 6 and 7 did not differ from each other. While falling far short of statistical significance, we did notice informally a small and transient increase in sharing for one of the three rats in Condition 6. Recall that in this condition, trial durations were unequal following social and food choices; trials with social release ended after 30 s (the duration of social contact), trials with food production lasted until the food had been consumed – nearly always by the focal rat. There were occasional trials in this condition, however, in which a rat would produce and consume some, but not all, of the 5 pellets, and at some time later in the trial (with latencies typically in excess of 30 s from the time of food production) would release the partner rat. If the partner rat then consumed any of the remaining food pellets, it would meet our operational definition of sharing, though appeared less a deliberate act of sharing (i.e., producing food and social release in relatively quick succession) than a satiated rat leaving food. Equalizing the trial duration to 30 s for both trial types in Condition 7 meant any food produced but not consumed within 30 s became unavailable until the following trial. This small change effectively eliminated sharing (xx% of total food). To further test this satiation hypothesis, we

compared the number of leftover pellets (i.e., pellets remaining at trial's end) in Condition 7 to that in Condition 5. Because only food but no rat or social release available in Condition 5, any food left would presumably be due entirely to satiation. The number of leftover food pellets in these conditions was comparable (xx), confirmed by..

Discussion

The present experiment was designed to replicate and extend some key conditions from the Ben-Ami Bartal et al. (2011) study, in which rats chose between social release and food. The present research focused on two main findings and related conclusions from that study: (1) rats chose food and social release with similar latencies, and therefore, food and social release are equally valued; and (2) rats willingly share food with their social partner, even if it comes at a cost to the individual. Taken together, these findings provide key support for the authors' claims of altruistic food sharing. Because occurrences of such unreciprocated food sharing are rare in the published literature, they warrant further scrutiny.

With respect to the first claim of equal reward value of social release and food, we found that relative value of food and social release varied systematically across conditions. More specifically, when food and social motivation were low (unrestricted homecage access outside the session) and food quantity was high (4-5 pellets per trial), food and social release were chosen about equally often (Conditions 4-6), consistent with the Ben-Ami Bartal (2011) findings. When food motivation was high (restricted access to food outside the session), however, rats strongly preferred food over social release (Conditions 1-3). This finding is consistent with the Hiura et al. (2018) findings, showing strong and reliable preference for food over social release when food is restricted outside the session (see also Blystad et al., 2019). Taken as a whole, then, the presents results show that relative preference between social and food is not invariant,

but rather, is subject to reward and motivational variables (food quantity and overall food access). The relative value of social release and food are always subject to these (and other) variables, and it would therefore be premature to draw broad conclusions about their relative value from sampling only a limited range of conditions.

The changes in preference across manipulation of food quantity in the first three conditions were driven mainly by changes in the number of food choices per session. This is partly due to economic factors (i.e., because the number of pellets per choice was increasing across these conditions, fewer food choices were needed to maintain comparable levels of food consumption), and partly due to satiation. Given the low price (1 response) and the dozens of choice opportunities each session, rats were producing and consuming large numbers of sucrose pellets each session (xx-xx, across rats). And when coupled with unlimited food access outside the session in Condition 4, the procedures combined to produce conditions of low food need. Indeed, our rats had such an abundance of food, there was often food left at the end of the session (xx). That rats did not consume rewards as highly valued as sucrose pellets suggests a high degree of satiation.

Despite such low levels of food need, there was very little evidence of food sharing – the second and most controversial claim set forth by Ben-Ami Bartal et al. Behavior that met our operational definition of sharing (i.e., producing food and then releasing the rat while food remained available) was exceedingly rare across all conditions in the experiment (xx%, across all subjects and conditions), even late in the sessions when much of the social release occurred (Figure 3?). It did not matter whether social and food access outside the session were restricted (Conditions 1-3) or not (Conditions 4-7); nor did food quantity (Condition 1-3) matter: rats rarely shared with the other rat any of the hundreds of food pellets they produced each session. Even in

the final three conditions, with procedures that most closely matched the original study (i.e., symmetrically arranged food locations, 5 sucrose pellets, and unrestricted access to food and social contact outside the session), sharing was seldom observed. Thus, on the whole, we found no evidence to support Ben-Ami Bartal et al. claim that a rat willingly shares food with another rat.

It is difficult to reconcile the food sharing reported by Ben-Ami Bartal et al. (2011) with the near complete absence of sharing in the present study. Low levels of food sharing cannot be explained in terms of reduced opportunities for sharing, as the number of social releases (hence, sharing opportunities) remained fairly constant across conditions for individual rats (see Table 2). This was accomplished by providing repeated exposure to a consistent duration of social contact (30 s) across the experiment. With long sessions and repeated trials, rats had ample opportunities to share the food they had produced; they simply did not do so.

The discrepant results also cannot be explained in terms of differing definitions of sharing between experiments. Ben-Ami Bartal et al. (2011) used a less stringent indirect measure of sharing (difference between food consumed with and without a rat available to release) than our behavioral definition of sharing (produce food, then social release with food remaining). This alone cannot be responsible for the different results, however, for even if we adopt the less stringent criterion, our rats showed no differences in food consumption with or without a rat available to release (Conditions 5 vs 6). This is important, as evidence of sharing-related costs are crucial to an altruistic food sharing explanation. Thus, by neither definition did our rats engage in sharing.

There are other differences between the procedures, and the only way to know for certain which factors are responsible for the discrepant results would be to begin with a *direct*

replication, an exact reproduction of the original procedures, and thereafter change one variable at a time. We chose instead to conduct a *systematic replication* (Sidman, 1960), in which some, but not all, of the original procedures are reproduced. Systematic replications are useful in assessing the generality of a finding, and this fit with our broader objectives of providing a more thorough characterization of preference and sharing. We sought not only to *replicate* but to *extend*, to assess the generality of the findings by exploring behavior across a range of conditions, including but not limited to, those of the original study. Indeed, sampling independent variables at multiple points on a function puts replication efforts into a broader context, changing the focus from *binary* questions with yes-no answers (e.g., Do rats value social release over food? Do rats share food with another rat?) toward *conditional* questions (e.g., Under what conditions is social release favored over food, and vice versa? Under what conditions does sharing occur?). Viewed in this way, the Ben-Ami Bartal et al. findings are not so much incorrect as they are incomplete; they are part of more general relationships between preference and sharing and the variables of which they are a function.

Exploring such functional relationships across a parametric range can also shed light on theoretical disputes. For example, when examined at only a single point on a function, social release can be interpreted either in terms of social reward (response-contingent access to social interaction) *or* in terms of empathy (acting out of concern for the other rat): both accounts make the same prediction, namely, that door opening will occur. The accounts begin to differ, however, as behavior is examined across a parametric range of conditions. For example, in procedures similar to those used here, Vanderhooft et al. (2019) established social release in rats. The price of social release (number of responses to produce it) was then systematically increased across sessions, generating demand functions. Overall, the functions (27 in all) were well

described by the Hursh and Silberberg (2008, 2017) essential value model (96% VAF), a model that has proven useful in quantifying the value of numerous other rewards, including food, water, drugs (refs). In other words, these functions were predictable, with a high degree of quantitative precision, on the basis of social reward functions. It is less clear, however, what, if anything, an empathy account would have to say about these data: it makes no obvious predictions about how empathy is affected by price – or other variables known to affect reward value (e.g., magnitude, delay, or probability) about which social reward makes clear and testable predictions. And if predictions could be derived from an empathy account (e.g., by assuming that empathy mirrors social reward functions), they would be indistinguishable from the more parsimonious social reward account, and would therefore add little to the explanation. This is not to deny the importance of empathy as a topic worthy of scientific study; it is, rather, to recommend more stringent tests of it, especially in domains in which simpler explanations already exist.

Table 2. Sequence of conditions and number of sessions conducted at each.

Phase	Condition	Pellets per response	Number of sessions		
			R4	R6	R8
1	1	1	11	11	5
	2	2	9	9	4
	3	4	13	9	5
	4	4	5	5	8
2	5	5	7	5	7
	6	5	6	6	6
	7	5	6	7	5

Figure 1. Apparatus

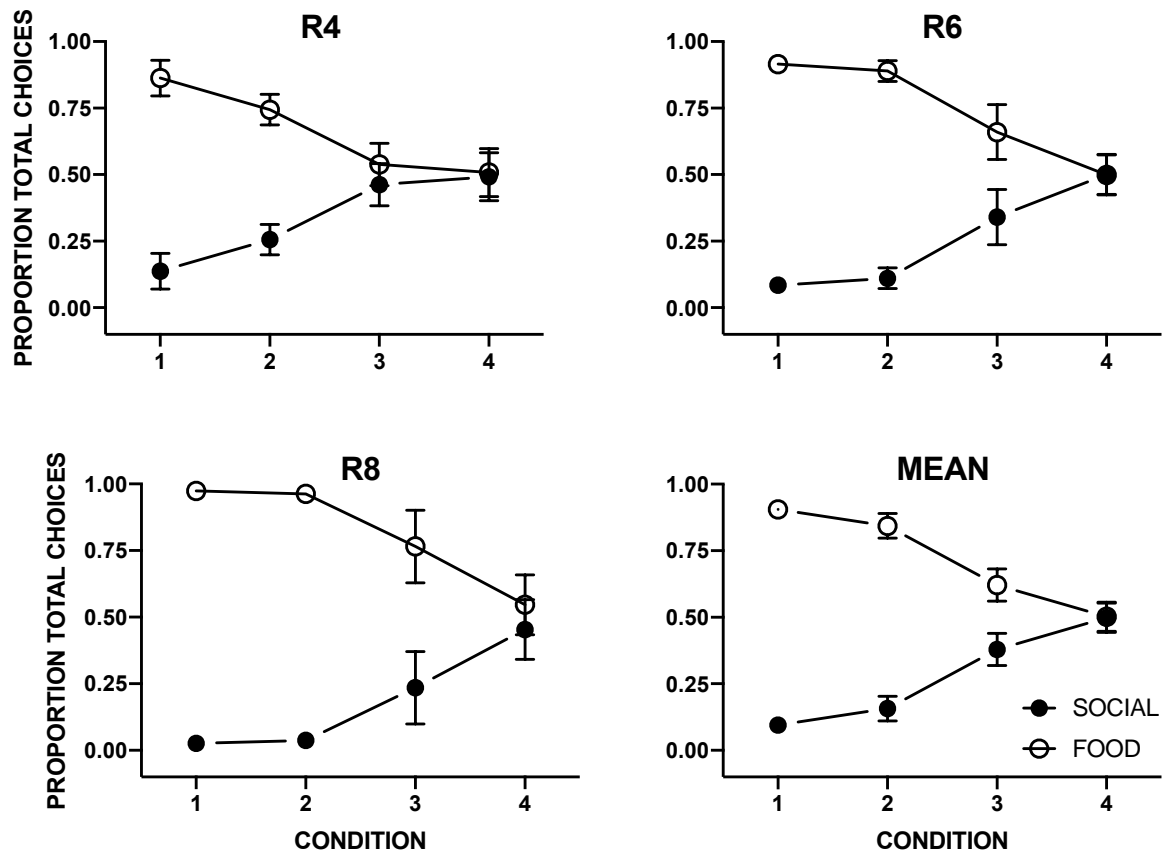


Figure 2. Mean proportion total choices allocated to food and social options across the four conditions of Phase 1. Error bars represent 95% confidence intervals.

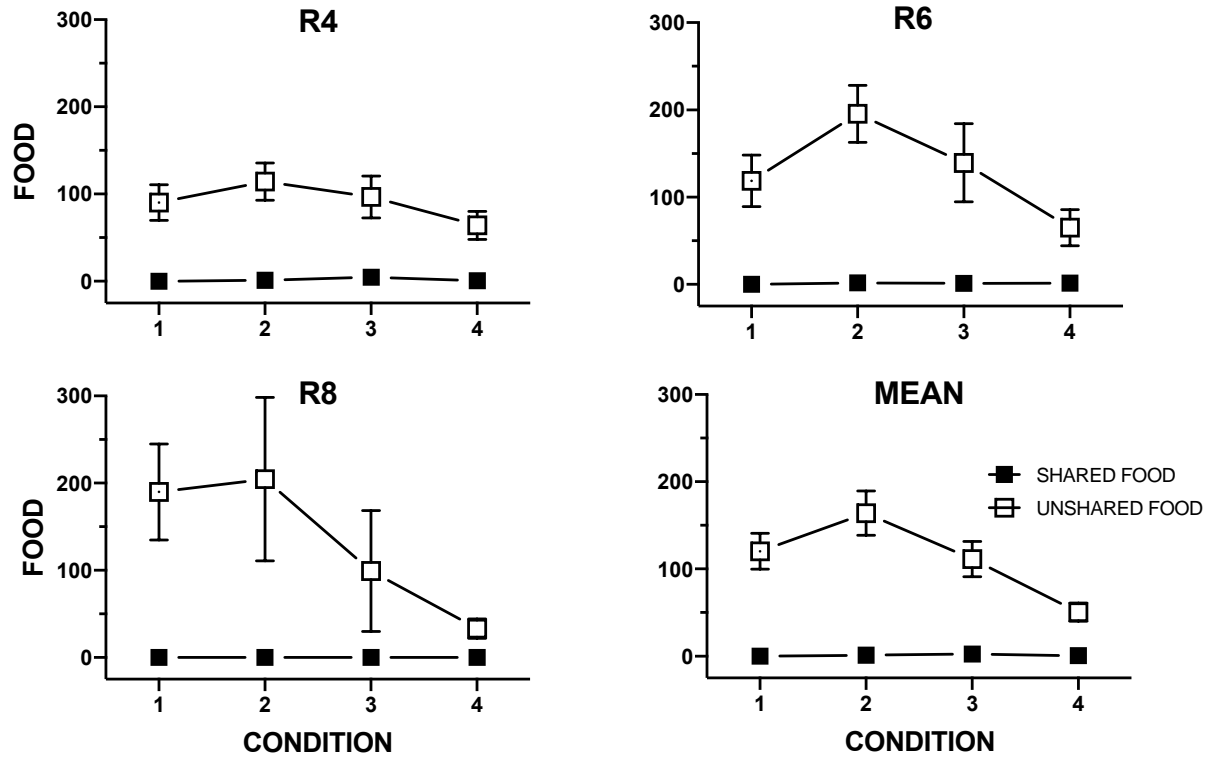


Figure 3. Mean shared and unshared food consumption of across the four conditions of Phase 1. Error bars represent 95% confidence intervals.

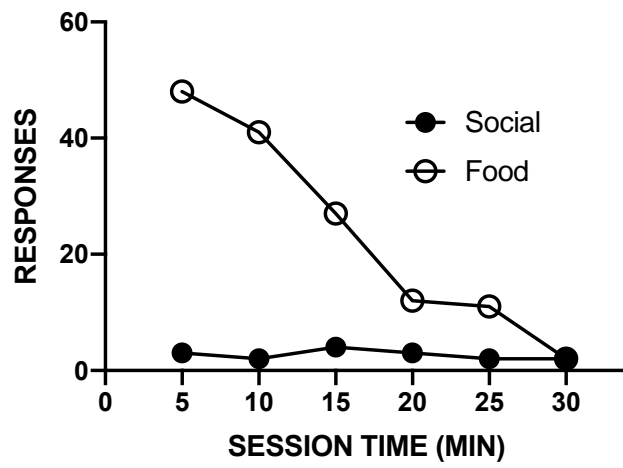


Figure 4. Mean within-session food and social responses in 5-min blocks.