

Social preference in rats

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Rats were given repeated choices between social and nonsocial outcomes, and between familiar and unfamiliar social outcomes. Lever presses on either of 2 levers in the middle chamber of a 3-chamber apparatus opened a door adjacent to the lever, permitting 45-s access to social interaction with the rat in the chosen side chamber. In Experiment 1, rats preferred (a) social over nonsocial options, choosing their cagemate rat over an empty chamber, and (b) an unfamiliar over a familiar rat, choosing a non-cagemate over their cagemate. These findings were replicated in Experiment 2 with 2 different non-cagemate rats. Rats preferred both non-cagemate rats to a similar degree when pitted against their cagemate, but were indifferent when the 2 non-cagemates were pitted against each other. Similar preference for social over nonsocial and non-cagemate over cagemate was seen in Experiment 3, with new non-cagemate rats introduced after every third session. Response rates (for both cagemate and non-cagemate rats) were elevated under conditions of nonsocial (isolated) housing compared to conditions of social (paired) housing, demonstrating a social deprivation effect. Together, the experiments contribute to an experimental analysis of social preference within a social reinforcement framework, drawing on methods with proven efficacy in the analysis of reinforcement more generally.

Key words: social preference, social reinforcement, concurrent schedules, lever press, rats

Keller and Schoenfeld (1950) defined as social, “behavior for which the reinforcing or discriminative stimuli are, or have been, mediated by the behavior of another organism” (pp. 257-258). One important type of reinforcing consequence mediated by another organism is the opportunity to engage in social interaction; and indeed, social reinforcement effects have been reported in a range of species, including humans (Jones et al., 2011) chimpanzees (Mason et al., 1962), capuchin monkeys (Dettmer & Fragaszy, 2000), horses (Søndergaard et al., 2011), foxes (Hovland et al., 2011), calves (Holm et al., 2002), pigs (Kirkden & Pajor, 2006), mice (Martin et al., 2014), and rats (Evans et al., 1994; Wilsoncroft, 1968) (see review by (Trezza et al., 2011).

Over the past decade, social reinforcement effects in rats have been analyzed extensively in social-release procedures, in which animals are given opportunities to release social partners (typically a familiar cagemate) from a tube restraint (Bartal et al., 2011; Bartal et al., 2014; Hachiga et al., 2018; Hiura et al., 2018; Sato et al., 2015; Schwartz et al., 2017; Silberberg et al., 2014; Vanderhooft et al., 2019). In the original Bartal et al. (2011) study, for example, one rat learned to open a door at one end of a tube restraint, releasing a familiar cagemate rat from the restraint into the larger surrounding environment for a period of sustained social interaction (the remainder of the 60-min session) with the other rat. Most of the rats eventually learned to do this, and continued to do so at relatively short latencies once the door-opening response had been acquired.

While these authors deemphasized the role of social reinforcement, the results from these and subsequent studies (Bartal et al., 2014; Sato et al., 2015) are most parsimoniously explained in social reinforcement terms, as contingent access to social interaction (Hachiga et al., 2018; Hiura et al., 2018; Silberberg et al., 2014; Vanderhooft et al., 2019). Hiura et al. (2018), for example, arranged a procedure in which a rat’s lever pressing raised a guillotine-type door at one

The research was supported in part by Summer Scholarship funds from Reed College. Portions of these data were presented at the 2016 meeting of the *Association for Behavior Analysis International*. We are indebted to Greg Wilkinson for his expert technical assistance, to Marisol Lauffer and Shirin Porkar-Aghdam for help conducting the sessions, and to Francesca degli Espinosa for comments on an earlier version of the manuscript. All procedures were in accord with the Reed College Institutional Animal Care and Use Committee.

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doi: 10.1002/jeab.686

end of the tube, permitting the restrained rat entry into the social compartment. Following a designated period of social interaction, the partner rat was returned to the tube, permitting repeated opportunities to respond. Responding for social access was maintained within and across dozens of sessions, and fell to low levels under extinction conditions, demonstrating a reinforcing function of social access.

Vanderhooft et al. (2019) extended these findings using economic demand methods to better quantify social reinforcement value. Using social-release procedures, rats' lever presses produced social access to a familiar cagemate, with the fixed ratio (FR) price and reinforcer duration varied systematically on a within-subject basis, generating a total of 27 separate demand functions across six rats. Overall, the data were well described by the Hursh and Silberberg (2008) essential value model (96% VAF), which has been applied successfully to a range of other reinforcers for rats (Barrett & Bevins, 2012; Bentzley et al., 2013; Cassidy & Dallery, 2012; Christensen et al., 2008; Fragale et al., 2017; Rasmussen et al., 2016). That similar functions are generated with both social and nonsocial reinforcers suggests that social contact shares important functional properties with other reinforcers.

While social-release methods have been used effectively for analyzing social reinforcement, the procedure itself was originally designed for a different purpose, namely, as a way to induce distress in the restrained rat as a basis for empathic motivation in the other rat (Bartal et al., 2011). In point of fact, however, evidence does not support an aversive function of the restraint (or accompanying distress in the restrained rats), as required by an empathy-based account. First, ultrasonic vocalizations, as markers of distress, do not correlate with social release (Bartal et al., 2011); and second, rats freely enter the restraint, suggesting a reinforcing rather than an aversive function (Hachiga et al., 2020). Nevertheless, the social release procedures in general bear the mark of these questions they were originally designed to address, and it may therefore be useful to explore methods that do not rely on the restraint as a potential motivating variable. Doing so would not only expand the analysis of social reinforcement, it would leave silent those accounts which appeal to distress-based

empathy motives (e.g., Bartal et al., 2011; Sato et al., 2015).

The present study was designed to build on our prior research assessing social reinforcement effects with operant methods, but without the use of a tube restraint. Instead, the *target* rats (the rats to which social access was provided) occupied side compartments through which *focal* rats (the rats with respect to which the contingencies were arranged) could enter for designated periods (45 s) of social interaction. The 45-s duration was within the range of durations used successfully in prior research with similar procedures (Hiura et al., 2018; Vanderhooft et al., 2019). In addition, while prior work has focused on simple schedules, the present study expanded the analysis to include concurrent schedules in order to explore social preferences. Rats were given repeated choices between social and nonsocial outcomes, and between different social outcomes. Lever presses on either of two levers opened an adjacent door, permitting access to a side compartment. In some conditions, rats chose between a familiar (cagemate) rat and an empty chamber; in other conditions, rats chose between their cagemate and an alternate (non-cagemate) rat; in still other conditions, rats chose between two non-cagemate rats. Preferences were assessed over blocks of sessions, providing extensive experience with the procedures, ensuring that choices were well informed by their outcomes. In some conditions, we explored the effects on preference of social motivation (social or isolated housing outside the experiment), a crucial but underanalyzed variable in the experimental analysis of social reinforcement. Together, the experiments provide a preliminary investigation of social preference within a social reinforcement framework, drawing on methods with proven efficacy in the analysis of reinforcement more generally.

Experiment 1

This experiment was an initial exploration of social preference using the methods we have used previously to study social release, but without the use of a tube restraint. Focal rats were given repeated choices between (A) a familiar (cagemate) rat and an empty chamber, and (B) a familiar and an unfamiliar (non-cagemate) rat. Choices were made by

pressing one of two levers, which raised a door adjacent to the lever, permitting access to the chosen side chamber. Rats in side chambers wore an elastic harness loosely tethered to the side wall, patterned after methods commonly used to study social preference in voles (Beery et al., 2018). The harness and tether enabled the rats nearly full range of the side chamber but no access to the middle chamber. The focal rat thus initiated the social contact by entering the side compartment. To assess the stability of preferences over time, we ran the initial (A) conditions for an extended period of time, systematically changing conditions on an individual basis. Two of the three rats required some remedial training, which necessitated a departure from the conditions as initially planned. While this required an individualized sequence of conditions, we are reporting the experiment here in the interest of completeness, as it served as a precursor to Experiments 2 and 3.

Method

Subjects

Six female Long Evans rats served as subjects. The rats were experimentally naive, and were pair-housed in stainless steel cages in a temperature- and humidity-controlled environment, with a 12-hr light/dark cycle. Rats had free access to standard rat chow (Purina Rat Diet 5012[®]) and water throughout the experiment. One rat in each pair was randomly assigned as the *focal* rat (the one with respect to which the contingencies were arranged) and the other as the *target* rat (the one in the side chamber to which access was provided).

Apparatus

The apparatus consisted of three adjoined chambers (32 cm x 25.5 cm x 20 cm each), with Plexiglas barriers (see Fig. 1). Circular openings (7.5 cm in diameter) were cut into the Plexiglas barriers, but the openings were blocked by a metal door hinged at the back of the chamber and opened upwards at a 90-degree angle. Each side chamber contained an eye hook, onto which a rat harness was attached via a chain tether. The harness was made of two elastic hair bands looped together and around the shoulders of the rat. The chain permitted free-ranging activity within the side chamber but no access to the middle chamber. The center chamber contained two levers (5 cm x 1.5 cm x 1.5 cm), mounted 6 cm above the floor and positioned equidistant from a centrally located food receptacle (not used in the present study). Stimulus lamps, which could be illuminated with white light, were positioned 4.5 cm above each lever. The side chambers each also contained a lever and food receptacle, though none of these were used in the present study. The chamber was sprayed and wiped with a sanitizer solution between sessions to reduce residual odors. Experimental events were controlled by a Macintosh[®] computer, running Microsoft Visual Studio 2008[®] in a parallel operating system (Windows 7[®]).

Preliminary Training

Before the experiment proper, several weeks of structured preliminary training was conducted with both rats in the dyad. Focal rats were first trained to press the left lever via reinforcing successive approximations by raising the

Figure 1

Apparatus Used in the Present Research



left door, behind which the target rat resided. The door remained open for 45 s, during which the rats could freely enter either the left or center chamber. At the end of this 45-s reinforcement period, the door closed and the rats were returned to their respective chambers. A white cue light above the left lever was on during periods when lever pressing was trained, and off during reinforcer periods. Once lever pressing had been established, the training contingencies shifted to the right lever, signaled now by the right cue light, and the target rat moved to the right chamber. This continued until right lever pressing had been established, about 10 sessions in total for both levers. At this point, target rats underwent a 14-day period of adaptation to the harness, consisting of (a) wearing the harness in an open area (4 days) (b) wearing the harness in a side chamber of the apparatus (2 days), (c) wearing the harness in a side chamber with the chain tether not attached (1 day), and (d) wearing the harness in a side chamber attached to the tether (6 days). To familiarize the focal rats with the new conditions in the side chambers, they received five sessions of noncontingent access to both side chambers, during which the side doors were open, one side empty and the other with the cagemate rat in the harness tethered to the side. This was followed by three sessions, during which lever pressing was reestablished.

Procedure

Once training was complete, focal rats were given repeated choices between the two side chambers in a discrete-trial choice format in 25-min sessions conducted 5 days per week. The first two trials of each session were forced-choice trials, in which only one option was available, signaled by a cue light above the active lever. The location of the active lever alternated across these two trials, ensuring

direct contact with the consequences of either option at the start of each session. There was no time limit placed on the forced-choice trials, but these generally took no more than the first few minutes of the 25-min session. The remaining trials in the session were choice trials, in which both options were available, signaled by cue lights above each lever. A lever press on either lever extinguished both cue lights, terminating the choice phase of the trial, and opened the door adjacent to the chosen lever. This initiated the reinforcer phase, in which the side chamber was accessible for 45 s, after which the focal rat was manually returned to the center chamber and the next choice trial initiated (signaled by the cue lights above each lever). If the side chamber was not entered within 30 s of door opening, the door closed and the 45-s reinforcer period was spent in the middle chamber. The location of the two options remained constant within each session, and strictly alternated across sessions. This session-to-session alternation was designed to reduce position biases commonly seen in choice studies with rats.

Experimental Design

Table 1 shows the sequence of conditions and the number of sessions conducted at each. The experiment was conducted on a within-subject basis across three conditions. In the initial (A_1) and subsequent (A_2) conditions, one side chamber was empty and the other side chamber contained the familiar cagemate rat. In the (B) condition, one side chamber contained the same familiar rat and a second chamber contained an unfamiliar non-cagemate rat. In the (C) condition (conducted with R1 only), one side chamber contained the familiar rat and the other (otherwise empty) side chamber contained an empty harness, designed to assess the potential

Table 1

Sequence and Number of Sessions per Condition for Each Rat in Experiment 1

Condition	Rat 1	Rat 2	Rat 3
A ₁ : cagemate vs. empty chamber	11	17	21
B: cagemate vs. non-cagemate	11	12	21
A ₂ : cagemate vs. empty chamber	14	-	21
C: cagemate vs. empty chamber + harness	12	-	-

reinforcing efficacy of access to the harness alone. The cagemate rat was thus constant across all three conditions; what varied was the alternate outcome: either empty (A), unfamiliar non-cagemate rat (B), or empty + harness (C). The rats underwent a sequence of conditions that varied somewhat across rats depending on their performance, as described below.

Because the methods were novel, we conducted the initial (A) baseline conditions for several weeks, making procedural adjustments as needed. For R2 and R3, responding was inconsistent, and so differential reinforcement procedures were reintroduced after 25 sessions, with the active lever (the one producing door openings on the side with target rat) alternating across sessions. The baseline (A) sessions were reinstated when consistent responding had been reestablished, requiring 22 and 2 sessions for R2 and R3, respectively. For R1, various procedural irregularities (equipment malfunctions, experimenter error) required a more extended baseline. The number of sessions listed in Table 1 for the initial (A) condition include only these final baseline sessions beyond the procedural irregularities (for R1) or the additional training sessions (for R2 and R3).

Results and Discussion

Table 2 shows mean response and reinforcement rates for both options under all conditions for each subject. The rates are exclusive of reinforcer periods and forced-choice trials; reinforcement rates are obtained rates

Table 2

Mean Responses and Reinforcers per Minute in Experiment 1

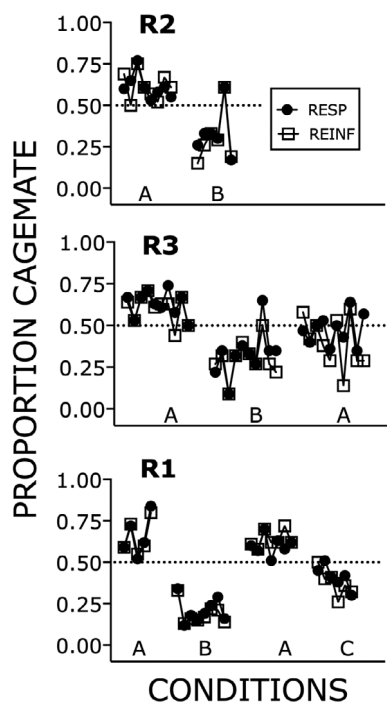
Rat	Condition	Resp/min		Reinf/min		
		CM	ALT	CM	ALT	CTR
R1	A	0.53	0.30	0.45	0.20	0.04
	B	0.27	0.99	0.17	0.73	0.03
	A	0.71	0.49	0.59	0.28	0.05
	C	0.43	0.61	0.33	0.47	0.09
R2	A	0.65	0.45	0.47	0.21	0.09
	B	0.25	0.70	0.19	0.41	0.10
R3	A	0.24	0.13	0.19	0.11	0.02
	B	0.16	0.33	0.13	0.29	0.02
	C	0.18	0.24	0.14	0.16	0.06

Note: CM = cagemate, ALT = alternate, CTR = center.

(i.e., side-chamber entries) rather than programmed rates (i.e., door openings). Trials in which a door was opened but not entered are listed in Table 2 as CTR (center) reinforcers, as the reinforcer period was spent in the center chamber.

A more detailed characterization of performance can be seen in Figure 2, which shows choice proportions (relative response and reinforcement rates), averaged across two-session blocks in each condition of the experiment for each rat. The two-session block was selected to partially correct for the effects of side biases that developed with prolonged exposure to the procedures. Because the sides alternated each session, aggregating across the two sessions dampened the impact of such position biases, roughly equalizing the time each option was associated with each side. In conditions with a non-even number of sessions, the first session

Figure 2
Proportion of Choices for Cagemate Across Conditions



Note. Proportion of response (filled circles) and reinforcement (open squares) for the cagemate option per rat across conditions in Experiment 1, expressed as two-session means. A = Cagemate vs. Empty, B = Cagemate vs. Alternate, C = Cagemate vs. Empty + Harness. See text for additional details.

of the condition was omitted from the analysis shown in Figure 2 (though it was included in the absolute rates shown in Table 2, averaged across the entire condition). Relative response rates were computed with respect to the cagemate choice: (cagemate responses) / (cagemate responses + alternate responses). Relative reinforcement rates were computed similarly, except that the denominator also included CTR reinforcers (reinforcer periods spent alone in the center chamber): (cagemate reinforcers) / (cagemate reinforcers + alternate reinforcers + center reinforcers). A reference line in the figure at 0.50 indicates indifference, with points above indicating preference for the homecage rat and points below indicating preference for the alternative: empty chamber (A) or unfamiliar rat (B).

Despite some between-subject differences, all three rats showed a small preference for the familiar (cagemate) rat over the empty chamber in the initial (A) condition, as evidenced by mean relative response proportion = 0.62 (range = 0.60-0.64), and all of the two-session means above the indifference line in Figure 2. Preference for the cagemate reversed in favor of the alternate rat for all three rats in (B) conditions, and did so within the first few sessions following the introduction of the unfamiliar rat (Fig. 2). This preference for the alternate rat was seen both in the mean relative response rates (mean = 0.72, range = 0.66-0.79) and in the two-session means in Figure 2, 92% of which favored the side with the alternate rats. It is also worth noting that the highest overall response rates for each rat were generated by access to the alternate rat (Table 2).

The return to the second (A) condition produced more mixed results. For R1, a rapid recovery of preference was seen, comparable to the initial (A) condition (mean = 0.60), with all points above the indifference line in Figure 2. For R3, on the other hand, no systematic preference for either option was seen. This was not due to a decrease in overall responses rates, as these were comparable to the initial (A) condition (see Table 2). It may instead have resulted from a decrease in social motivation. This rat spent a higher proportion of reinforcer periods in the center chamber in this condition (CTR reinforcers in Table 2), a consequence of long (> 30 s) latencies to access the chosen side chamber. The frequency of these trials occurred

to a much greater extent in this condition than in the initial (A₁) conditions for R3, in which clearer patterns of preferences were seen, perhaps reflecting differences in reinforcer value across these two conditions. Because FR 1 schedules maintain a strong correspondence between relative response rates and relative reinforcement rates, any discrepancy between them is due to CTR reinforcers (i.e., reinforcers produced but not "consumed"). For this reason, the frequency of CTR reinforcers became a useful metric for assessing experimental control.

Beginning in the (B) condition, and carrying through to the subsequent (A) condition, R1 began chewing on the harness of the target rats during the social reinforcer periods. To determine whether the opportunity to chew on the harness contributed to the value of the social reinforcer, we conducted a control condition (C), identical to A except that an empty harness was available in the otherwise empty chamber. The focal rat allocated some responding to both options each session in this condition, but showed a small (mean = 0.58) but consistent (83% of two-sessions means in Fig. 2) preference for the harness alone to the cagemate rat with harness. This suggests that opportunities to engage with the harness were, for this rat, at least as reinforcing as opportunities to engage with the familiar rat in the harness.

On the whole, across the three rats, we found small but generally consistent preference (4 of 5 conditions) for the familiar cagemate rat over the empty chamber, and an even stronger and more consistent (3 of 3 cases) preference for the alternate (non-cagemate) rat over the familiar rat. And while we were able to generate and sustain responding over extended blocks of sessions, responding grew weak at times, requiring shaping procedures to reestablish for two of the rats (R2, R3). In some cases (as for R1), problems seemed to arise from various issues with the harness (e.g., target rat escaping from the harness, focal rat chewing on the harness). Moreover, the harness introduced factors extraneous to social interaction, and its use is thus less than ideal in a method aimed at assessing social reinforcement value. In the subsequent experiments we therefore abandoned the harness, and considered alternative ways of programming social reinforcement.

Experiment 2

As in Experiment 1, focal rats were given a series of choices involving various combinations of cagemate rats, alternate (non-cagemate) rats, and empty chambers. Unlike Experiment 1, the target rats in the side chambers were free roaming, permitting less constrained forms of social interaction with the focal rat. Our aim was to replicate and extend the two main findings from Experiment 1—preference for cagemate over empty chamber, and preference for non-cagemate over cagemate—with this type of direct reciprocal social interaction. In addition to the critical comparisons between (a) cagemate and empty chamber and (b) cagemate and an alternate (non-cagemate) rat, we also included a second non-cagemate rat. This permitted two additional comparisons, one between the cagemate and the second alternate rat, and one between the two non-cagemate alternate rats. In an effort to increase response rates, we used fixed ratio (FR) 5 schedules, in which the reinforcers depended on 5 responses rather than a single response, as in Experiment 1.

Method

Subjects

Sixteen female Sprague–Dawley rats, approximately 60 days old at the start of training, served as subjects. Rats were housed in pairs in Ancare[®] transparent polycarbonate rodent cages (measuring 26.5 cm x 48.2 cm x 20.3 cm). Four of the rats (from different cages) were arbitrarily deemed *focal* rats, whereas the other eight were deemed *target* rats, as defined above. Four of the target rats were pair-housed with the four focal rats; the other eight were pair-housed with each other in four other cages. Other conditions of feeding and housing were as described above.

Apparatus

The apparatus was the same as in Experiment 1, supplemented to include flap doors that opened into the side chambers, designed to permit one-way access to the side chambers (i.e., from center to side, but not vice versa). The chamber was sprayed and wiped after each session, as described above.

Preliminary Training

To familiarize the rats with the training environment, several adaptation sessions were

conducted. Target rats were placed in one side chamber or the other (the location alternated across sessions). In separate sessions, focal rats were placed in the middle chamber but with the guillotine doors propped open, enabling the rats to explore all three chambers. When the focal rats were consistently entering the side chambers through the flap doors, lever-press training was initiated. Similar to Experiment 1, successive approximations were reinforced by door openings on the side adjacent to the lever, permitting access to the side chamber for 45 s (timed from door opening). The door was closed when the focal rat entered the side chamber. The focal rat was returned to the middle chamber at the end of the outcome phase, whereupon the next choice trial ensued. Sessions lasted for 20 min, preceded by 10 min adaptation (5 min each for the focal and partner rat alone in the apparatus). Once lever pressing was established, the FR requirements were systematically increased across sessions until consistent responding was obtained at the terminal value of FR 5, in which five responses were required to open the door. This phase of training required 16 sessions for R7, and 24 sessions for the other three rats.

Procedure

When the focal rats were consistently pressing both levers and entering both side chambers, they underwent a sequence of conditions constituting the experiment proper. Similar to Experiment 1, focal rats were given repeated choices between two side chambers in a discrete-trial choice format in 25-min sessions conducted 5 days per week. The first two trials each session were forced-choice trials, and the remainder were choice trials. The first-trial location of the forced-choice trials varied randomly across sessions, and the locations of the two options strictly alternated across sessions, as in Experiment 1. In the subsequent choice trials, signaled by the cue lights above each lever, concurrent FR 5 schedules were arranged, in which five (nonconsecutive) responses turned off both cue lights, and opened the door adjacent to the lever for the 45-s reinforcer period. The flap on the door prevented the target rat from exiting the side chamber before the focal rat could enter. Once the focal rat entered the side chamber,

the door closed, thereby preventing either rat from moving into the center chamber. At the end of this reinforcer period, the focal rats were manually returned to the middle chamber, whereupon a new choice trial was initiated, signaled by the cue lights above each lever. An attempt was made to place the rat in the center or rear of the chamber, facing sideways, perpendicular to rather than facing the levers, so as to not differentially favor either side. Responses on both levers were reset to 0 at the end of each trial, such that each choice trial had the same FR 5 requirements.

Experimental Design

Table 3 shows the sequence of conditions and the number of sessions per condition for each rat. The experiment consisted of four phases, manipulated on a within-subject basis: (A) *cagemate vs. empty*, in which focal rats chose between their cagemate and an empty chamber, (B₁) *cagemate vs. alternate rat 1*, in which rats chose between their cagemate and a non-cagemate rat, (C) *alternate rat 1 vs. alternate rat 2*, in which rats chose between the non-cagemate rat from Condition B and a second non-cagemate rat, and (B₂) *cagemate vs. alternate rat 2*, in which rats chose between their cagemate and the second non-cagemate rat from Condition C.

Given the novelty of the procedures with the unrestrained target rats, and the only moderate preferences observed in the first few weeks of the initial (A) baseline conditions, we included some forced-choice sessions, in which the only functional alternative was the option providing access to the cagemate rat; responses on the lever adjacent to the empty chamber produced no programmed consequences, and the cue light above this lever was off. These had no substantial effects on preference, and were withdrawn after 7-10 sessions.

The baseline conditions with the concurrent options were then reinstated for the final five sessions of the condition. The remaining conditions (B₁, C, and B₂) were in place for a minimum of five and a maximum of 10 sessions (see Table 3).

Results and Discussion

Table 4 shows mean overall response and reinforcement rates across conditions, computed as before. (Due to a programming error, baseline reinforcement rates were unavailable.) Figure 3 shows relative response and reinforcement rates in two-session blocks, per condition for each of the rats, computed as before. The break in the function in the baseline (A) conditions indicates where the forced-choice sessions occurred. Subject R6 showed a strong (relative response rate = 0.78) and consistent (all two-session means favoring the social option) preference for the familiar rat over the empty chamber. For R5 and R7, a smaller and less systematic preference for the cagemate was evident across the entire condition (Table 4), though a fair number (> 20%) of the two-session means favored the empty chamber (Fig. 3). Subject R4 did not develop consistent preference for either option, due in large part to a strong position bias we were unable to rectify, and so was not run in the subsequent conditions.

Overall, the results were clearest in the (B) conditions, in which the familiar (cagemate) rats were pitted against unfamiliar (non-cagemate) rats. Consistent preferences for the non-cagemate were seen in all three rats in the B₁ conditions: mean proportion = 0.64 (range = 0.60-0.67), with all two-session means favoring the unfamiliar (non-cagemate) rats. In choices between non-cagemate rats in condition (C), no clear preference was seen:

Table 3

Sequence and Number of Sessions per Condition for Each Rat in Experiment 2

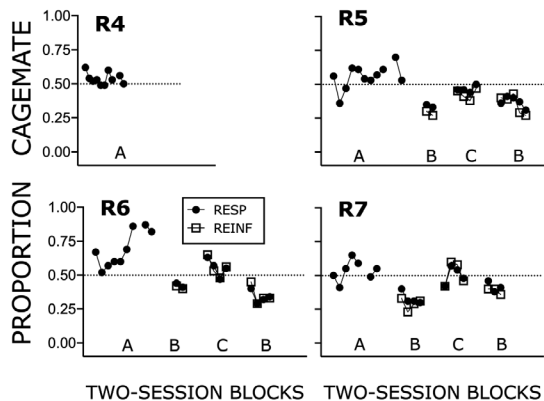
Subject	Rat 4	Rat 5	Rat 6	Rat 7
A: cagemate vs. empty chamber	19	23	20	15
B ₁ : cagemate vs. alternate 1	-	5	5	9
C: alternate 1 vs. alternate 2	-	8	8	8
B ₂ : cagemate vs. alternate 2	-	10	8	7

Table 4*Mean Responses and Reinforcers per Minute in Experiment 2*

Rat	Condition	Resp/min		Reinf/min		
		CM	ALT	CM	ALT	CTR
R4	A	0.92	0.77	-	-	-
R5	A	2.25	1.74	-	-	-
	B ₁	1.46	2.64	0.23	0.46	0.03
	C	2.03	1.78	0.37	0.29	0.01
	B ₂	1.37	2.30	0.23	0.42	0.00
R6	A	1.53	0.87	-	-	-
	B ₁	0.70	1.03	0.13	0.20	0.00
	C	1.47	1.80	0.34	0.27	0.01
	B ₂	0.86	1.79	0.17	0.33	0.00
R7	A	0.87	0.69	-	-	-
	B ₁	0.96	1.98	0.16	0.37	0.01
	C	1.43	1.45	0.26	0.27	0.00
	B ₂	1.15	1.43	0.20	0.26	0.00

Note: CM = cagemate, ALT = alternate, CTR = center.

Figure 3
Proportion of Choices for Cagemate Across Conditions



Note. Proportion of response (filled circles) and reinforcement (open squares) for the cagemate option per rat across conditions in Experiment 2, expressed as two-session means. A = Cagemate vs. Empty, B = Cagemate vs. Alternate, C = Alternate 1 vs. Alternate 2. See text for additional details.

Response rates remained high in this condition (Table 4), but preferences fluctuated from session to session, hovering around indifference (0.50) overall. When the cagemate returned in Condition B₂, but now pitted against the second non-cagemate (alternate rat 2) for the first time, preference shifted back in favor of the less familiar rat: mean proportion = 0.62 (range = 0.55-0.68), with all two-session means favoring the unfamiliar (non-cagemate)

rats. Preferences across the two B conditions were comparable. On the whole, the consistent preference for the alternate over the cagemate rats seen here replicates the preference for novel over familiar rats observed in Experiment 1.

Because the procedures involved the experimenter manually returning the focal rat to the center chamber prior to each trial, it is possible that the placement of the rat at trial onset may have affected responding on that trial. We did not video record each session, but in the few sessions in which video recordings were available, we found no evidence that either the position (front/rear of the chamber) or the orientation (facing cagemate or empty chamber) predicted the location of the next lever press. Given the possibility of unconscious experimenter bias on procedures like these, however, it would be desirable in future research to analyze data from additional sessions in this fashion to rule out this potential confound.

Experiment 3

Taken together, the results of Experiments 1 and 2 show consistent preference for the alternate (non-cagemate) rat, suggesting that familiarity may be an important determinant of social preference. With the repeated and prolonged exposure to the alternate rats in the present procedures, however, these non-cagemate rats became progressively more familiar to the focal rats over time. In other words, social familiarity varied directly with exposure to the procedure. To hold constant relative social familiarity, we repeated the main comparisons (i.e., cagemate vs. empty, and cagemate vs. non-cagemate) in the present experiment, but in conditions with non-cagemate rats, new alternate rats were introduced every three sessions, thereby holding social familiarity constant. If social familiarity reduces social reinforcer value, as suggested by the preference for the less familiar to the more familiar rats seen in the first two experiments, then one might expect even stronger preference for the relatively less familiar rats in this experiment than in Experiment 2. We also examined the effects of social motivation on social preference by manipulating housing conditions outside the experiment; focal rats were either pair-housed with a cagemate or

housed alone. If this type of social restriction acts as a motivating operation (Keller & Schoenfeld, 1950; Michael, 1982), increasing the reinforcing value of social reinforcement in the session, one might expect higher responding under conditions of social deprivation than under conditions of unlimited social contact in the home cage.

Method

Subjects

Eighteen female Sprague–Dawley rats served as subjects. Six of these were focal rats that served in Experiment 2 (Rats 5, 6, and 7, along with their cagemates); the other 12 were experimentally naïve target rats. Rats were housed in pairs, except in the social isolation conditions, when the focal rats and their cagemates were housed alone. All other conditions of feeding and housing were as described above.

Apparatus

The apparatus was the same as in Experiment 2, as were conditions of cleaning and maintenance.

Procedure

The focal rats had previously served in Experiment 2, so preliminary training was unnecessary. The basic procedure was similar to Experiment 2, in that focal rats were given repeated choices between two side chambers in a discrete-trial choice format in 25-min sessions. The trial structure was also the same, with trials separated into choice (concurrent FR 5 FR 5) and reinforcer (45 s access to the side chamber) periods, and two (forced-choice) trials each session (one for each option). One difference was that in this experiment the alternate (non-cagemate) rat rotated after every third session, maintaining a relatively constant level

of familiarity between the focal and alternate rats. (Occasionally fewer than three sessions occurred due to scheduling logistics, that is, the target rat had already been used in a session the same day.) A second difference concerned social housing conditions. In some conditions, rats were socially housed (with cagemate partners) outside the sessions, whereas in others they were socially isolated (housed alone). (The cagemates were also housed individually in these social isolation conditions.) The alternate rats continued to be pair-housed throughout the experiment.

Experimental Design

Table 5 shows the order of conditions and the number of sessions conducted at each. Experimental conditions were arranged on a within-subject basis, with each rat exposed to four conditions: (A₁) *cagemate vs. non-cagemate/ socially housed*; (B) *cagemate vs. empty chamber/ socially isolated*; (C) *cagemate vs. non-cagemate/ socially isolated*; and (A₂) *cagemate vs. non-cagemate/ socially housed* (replication of A₁).

Results and Discussion

Table 6 shows mean overall response and reinforcement rates per condition, and Figure 4 shows relative response and reinforcement rates in two-session blocks across conditions for each rat in Experiment 3. We chose the two-session blocks to maintain consistency with the first two experiments. We also analyzed choice proportions with respect to target rat (changed about every three sessions), but found no systematic pattern either across blocks of sessions with a given target rat, or in transition from one target rat to another. Also, when analyzed across focal rats, we found no evidence of differential preference for particular target rats.

Table 5

Sequence and Number of Sessions per Condition for Each Rat in Experiment 3

Condition			Subject		
	Choice	Housing	Rat 5	Rat 6	Rat 7
A ₁ :	cagemate vs. non-cagemate	social	18	19	17
B:	cagemate vs. empty chamber	nonsocial	7	7	5
C:	cagemate vs. non-cagemate	nonsocial	6	6	6
A ₂ :	cagemate vs. non-cagemate	social	9	9	8

Table 6

Mean Responses and Reinforcers per Minute in Experiment 3

Rat	Condition	Resp/min		Reinf/min		
		CM	ALT	CM	ALT	CTR
R5	A ₁	0.57	0.75	0.07	0.12	0.05
	B	1.22	1.21	0.20	0.03	0.18
	C	1.14	1.66	0.19	0.32	0.04
	A ₂	0.31	0.76	0.04	0.14	0.02
R6	A ₁	0.39	1.36	0.03	0.22	0.04
	B	1.03	0.38	0.15	0.01	0.05
	C	0.67	1.88	0.12	0.35	0.00
	A ₂	0.41	1.72	0.04	0.26	0.02
R7	A ₁	0.24	0.49	0.03	0.09	0.01
	B	1.45	1.00	0.19	0.07	0.08
	C	1.41	2.05	0.25	0.36	0.00
	A ₂	0.43	0.85	0.07	0.17	0.00

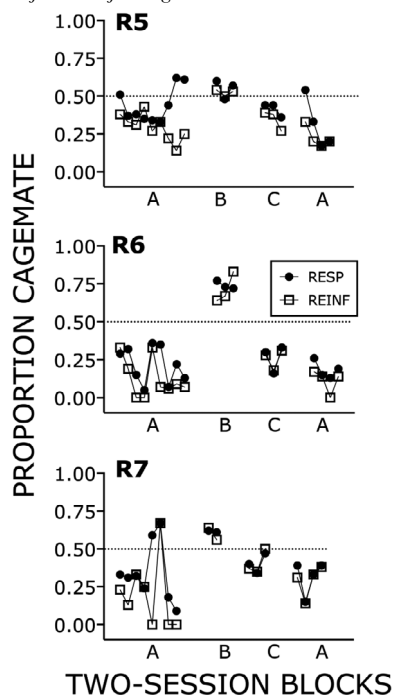
Note: CM = cagemate, ALT = alternate, CTR = center.

The effects shown in Figure 4 were clearest in R6 and R7. In the initial (A₁) conditions, with familiar cagemate rats pitted against the alternate (unfamiliar) rats, choice proportions for both rats favored the alternate rats: mean overall proportions equal to 0.77 and 0.68, respectively, and with 88% of the two-session means in Figure 4 favoring the alternate (unfamiliar) rats. In the B conditions, with the cagemate rats pitted against an empty chamber, preference reversed in favor of the cagemate: mean overall proportions equal to 0.73 and 0.63, respectively, for R6 and R7, with all of the two-session means in Figure 4 favoring the cagemate rats. In the C and A₂ conditions, with the cagemate again pitted against non-cagemate rats, preferences reversed back in favor of the alternate rats: mean overall choice proportions equal to 0.77 and 0.68, respectively, for R6 and R7, and with all of the two-session means in Figure 4 favoring the alternate (unfamiliar) rats. On the whole, and consistent with the earlier findings, these rats preferred the less familiar non-cagemate rats to the familiar cagemate rat (all six conditions in which such choices were assessed), and preferred the cagemate rat to the empty chamber (both conditions in which such choices were assessed).

The effects for R5, however, were less clear. Although the overall rates favored the alternate rats (Table 6), the time course data (Fig. 4) were mixed. Relative response and reinforcement rates favored the alternate rats for most of

Figure 4

Proportion of Choices for Cagemate Across Conditions



Note. Proportion of response (filled circles) and reinforcement (open squares) for the cagemate option per rat across conditions in Experiment 3, expressed as two-session means. A = Cagemate vs. Alternate (Social), B = Cagemate vs. Empty (Non-social), C = Cagemate vs. Alternate (Non-social). See text for additional details.

the condition, but response proportions shifted in favor of the cagemate over the final three blocks. The discrepancy between response and reinforcement rates in this condition was relatively rare in the experiment as a whole, as the measures generally closely tracked. The discrepancy in this case was due to an increasing proportion of trials with reinforcer periods spent in the center chamber (CTR reinforcers in Table 6), a sign of reduced control by the side-chamber reinforcers. This coincided with a strong right-lever bias in this condition, as disproportionately fewer reinforcers were obtained on the left side. Such position biases continued to interact with the choice patterns of this rat in the subsequent conditions, yet consistent preference for unfamiliar rats was still discernible in Conditions C and A₂: mean choice proportions of

0.58 and 0.71 (Table 6) and 86% of the two-session means (Fig. 4) favoring the alternate (unfamiliar) rats.

Effects of housing conditions on social preference can be seen by comparing the conditions in which focal rats were socially housed (Conditions A₁ and A₂) under otherwise comparable but socially isolated conditions (Condition C). Although relative response allocation was generally comparable (if not slightly higher in A than in C conditions), absolute response rates were higher for all three rats in Condition C, when social access was restricted, than under conditions of social housing (see Table 6). Similarly, response rates were higher for the familiar cagemate under the conditions of social isolation (B) than under the social housing conditions (A, C).

It is also worth noting that different genetic rat strains were used across experiments: Long-Evans rats in Experiment 1 and Sprague-Dawley rats in Experiments 2 and 3. The different strains were chosen here due to their availability at the time of the respective experiments. While it was not our intent to conduct strain comparisons, we observed no consistent differences in performance between these rat strains. Responding was comparable across experiments, and largely in line with previous findings from similar procedures with rats of the Long-Evans strain (Hiura *et al.*, 2018; Vanderhooft *et al.*, 2019).

General Discussion

In the present research, responding was maintained by contingent access to another rat, demonstrating a reinforcing function of social interaction. As such, the findings contribute to an expanding body of research with similar methods (Hiura *et al.*, 2018; Vanderhooft *et al.*, 2019), in which rats respond for access to social interaction in much the same way that they respond for access to other reinforcers (e.g., food, water, drug), suggesting functional parallels between social and nonsocial reinforcers. The present research expands this analysis to the domain of social preference, using concurrent-schedule procedures to investigate choices between social and nonsocial outcomes, and between different social outcomes.

In choices between social (familiar cagemate rat) and nonsocial (empty chamber) options, the rats showed a modest but consistent preference

for the social option. Across experiments, about 60% of the choices were for the social option over the empty chamber (see Tables 2, 4, and 6), with 32 of 40 (80%) of the of the two-session means favoring that option (Figs. 2-4). Although the rats allocated more responding to the social than the nonsocial option, the preferences were at times small, and most sessions included choices of both types. Thus, just as the opportunity to explore an empty tube restraint holds some reinforcing value (Hachiga *et al.* 2020), so too does the opportunity to explore an empty chamber in the present study. This finding underscores the need to include such nonsocial options as controls when assessing social reinforcement. It also serves as a useful reminder that the reinforced response (door opening, in this case) is multiply controlled by social reinforcers (opportunities for social interaction) and nonsocial reinforcers (opportunities to explore the side chambers). Additional nonsocial sources of reinforcement were evident in some conditions in Experiment 1, where harness chewing was observed in one rat. Because the harness had been perfectly correlated with the social option in earlier conditions, it required a procedural analysis (Condition C) to isolate the sources of control, verifying that an opportunity to engage with the harness was reinforcing in its own right. Thus, even in simplified laboratory procedures, behavior is multiply determined, and it sometimes requires additional control procedures to disentangle the social from nonsocial sources of control (Hake *et al.*, 1983).

The most robust finding in the present study was the consistent preference for the less familiar (non-cagemate) over the more familiar (cagemate) rat. Across experiments, the non-cagemate rats were selected over the cagemate rats in 17 of 18 conditions (see Tables 2, 4, and 6), in about a 2:1 ratio. These preferences were also seen across sessions within a condition, with 87 of 89 (98%) of the two-session means favoring the non-cagemate rat (Figs. 2-4). This consistent preference for the less familiar (more novel) rat parallels effects reported in the social preference test, the most widely used assessment of social choice in rodents (Crawley, 2004), though over a much longer time frame. Social preference tests typically last for only 10 min, whereas the preferences observed here were observed over hundreds of trials and dozens of sessions. The relationship between these highly popular brief

assessments of social preference and longer-term choice patterns is unknown, yet of high translational significance given the weight this test is afforded in rodent models of clinical disorders, including autism (Kaidanovich-Beilin et al., 2010; Moy et al., 2004).

The robust preference for less familiar over more familiar suggests that *social familiarity* may be an important determinant of social preference, though little is known about social familiarity as a variable or the mechanisms by which it might operate. In the present study, social familiarity was a joint product of experience with the procedures (with both cagemates and non-cagemates) and from the between-session homecage housing conditions (cagemate only). By virtue of the social housing conditions in place for most of the study, cagemate rats were orders of magnitude more familiar than the alternate rats. Thus, for all intents and purposes, social familiarity may have functioned not as a continuous variable (i.e., the less familiar the more reinforcing), but rather, as a dichotomous variable (i.e., cagemate vs. non-cagemate). The effects of social familiarity seen in the present study can be accounted for in these categorical terms.

Within the more restricted ranges of familiarity that accrued with contact with the procedures, no effects of familiarity on preference were seen. First, in choices between non-cagemate rats in Experiment 2, rats did not prefer the less familiar rat (alternate rat 2) to the more familiar rat (alternate rat 1), as would be expected from a consideration of differences in relative social familiarity. Second, in choices between cagemates and non-cagemates, rats did not exhibit a stronger preference for the alternate rats introduced every three sessions in Experiment 3 than the alternate rats that remained constant in Experiment 2. Third, there was no evidence of weakening preference across the block of three sessions per alternate rat in Experiment 3, nor was there any systematic enhancement of preference when a new rat was introduced. Thus, at least within this restricted range represented by the non-cagemate rats, choices were not sensitive to *relative* social familiarity. It is possible that with a wider range of values, a more graded function relating familiarity to value would be obtained, and this should be a priority for future research. The present data, however, only permit conclusions at the categorical level: cagemate vs. non-cagemate.

When viewed in this way, the consistent preference for non-cagemate over cagemate rats may be understood in terms of social motivation. That is, the conditions of social housing may have altered the reinforcing value of social interaction in the sessions, in much the same way that unrestricted homecage access to food or water decreases the value of these reinforcers in the session. In support of this, absolute response rates were elevated in the conditions of isolated housing in Experiment 3 than conditions of social housing. In Condition C, the increases in responding for cagemates and unfamiliar rats were roughly proportional (leaving relative preferences largely unchanged, Fig. 4), suggesting that the social deprivation effects were nonselective (i.e., restriction from cagemate increased the value of social interaction more generally). This social deprivation effect is broadly consistent with some prior findings showing that nonsocial housing conditions enhance social interaction (Templer et al., 2018; Varlinskaya & Spear, 2008), but procedural differences limit more direct comparisons to the present results. Using procedures more like those used here, Hiura et al. (2018) found some evidence of social enhancement, but the effects were mixed, more likely in conjunction with food deprivation than social deprivation by itself. Moreover, the research to date has been largely limited to one method of social deprivation: the binary removal (or not) of the cagemate between sessions. Future research should be directed at intermediate levels of social restriction to more fully characterize the function relating social motivation to reinforcer value. Given the importance of motivational variables in assessing reinforcer value, these types of manipulations are critical topics for future investigation.

Another set of variables brought to light through a reinforcement analysis concerns the type and arrangement of reinforcement schedules. The concurrent schedules used here were equal, although unequal schedules would be useful in analyzing relative value between different social outcomes, as well as reinforcer interactions. For example, holding constant the cost of obtaining *reinforcer A* (e.g., the familiar rat) while systematically increasing the cost (and thereby decreasing preference) for *reinforcer B* (e.g., the unfamiliar rat) would

permit an analysis of substitution effects (Green & Freed, 1993)—the degree to which preference decreases for B are compensated or replaced by increased preference for A. It would also be fruitful for research to explore a wider range of schedule types and to subject them to a parametric analysis. Extending to interval schedules, for example, would facilitate contact with the broader literature on choice and reinforcement value, the majority of which has utilized concurrent interval schedules (Herrnstein, 1970; McDowell, 2013). To the extent that interval schedules encourage changeovers between schedules, they may also reduce the strong position biases we observed for some rats that complicated interpretation of the results. While we attempted to reduce the impact of side biases by repeatedly alternating the locations of the choice alternatives across sessions and forcing exposure to each alternative in each session, position biases continued to interact with the observed preferences for some rats, posing threats to internal validity. This should be addressed in future research, perhaps by providing additional forced-choice trials to ensure repeated contact with both options.

Another variable in need of further systematic investigation is reinforcer quantity, operationalized in the present line of research as duration of social interaction. The 45-s social reinforcer duration used in these experiments falls within the range of durations (10-60 s) Vanderhooft et al. (2019) found to serve as effective social reinforcers. In that study, the shortest duration (10 s social access) was generally more effective than the longer (30 s, 60 s) durations, though the differences were not large, and need further replication. Research with food reinforcers suggests that choice patterns may be more sensitive than response rates to reinforcer duration (Neuringer, 1967). In light of this, it may be fruitful to systematically examine social reinforcer duration with concurrent procedures like those used in the present study.

Previous research has supported a distinction between *appetitive* (social approach) and *consummatory* (social contact and engagement) aspects of social interaction, finding that these two components of socially motivated behavior respond differentially to neuroanatomical (Diergaarde et al., 2005) and environmental (social housing) (Templer et al., 2018)

manipulations. The present study focused on what would be considered appetitive (tendency to work for and approach opportunities for social interaction) rather than consummatory (the social interaction itself). We observed several distinct social-affiliative response topographies (e.g., sniffing, grooming, play), but these responses were not systematically analyzed. Doing so in future research would shed light on the relationship between these different components of social interaction, and the degree to which they may be differentially sensitive to variables of interest (e.g., social motivation, social reinforcer quantity).

In the present research we studied female rats only, a choice guided by our experience with similar procedures, in which female rats showed consistently higher levels of social responsiveness than male rats (Vanderhooft et al., 2019). The generality of such sex-related differences awaits further research. Also, research to date has emphasized same-sex pairs, but should prove interesting to explore interactions between members of opposite sex (Evans et al., 1994), as well as between different strains of rats. Bartal et al. (2014), for example, found that rats would release rats of their own genetic strain but not rats of a different strain (i.e., Sprague–Dawley rats would release unfamiliar Sprague–Dawley rats but not unfamiliar Long-Evans rats). This strain-specific bias was overcome, however, by social experience: Sprague–Dawley rats that lived for a few weeks with a Long-Evans rat would release not only the particular Long-Evans rat with which it was familiar, but also unfamiliar Long-Evans rats (i.e., the social release response generalized to other rats of that strain). Moreover, Sprague–Dawley rats cross-fostered with Long-Evans rats would preferentially release Long-Evans rats even over rats of their native strain, suggesting that in some cases social experiences can override genetic relatedness as a determinant of social reinforcement value. The present procedures are especially well suited to an analysis of such strain-related preferences, permitting direct measurement of the relative value of genetic and social learning contributions to socially reinforced behavior.

In sum, the present research builds on prior research showing that opportunities to engage in social interaction serve reinforcing functions (Hachiga et al., 2018; Hiura et al., 2018;

Schwartz et al., 2017; Silberberg et al., 2014; Vanderhooft et al., 2019), expanding the analysis of social reinforcement to the domain of social preference. Demonstrating such reinforcing functions without the use of the tube restraint is conceptually significant, in that removing the restraint from the procedures also removes from consideration empathy-based explanations that require distress on the part of a restrained rat as a motivating condition. In the absence of any obvious source of distress on the part of the target rats, an empathy-based account cannot explain why a rat would choose a less familiar over a familiar rat; nor even why it would choose a social over a nonsocial option. A social reinforcement account, on the other hand, not only accommodates these findings, it provides a framework for extending them, bringing to bear variables known to be important in the analysis of reinforcement more generally. In addition to those variables considered here (e.g., social deprivation, reinforcement schedules, social reinforcer quantity), others (e.g., social discrimination, social discounting) could be explored as well. Given how little is currently known about even its most basic functions, studying social reinforcement within the context of well-established reinforcement principles is the most productive path forward, both for identifying commonalities and well as differences between social and nonsocial reinforcement.

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Received: May 3, 2020

Final Acceptance: February 24, 2021

Editor-in-Chief: Mark Galizio

Associate Editor: Matthew Bell