

# Functional Analysis of Mutual Behavior in Laboratory Rats (*Rattus norvegicus*)

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Three pairs of rats were trained to synchronize their lever pressing according to a mutual reinforcement contingency, in which alternating lever presses that fell within a 500-ms window were reinforced with food. In Experiment 1, rats worked in adjacent chambers separated by a transparent barrier, and the effects of the mutual reinforcement contingency were compared with those under yoked-control conditions that provided the same rate of food reinforcement but without the temporal coordination response requirement. In Experiment 2, coordinated behavior was compared with and without a barrier, and across different barrier types: transparent, opaque, wire mesh. In Experiment 3, the effects of social familiarity were assessed by switching partners, enabling a comparison of coordinated behavior with familiar and unfamiliar partners. The overall pattern of results shows that the coordinated behavior of 2 rats was (a) maintained by mutual reinforcement contingencies, (b) unrelated to the type or presence of a barrier separating the rats, and (c) sufficiently flexible to adjust to the presence and behavior of an unfamiliar partner. Taken as a whole, the study illustrates a promising approach to conceptualizing and analyzing behavioral mechanisms of mutual behavior, an important component of an integrated study of social behavior.

**Keywords:** social behavior, cooperation, temporal coordination, mutual reinforcement, rats

Intraspecies cooperation is widespread in the animal kingdom, and includes cooperative hunting, territory defense, reciprocal grooming, and food sharing, among others (Roberts, 2005; Stevens, Cushman, & Hauser, 2005). Until relatively recently, much of the comparative work on cooperation had been conducted with primates (e.g., Chalmeau & Gallo, 1995; Chalmeau, Lardeux, Brandibas, & Gallo, 1997; Chalmeau, Visalberghi, & Gallo, 1997; Cronin, Kurian, & Snowdon, 2005; Hattori, Kuroshima, & Fujita, 2005; Hirata & Fuwa, 2007; Mendres & de Waal, 2000; Visalberghi, Quarantotti, & Tranchida, 2000). The cross-species analysis of cooperation has proliferated in the past decade, however, and now includes, in addition to apes, corvids (Seed, Clayton, & Emery, 2008), African gray parrots (Péron, Rat-Fischer, Lalot, Nagle, & Bovet, 2011), wolves (Möslinger, Kotschal, Huber, Range, & Virányi, 2009), hyenas (Drea & Carter, 2009), dogs (Bräuer, Bös, Call, & Tomasello, 2013; Ostojic & Clayton, 2014), elephants (Plotnik, Lair, Suphachoksakun, & de Waal, 2011), and rats (Łopuch & Popik, 2011; Rutte & Taborsky, 2007; Schuster & Perelberg, 2004).

The present study was concerned with a type of cooperation termed *mutualism*, in which socially coordinated behavior produces gains for both animals. Experimental study of mutual behavior dates to a study by Crawford (1937), in which coordinated responding of two chimpanzees was required to produce food for both. In the Crawford study and in the majority of subsequent replications, the mutual response involved pulling a receptacle within reach of both animals (e.g., Hirata & Fuwa, 2007; Mendres & de Waal, 2000; Möslinger et al., 2009; Péron et al., 2011; Plotnik et al., 2011; Rutte & Taborsky, 2007). Other variations utilize a temporal coordination task, in which animals are required to respond synchronously on two separate operanda (e.g., Chalmeau & Gallo, 1995; Cronin et al., 2005; Łopuch & Popik, 2011; Visalberghi et al., 2000). In the Łopuch and Popik (2011) study, for example, pairs of rats in adjacent chambers were trained to respond in temporal synchrony (within 2000 ms of each other) to produce mutual sucrose reinforcement. Coordinated responding, defined as the proportion of responses that met the mutual reinforcement contingency, was established and then maintained across a series of conditions that manipulated the presence and type of barrier separating the rats.

Although Łopuch and Popik's (2011) results suggest that the rats coordinated their behavior, because there were no control conditions in which the mutual reinforcement contingency was disabled, it is unclear to what extent the coordinated behavior was under the functional control of that contingency. Seemingly coordinated behavior may instead come about as an incidental product of individual responding, so-called *byproduct mutualism*. For example, Chalmeau et al. (1997) found that seemingly mutually coordinated behavior of capuchin monkey pairs could be more simply explained as the coincidental synchronization of each monkey's individual responding (see also Visalberghi et al., 2000).

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Without additional control conditions, it is not possible to determine whether the [Łopuch and Popik \(2011\)](#) findings represented a clear case of socially contingent behavior, or whether it arose instead as an incidental by-product of the independent behavior of the individual rats.

Disentangling social from nonsocial sources of control, such as cues produced by a partner versus cues produced by the apparatus independent of a partner's behavior, requires control procedures in which both *mutual* and *individual* reinforcement contingencies are separately manipulated. Therefore, in the present study (Experiment 1), we compared coordination in rats under mutual reinforcement and yoked-control conditions with matched reinforcement rates. If coordinated behavior was primarily due to the mutual reinforcement contingency, then it should be high in the mutual reinforcement conditions and low in the yoked control conditions. In addition to these control conditions, we adopted a more stringent temporal criterion than that used by [Łopuch and Popik \(2011\)](#), and also analyzed multiple measures of coordinated behavior. The stricter response definition enhanced experimental control, and together with the control procedures, enabled a clearer analysis of the determinants of socially coordinated behavior in this task.

Previous research has shown familiarity and social bonds promote pro-social behavior in unrelated individuals (e.g., [Ben-Ami Bartal, Rodgers, Bernardez Sarria, Decety, & Mason, 2014](#); [Rutte & Taborsky, 2007](#); [St-Pierre, Larose, & Dubois, 2009](#)). It was therefore of interest to determine whether coordination was functionally related to social proximity, both inside and outside the sessions. In Experiment 2, we compared coordinated responding across barrier and no-barrier conditions to determine whether social proximity within the session facilitated coordinated responding on the task. In the [Łopuch and Popik \(2011\)](#) study, slightly higher levels of coordinated behavior were observed without barriers separating the rats than when mesh or opaque barriers were present, leading the authors to speculate that perhaps the direct social contact facilitated social coordination. In the present study, we replicated the barrier versus no-barrier comparison, while also expanding the barrier types: transparent, opaque, wire mesh.

In Experiment 3, we examined a different aspect of social proximity: housing conditions outside the sessions. The rats either worked in the sessions with their familiar cagemates or with an unfamiliar noncagemate (a rat from a different dyad). An attempt was made to pair rats with dissimilar baseline response rates, requiring the rats in some cases to change appreciably their rate of responding to maintain coordination. This provides a strong test of sensitivity to partner behavior, and the degree to which coordinated behavior depends on social familiarity.

Together, the experiments are aimed at a functional analysis of mutual behavior, an important behavioral component of many forms of cooperation with benefits for both animals ([West, Griffin, & Gardner, 2007](#)). Such mutual benefits have undoubtedly played an important role in shaping cooperative behavior, but the mechanisms by which they operate are not well understood. The present study sought to throw light on some behavioral mechanisms of mutual behavior, in part by a clearer specification of the target response. The use of a clearly defined and reproducible unit, *temporal coordination*, permits a robust baseline level of performance against which the effects of other variables (e.g., reinforcement rate, barrier conditions, social familiarity) can be assessed. A

standard behavioral unit may also help facilitate productive dialogue across disciplinary boundaries, which at present are often mired in terminological differences ([West et al., 2007](#)). The study also sought to better understand some important sources of stimulus control over coordinated behavior—the various stimulus cues (both social and nonsocial) that combine to produce behavioral synchronization in our temporal coordination procedure.

## General Method

### Subjects

Six male Long Evans rats (*Rattus norvegicus*), approximately 6 months old at the beginning of the experiment, served as subjects. They were pair-housed with a 12-hr light/dark cycle, identified by tail markings made with nontoxic colored markers. Rats were given free access to Purina rat chow in their home cages for 60–90 min immediately following experimental sessions, and were otherwise food restricted. The rats had previously been trained to lever press in a different chamber.

### Apparatus

The apparatus consisted of two adjacent chambers, each with a wire grid floor, measuring 31 cm × 25 cm × 22 cm. Each chamber had a response lever (5 cm × 1.5 cm × 1.5 cm) situated in the middle of the operant panel and a houselight situated 5.5 cm above the center of the lever. A MED-Associates (St. Albans, VT) feeder, that dispensed BioServ (Flemington, NJ) banana pellets, was located to the left of the lever, 6 cm from the left wall. The remaining walls were made of clear Plexiglas. A Plexiglas wall also separated the two chambers, but could be replaced by an opaque Plexiglas or wire mesh barrier. Experimental events were controlled by a Macintosh computer, running Microsoft Visual Studio (2008) in a parallel operating system (Windows 7).

### Procedure

Training and experimental sessions were conducted daily. Rats within each pair were assigned randomly to one of the two chambers (left or right), where they remained for the entire study. Due to their prior histories, lever pressing was quickly established with each rat trained separately in their assigned chambers. Pairs of rats were then run simultaneously on independent reinforcement schedules in both chambers, with a clear Plexiglas partition separating the rats. Following 8 sessions of continuous reinforcement (fixed-ratio 1, FR1), in which every lever press produced food, the rats received 14 sessions on a variable-ratio 5 (VR 5) reinforcement schedule, in which an average of five responses was required for food. Once responding was established for individual behavior, a mutual reinforcement contingency was arranged, in which food was presented to both rats if either rat responded within 500 ms of the other—an interresponse time (IRT) <500-ms schedule, with the restriction that the successive IRTs alternated between rats.

Experimental sessions were signaled by the houselights. Sessions were programmed to end at 25 min, but due to small timing discrepancies in the software and hardware systems, actual session durations were slightly longer, between 25 and 26 min. Session

time did not deviate systematically over the course of the experiment, however, or for different pairs of rats.

All experiments used within-subject/pair designs, with experimental conditions arranged systematically over time. Experimental conditions remained in effect until responding of all three pairs was deemed stable according to the following criteria: response rates showed no upward or downward trends over the last three sessions and the last five sessions did not contain a condition maximum or minimum.

## Analysis

The main dependent variables analyzed were (a) proportion of alternating IRTs <500 ms, (b) mean number of alternating responses, (c) responses per min, and (d) reinforcements per min. Due to the small sample size, nonparametric tests were used to assess effects of experimental conditions on responding. Data from the last five sessions of each condition were used in data analysis.

## Experiment 1

The objective of Experiment 1 was to identify more clearly the influence of mutual reinforcement contingencies on coordinated responding between a pair of rats. This was accomplished by comparing coordinated and individual behavior across a series of conditions in which the reinforcement contingencies were manipulated within pairs. Coordinated responding under a mutual reinforcement schedule was compared with two yoked conditions, arranged as follows: (a) response-independent food according to a variable-time (VT) schedule, and (b) response-dependent food according to a variable interval (VI) schedule. To ensure that comparisons were made across similar overall rates of food presentation, the programmed intervals comprising the VT and VI schedules were yoked to the obtained food rate from the immediately prior mutual reinforcement baseline condition. If coordinated behavior during the baseline condition was dependent on the mutual reinforcement contingency, and not simply a byproduct of reinforced response patterns of each rat separately, then we would expect substantially lower rates of coordination when reinforcement was delivered at the same rate but independent of coordination. On the other hand, if the apparently coordinated behavior is merely a by-product of individual response patterns maintained coincidentally by reinforcement, then coordinated behavior should be little affected by such changes to the contingencies.

## Method

Three main experimental conditions were arranged on a within-subject (pair) basis, according to an ABACA design, with the conditions as follows: (A1) *mutual reinforcement* (baseline), in which food was presented to both rats if the IRTs separating their successive presses was <500 ms; (B) *yoked response-independent food*, in which food was presented to both rats simultaneously and independent of lever presses according to a VT schedule; (A2) return to the baseline *mutual reinforcement* condition; (C) *yoked response-dependent food*, in which food was presented to both rats simultaneously when the responding of either rat satisfied a VI schedule; (A3) return to the baseline *mutual reinforcement* condition.

The VT and VI intervals were determined by a 12-element constant probability distribution (Fleshler & Hoffman, 1962). The difference between the VT and VI schedules was that in the former, food was delivered independent of lever presses, whereas in the latter, food was delivered contingent on a lever press by either rat. To hold food delivery rate constant, the mean VT and VI schedules were yoked to the average obtained food rates obtained by each pair of rats in the final five sessions of the immediately prior A condition (i.e., VT to A1 and VI to A2). Consequently, the scheduled intervals for the VT and VI schedules differed slightly for each pair: 9 s, 6 s, and 8 s in the VT condition (B), and 8 s, 7 s, and 8 s, in the VI condition (C) for rat pairs 32, 37, and 42, respectively.

Table 1 shows the sequence of conditions and the number of sessions conducted at each. Conditions were changed when the stability criteria described above were met.

## Results and Discussion

The top panel of Figure 1 shows the mean proportion of total responses that met the criteria for mutual reinforcement (i.e., alternating responses with IRTs <500 ms) across conditions in Experiment 1. Coordinated responding was high in the first baseline condition, and increased for two of the pairs (32 and 42) over time. Relative frequencies of coordination decreased markedly and to a roughly similar degree in both the yoked VT and yoked VI conditions. A Friedman test found a significant effect of condition (baseline, VT or VI) on rates of coordination  $\chi^2(2, n = 3) = 9.87, p < .05$ .

The bottom panel of Figure 1 shows the mean total alternating responses (i.e., responses made successively by each rat within the pair), including but not limited to the target IRT length. Alternating responding was high in all mutual reinforcement conditions, but decreased to low levels in the yoked VT condition (when food was delivered independently of responding). In the yoked VI condition, alternating responding occurred at higher levels than in the VT condition, although only a small proportion of these responses met the IRT requirement (upper panel of Figure 1). A Friedman test found a significant effect of condition (baseline, VT or VI) on total alternating responses,  $\chi^2(2, n = 3) = 11.47, p < .001$ .

Figure 2 shows alternating IRT frequency distributions under baseline and both yoked-control conditions for each pair of rats. Each IRT was initiated by one rat and completed by its partner. Shaded portions correspond to the target IRT class. The distributions clearly differed across conditions. Under baseline conditions, the modes of the distribution fell within the target region, less than 500 ms. The yoked VI distributions peaked somewhat later, cor-

Table 1  
Sequence of Conditions and Number of Sessions in Experiment 1

Phase	Condition	No. of sessions
A1	Baseline mutual reinforcement	29
B	Yoked variable time	12
A2	Baseline mutual reinforcement	29
C	Yoked variable interval	12
A3	Baseline mutual reinforcement	10

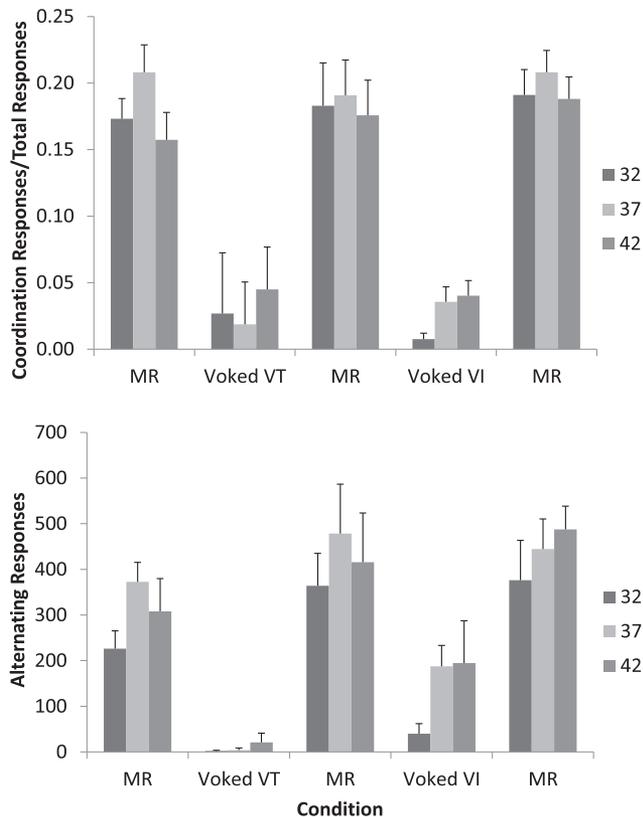


Figure 1. Mean relative frequency of coordinated responses (upper panel) and mean number of alternating responses (lower panel) for each pair of rats in the final five sessions of baseline mutual reinforcement (MR), yoked variable time (VT), and yoked variable interval (VI) conditions in Experiment 1. Error bars plot the upper bound of the 95% confidence interval.

responding to lower alternating response rates. Little responding occurred under the yoked VT conditions, hence the flat distributions.

The top panel of Figure 3 shows the mean number of total responses per session by each rat in the pair. For one pair (37), the two rats responded at approximately equal rates. For the other two pairs, differential response rates were seen, with one rat responding at a considerably higher rate than its partner. These differential rates persisted across all three baseline conditions, and became even more pronounced under the yoked VI conditions, in which responding by only one rat was needed to meet the contingency. In the yoked VI conditions, for all three pairs of rats, one rat responded at substantially higher rates than its partner.

The bottom panels of Figure 3 show the mean number of reinforcers produced by each rat (i.e., the number of times each rat made the terminal response completing the mutual reinforcement contingency). Note that these values are zero in the yoked VT condition, as food was independent of responding. In the pair with similar overall response frequencies (37), completed sequences were roughly equivalent across rats. In the other two cases, however, overall response rates were negatively related to sequence completion rates: the rats with the lower response rates terminated a disproportionately greater share of the sequences. A Spearman

rank-order correlation confirmed a significant negative relationship between response rates and reinforcers earned in the baseline conditions (Spearman's  $\rho = -0.61$ ,  $p < .01$ ); rats with higher overall response rates initiated more and terminated fewer of the reinforced IRTs.

In the yoked VI condition, the within-pair difference in the initiation and termination of reinforced IRTs (bottom panels of Figure 3) was related to the bidirectional changes in response rates (top panels of Figure 3). Because the VI reinforcement contingency required only one response by either rat, the rats with higher response rates tended to meet the VI reinforcement contingency more frequently than their partners. These disparities were sharply reduced on return to the baseline conditions, as the response rates again converged.

In sum, the results from Experiment 1 show that coordinated behavior was not merely a byproduct of independent responding by the individual rats. Coordination was sensitive to reinforcement contingencies and decreased markedly when either the response requirement (in the yoked VT condition) or the response contingency (in the yoked VI condition) for reinforcement was removed. Rats within each pair had somewhat different response profiles, determined by their relative response rates; high-rate responders tended to initiate, whereas low-rate responders tended to complete the reinforced sequences.

## Experiment 2

In the Łopuch and Popik (2011) study, coordination rates were higher in conditions without a barrier separating the two rats than with a barrier present. Without a barrier present, the rats interacted more and perhaps became more socially responsive to each other. This enhanced social contact may account for increased cooperation levels. No-barrier conditions, however, not only permit direct social contact between the rats, they also allow maximum levels of sensory contact from all sources, both social and nonsocial, and in various sensory modalities; these may combine to enhance stimulus control.

In the present experiment, we replicated the barrier versus no-barrier condition from the Łopuch and Popik (2011) study, comparing coordinated behavior with and without the transparent barrier (identical to that used in Experiment 1). Unlike Łopuch and Popik, however, who trained rats with no barrier, our rats were trained to coordinate with a transparent barrier. Coordinated behavior was therefore already well established, and provided a sensitive baseline for assessing the effects of the other barrier conditions. In addition to the barrier versus no-barrier comparisons, we also included wire mesh and opaque barrier conditions, comparing coordinated responding between them and between the standard transparent barriers. By attenuating some forms of sensory contact, these latter conditions were designed to explore in further detail some of the stimulus cues controlling coordinated behavior.

## Method

**Subjects and apparatus.** Same as in Experiment 1.

**Procedure.** The experiment was divided into two phases, each using within-subject/pair experimental designs. In Phase 1, the partition separating the two experimental chambers was systemat-

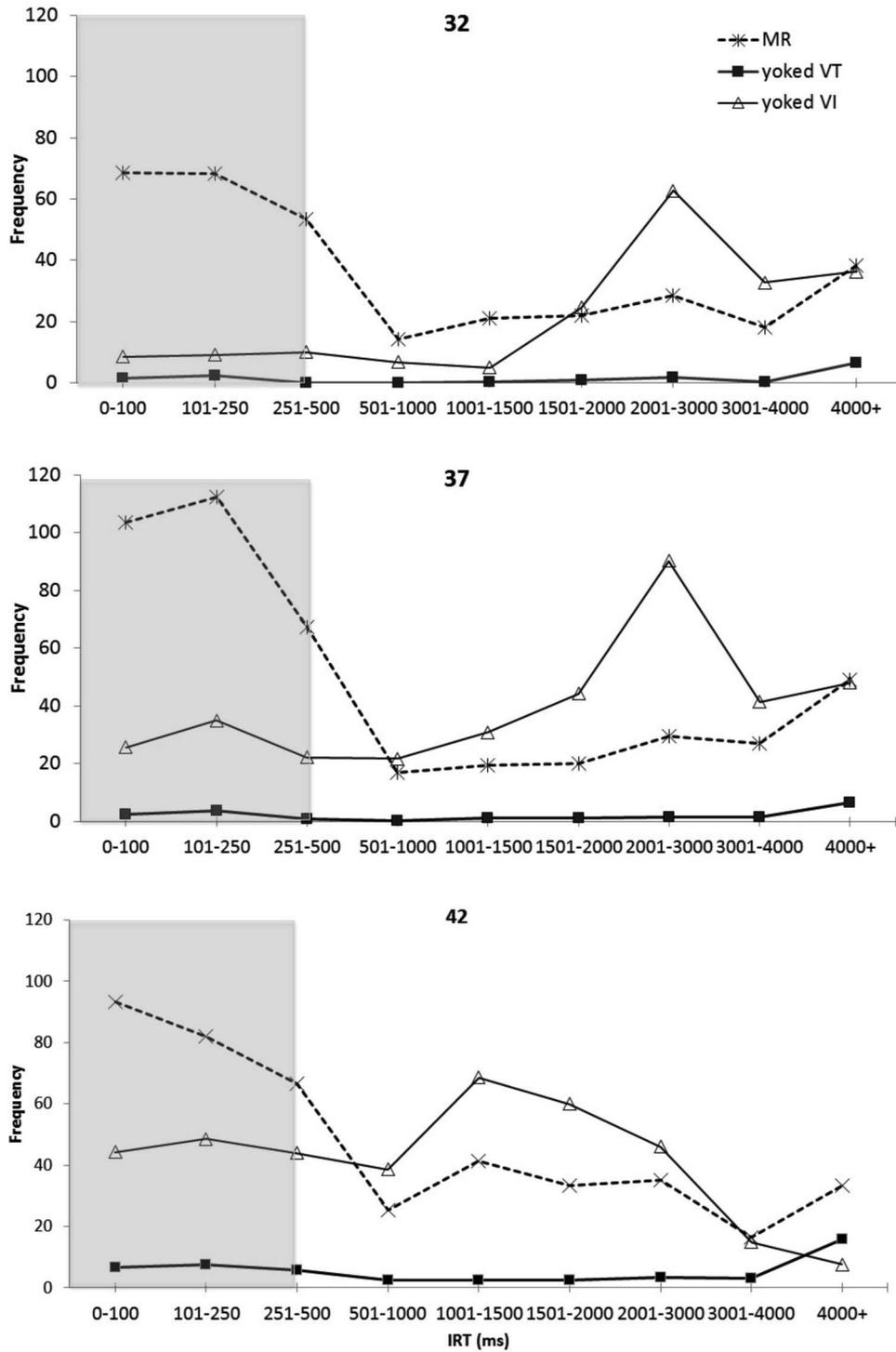


Figure 2. Alternating IRT distributions for each pair of rats under baseline, yoked variable time (VT), and yoked variable interval (VI). Data are averaged over the final five sessions of each condition in Experiment 1. The baseline data are averaged across three baseline conditions. The shaded area delineates the target interresponse time (IRT) region. MR = baseline mutual reinforcement condition.

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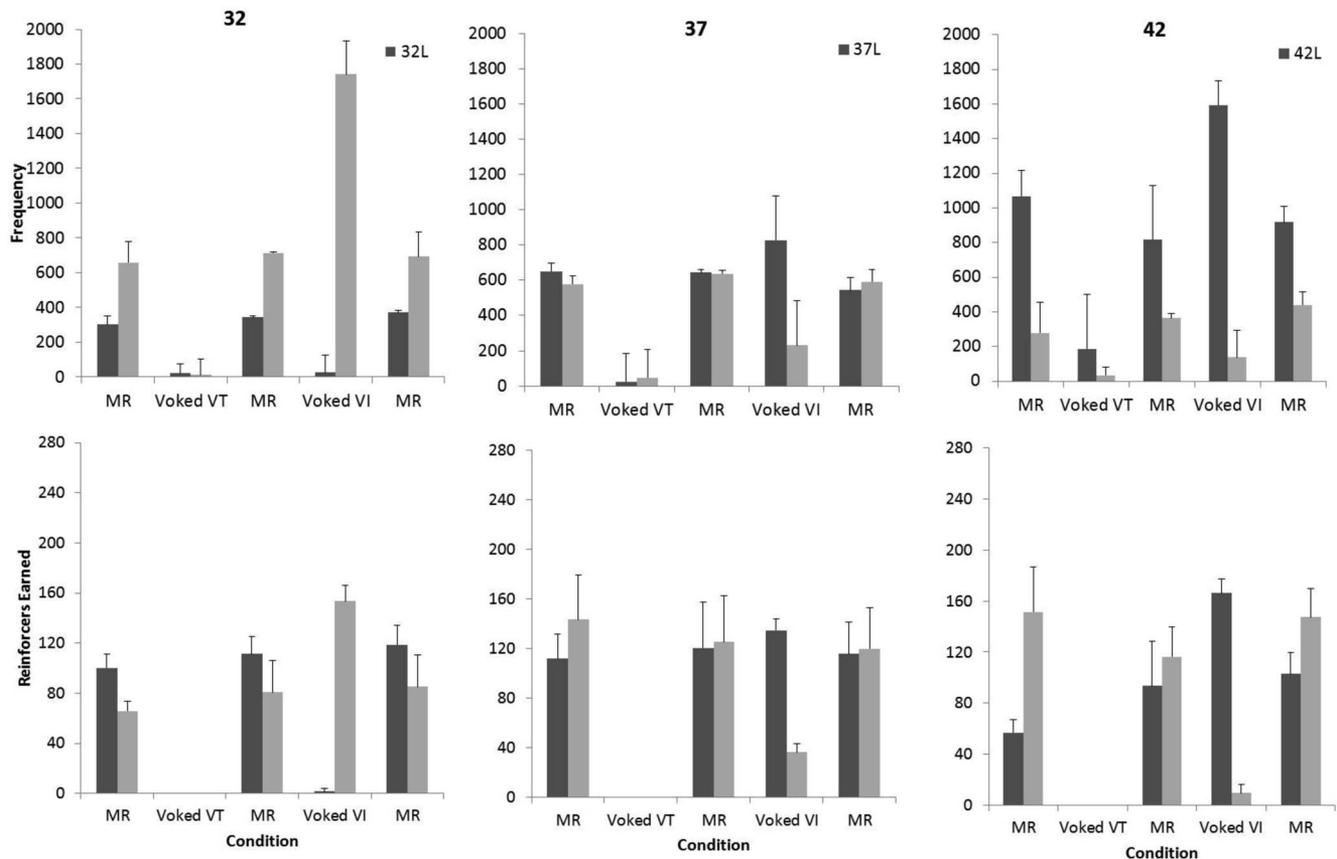


Figure 3. Mean total responses (upper panel) and reinforcers earned (lower panel) per session by each rat in each pair across the final five sessions in Experiment 1. Error bars show the upper bound of the 95% CI. MR = baseline mutual reinforcement condition; VT = variable time; VI = variable interval.

ically altered across conditions: (A) clear Plexiglas barrier, (B) opaque barrier, and (C) wire mesh. Each comparison was preceded and followed by a return to baseline (A) conditions. The design can thus be conceptualized as an ABACA within-subject/pair design. In Phase 2, conducted approximately three months after Phase 1, the barrier condition (A) was compared with a no-barrier (D) condition, in which the barrier dividing the experimental chambers and was removed, permitting direct interaction between rats. These conditions were alternated in an ADA design.

Table 2 shows the sequence of conditions and number of sessions in each condition. Conditions were changed when respond-

ing was deemed stable according to the criteria described in the General Method.

## Results and Discussion

The mean proportion of total responses that met the coordination criteria (alternating IRTs <500 ms) is shown for each pair of rats in the top panels of Figure 4. Coordination did not differ markedly as a function of barrier type, according to Friedman's test,  $\chi^2(4, n = 5) = 7.2, ns$ . Additionally, coordination was not significantly different when barriers were removed and rats had free access to both levers and each other,  $\chi^2(2, n = 3) = 2.0, ns$ , although all pairs showed slightly higher rates of coordination with no barrier relative to the preceding baseline cooperation condition (with a clear Plexiglas barrier).

The bottom panel of Figure 4 shows the frequency of alternating responses for all pairs of rats across conditions. No significant difference was found in the number of alternating responses with opaque or mesh barriers,  $\chi^2(4, n = 5) = 8.00, ns$ . Similarly, there was no significant change in alternation rates when the barrier was removed,  $\chi^2(2, n = 3) = 2.0, ns$ . In the latter sequence of conditions, alternating response frequencies increased for Pair 37 in this phase, but this did not alter the proportion of reinforced alternations (top panel).

Table 2

### Sequence of Conditions and Number of Sessions for Experiment 2

Phase	Condition	No. of sessions
1-A	Clear (baseline)	10
1-B	Opaque	15
1-A	Clear (baseline)	11
1-C	Mesh	15
1-A	Clear (baseline)	15
2-A	Clear (baseline)	13
2-D	No barrier	11
2-A	Clear (baseline)	11

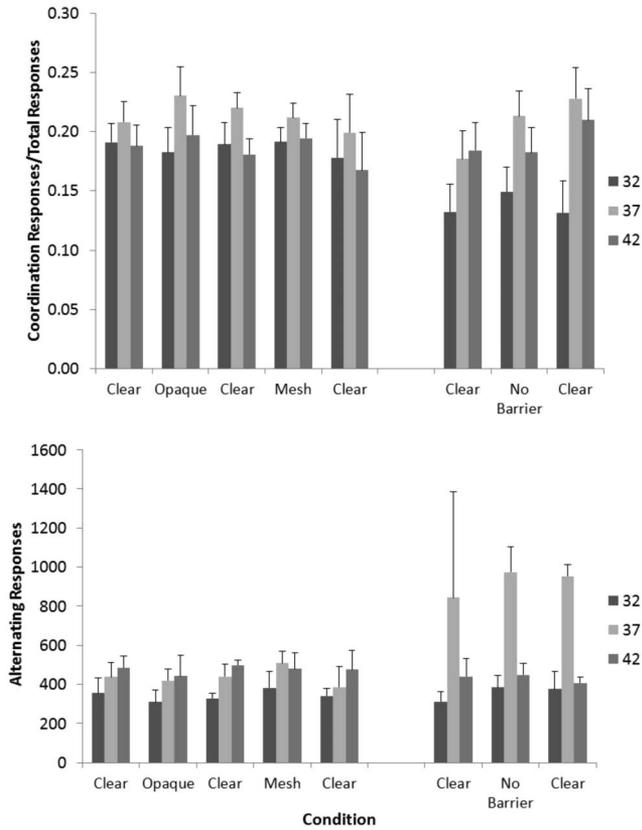


Figure 4. Mean relative frequency of coordinated responses (upper panel) and mean frequency of alternating responses (lower panel) across the final five sessions in each condition in Experiment 2. Error bars show the upper bound of the 95% confidence interval.

Figure 5 shows the mean number of total responses made by each rat in the pair. The same patterns of differential responses seen for Pairs 32 and 42 were evident again here, with one rat responding more than its partner. For Pair 37, which produced approximately equal response rates in Experiment 1, differential responding developed in the latter half of the experiment. These differences did not differ significantly across barrier conditions, however. Friedman tests found no significant differences in mean response number across conditions when the barriers were changed,  $\chi^2(4, n = 5) = 4.67, ns$ , or when they were removed entirely,  $\chi^2(2, n = 3) = 0.33, ns$ . These results suggest that the type of barrier, or lack thereof, had no systematic effect on response rates coordinated responding.

In sum, coordination did not change when barriers were changed from clear solid to opaque solid to wire mesh to no barrier. This pattern of findings differs from previous research (Łopuch & Popik, 2011), in which more restrictive barriers appeared to slightly decrease coordinated behavior. It is unclear what is responsible for these inconsistencies across studies, though some procedural differences may be relevant. Having served already in Experiment 1, our rats had extended histories with the coordination task, and may therefore have been less resistant to change by the different barrier types than the less-experienced rats in the Łopuch and Popik (2011) study.

Additionally, Łopuch and Popik's (2011) rats were trained initially with no partition. This may have produced greater reliance on contact-dependent cues that were unavailable to the rats in the current experiment, all of which received extensive training with clear Plexiglas barriers separating the experimental chambers. In the baseline mutual reinforcement conditions, both here and in Experiment 1, the sight and sound of the lever may both have contributed to stimulus control (i.e., a compound stimulus). When the visual cues were blocked in the opaque barrier conditions of Experiment 2, the auditory stimuli may have continued to exert

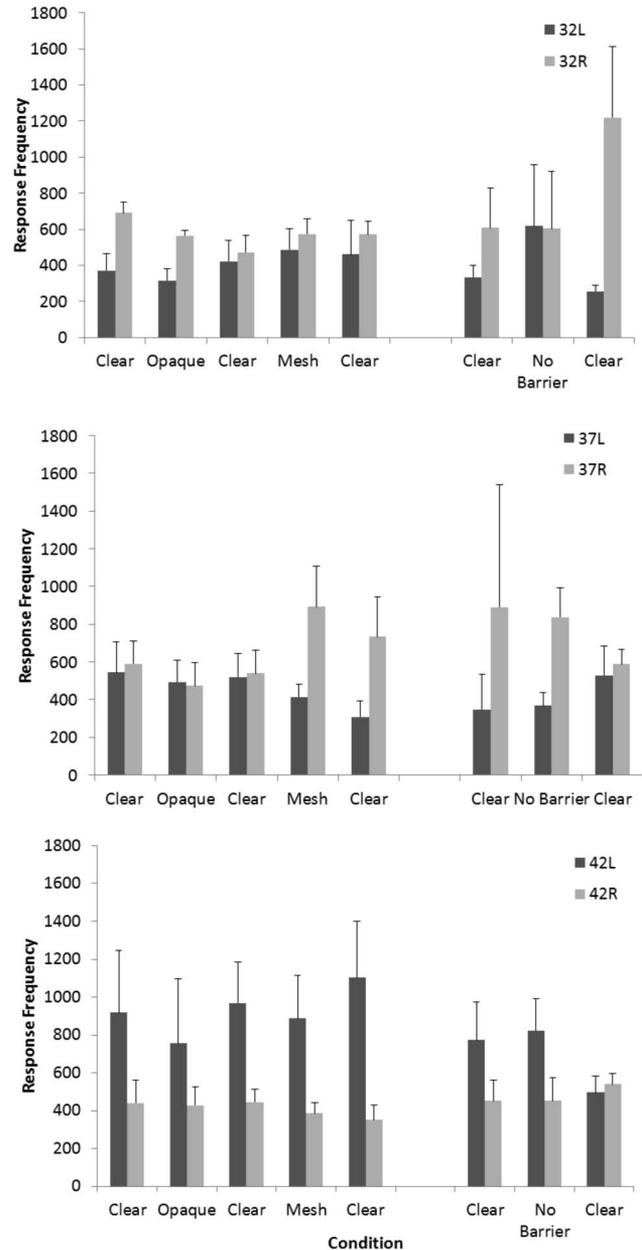


Figure 5. Mean session total response frequency for each rat in each of the cagemate pairs across the final five sessions in Experiment 2. Error bars show the upper bound of the 95% confidence interval.

stimulus control over responding, signaling when short IRTs would be reinforced with food.

This is consistent with findings reported by Hake, Donaldson, and Hyten (1983), in which coordinated responding between two rats was attenuated but not eliminated in conditions in which visual access was blocked. The role of the correlated auditory stimuli (i.e., the sound of the partner's lever presses) was verified in subsequent conditions with auditory masking by white noise. Including such masking conditions in the present procedures would shed further light on the role of the partner's response-produced cues in maintaining the coordinated behavior.

### Experiment 3

The rats within each pair had not only shared a common training history over the course of the two experiments, but also shared a home cage since entering the colony at an early age. The rats were thus quite familiar with each other, and it is reasonable to ask whether, or to what extent, the coordinated responding was limited to interactions with the familiar cage mate with whom the rats shared an extensive social history. This was tested in the present experiment by switching the rat partners across experimental conditions. An attempt was made also to match rats on the basis of disparate baseline response rates, thereby requiring adjustments to the behavior of a new rat.

The current experiment also tests whether the successful coordination was based on pair-specific response patterns that had developed over training. If pairs had developed idiosyncratic, coordinated, behavior patterns over training that met the reinforcement contingencies but were relatively insensitive to social cues, social coordination would be limited to familiar rats and we would expect marked disruptions in coordinated behavior when the partners are switched. If the training with the mutual reinforcement contingencies in the earlier experiments generalized beyond the familiar partner, however, we would expect adjustments to the behavior of the new partner in such a way to maintain coordination. Such conditions are important in determining whether coordination is socially mediated, in the sense of being flexible in the face of changing social circumstances, or whether it is limited to familiar partners.

### Method

**Subjects and apparatus.** Same as in Experiments 1 and 2.

**Procedure.** The same alternating IRT contingency from the first two experiments was in effect throughout Experiment 3. The main experimental variable was the familiarity of the partner, manipulated across conditions in an ABA sequence. In the first condition (A), the IRT contingency was arranged with familiar rats. In the second condition, the same contingency was arranged but with unfamiliar rats; each rat was assigned a rat from one of the other pairs of rats. These new partners were equally experienced but had been trained with a different partner. An attempt was made to match rats with disparate response rates. Rat 32L was paired with 42R, 37L was paired with 32R, and 42L was paired with 37R. In the third (A) condition, rats were returned to their original pairings. Table 3 shows the sequence and number of sessions per condition. Stability criteria were as described earlier.

Table 3  
*Sequence of Conditions and Number of Sessions in Experiment 3*

Phase	Condition	No. of sessions
A	Familiar partners	15
B	Unfamiliar (switched) partners	13
A	Familiar partners	11

### Results and Discussion

The switch to novel partners had no discernible effects on steady-state coordinated responding. Figure 6 shows the mean proportion of reinforced responses before, during, and after partners were switched, over the final five sessions of each condition. Coordination did not change significantly when rats were paired with an unfamiliar partner, according to Friedman's test,  $\chi^2(2, n = 3) = 0.67, ns$ , though for some pairs (32 and 42), coordination appeared to increase slightly with new partners.

Figure 7 provides a more detailed characterization of the adjustment to novel partners, showing overall response rates for each rat across individual sessions before and after the switching of pairs. Unfamiliar pairs are plotted on the same panel. Thus, only in the middle (switched pairs) condition are the rats whose data are shown in each panel paired. For comparison, response rates during baseline and after the switch are plotted for the switched pairs. Response rates of individual rats adjusted to the mutual reinforcement contingency, in some cases reversing the role of high-rate and low-rate responder. For example, prior to pairing Rat 32R and 37L, Rat 32R was a high-rate responder (when paired with 32L) whereas Rat 37L was a low-rate responder (when paired with 37R). Following the switch, however, relative response rates reversed, such that 37L assumed a higher rate and 32R a lower rate (middle panel). In another case, postswitch response of two high-rate responders (37R, 42L) decreased and converged, with high and low-rate roles reversing at least once before stabilizing. Postswitch adjustments in response rates were smaller for the third pair (top panel). Preswitch response rates were less differentiated for these rats, and the postswitch period was characterized by several rate reversals. In the return to baseline, individual response rates adjusted again to those of their original partners.

Figure 8 shows the frequencies of reinforcers produced per rat in each pair. Most rats switched roles with their new partners; rats that earned a relatively greater number of reinforcers with their original partner earned relatively fewer with their new partner and vice versa. For instance, Rat 32L earned on average more reinforcers than its partner, 32R, in the baseline condition, but after the switch earned considerably less than its new partner, 42R, who had originally earned less reinforcers on average than its baseline partner, 42L. Similar patterns can be seen in Rats 37L and 32R.

In sum, switching to novel partners had no substantive effect on social coordination. Over a period of adjustment to the new partner, rats developed coordinated response patterns and reinforcement rates that were comparable to conditions with familiar rats. This suggests that coordination behavior is flexible, and adaptable to new social partners and situations.

**General Discussion**

The present study was aimed at identifying some functional properties of coordinated behavior in rats. Pairs of rats learned to temporally coordinate their responding under the control of a mutual reinforcement contingency. The important role of the mutual reinforcement contingency in maintaining the coordinated behavior was shown repeatedly throughout the study, each time the baseline conditions were replicated. The unit of focal concern in the present study (alternating IRTs) showed functional control by the contingencies, and holds promise as a basis for a common analytic unit of social coordination. This type of reproducibility is an important characteristic of an analytic unit with the potential for cross-species generality.

The general pattern of findings builds on prior research, especially that of [Lopuch and Popik \(2011\)](#), but extends it in several important ways. First, the more stringent contingency for defining coordinated behavior (alternating IRT <500 ms) produced sharper temporal differentiation, as depicted in the IRT distributions (see [Figure 2](#)). Second, we carried out a series of control conditions that isolated important functional variables. In the yoked VT condition of Experiment 1, the mutual reinforcement contingency was removed while the overall rate of food delivery was held constant; in the yoked VI condition, the contingency was removed while holding constant both the overall rate of food delivery *and* the dependency between responding and food delivery. The large differences in the rates of coordinated responding when it produced differential consequences (mutual reinforcement conditions) compared with when it did not (yoked conditions) demonstrate the critical role of mutual reinforcement in the development and maintenance of coordinated behavior. That the yoked VI condition maintained moderate rates of responding, but not coordinated responding, shows the coordinated behavior was not merely a byproduct of higher rates of responding per se, but rather, a direct product of the mutual reinforcement contingency.

Such mutual behavior sometimes occurred in the context of large differences in individual response rates. For two of the three

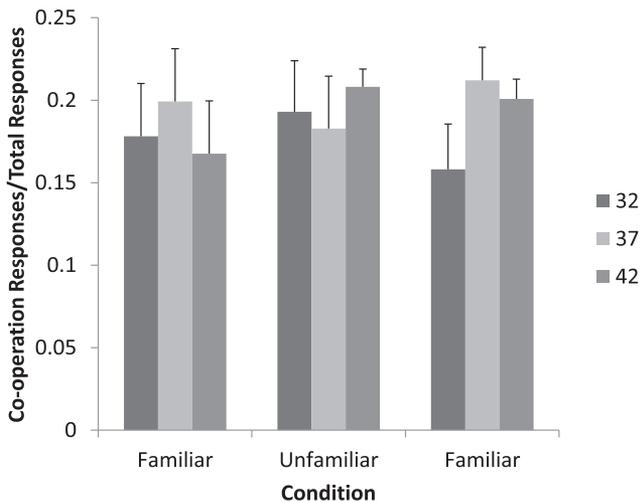


Figure 6. Mean relative frequency of coordinated responses across the final five sessions in all conditions in Experiment 3. Error bars show the upper bound of the 95% confidence interval.

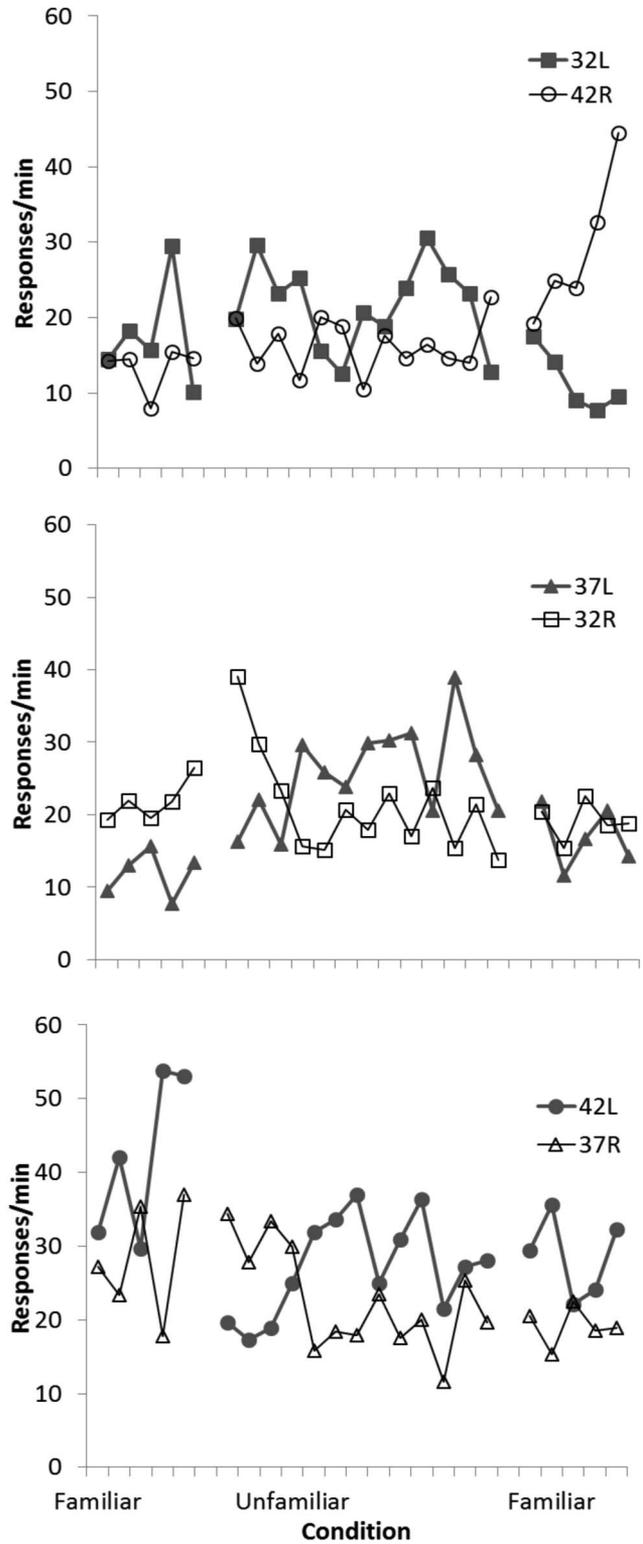


Figure 7. Response rates across blocks of sessions conducted in baseline (BL) and in the switched pairs condition with unfamiliar partners in Experiment 3. Note that the data in each panel are from rats paired in the middle (switched pairs) condition. See text for details.

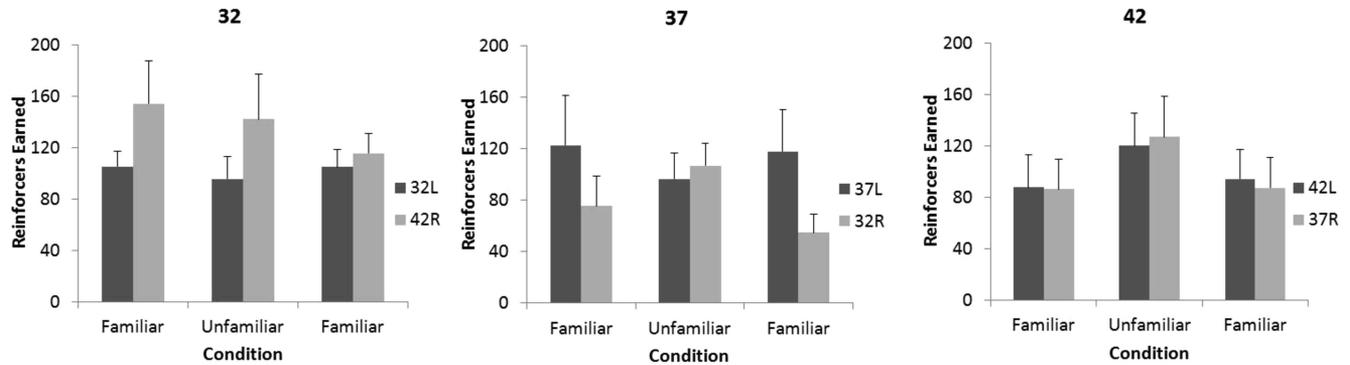


Figure 8. Mean food reinforcer frequencies earned by each rat before and after pairs were switched across the final five sessions in Experiment 3. Error bars show the upper bound of the 95% confidence interval.

pairs of rats, partners developed high-rate and low-rate roles; within these pairs, the high-rate responder would initiate most of the IRT units, whereas the low-rate responder would terminate them, producing reinforcement for both rats. In the third pair, responding was divided more equally; the rats initiated and terminated the units at roughly equivalent rates. When we switched pairs in Experiment 3, rats adjusted their responding to more closely match their partner, maintaining similar rates of coordination and reinforcement. High-rate and low-rate roles also switched with partners for some rats. These results show that successful cooperation was not partner-specific, but rather, flexible and sensitive to the response patterns of a novel rat.

The latter findings are similar to those reported by Drea and Carter (2009) with hyenas. The animals learned quickly to coordinate their behavior in a mutual reinforcement task, and were then tested with novel partners that were either experienced or naïve to the task. The experienced hyenas adjusted their behavior to that of the novices, maintaining proximity until successful coordination occurred. Even quicker transitions to successful coordination were seen when experienced hyenas were tested with other experienced hyenas. This latter condition is closer to the present study, in which the rats adjusted to the behavior of novel rats experienced in the task.

One of the major aims of the present study was to delineate various sources of discriminative stimulus control over coordinated behavior. That coordinated behavior was not appreciably altered across the various barrier conditions in Experiment 2 may raise questions about whether the behavior is actually social. With visual access attenuated, how was coordination achieved? The most likely explanation is the response-produced auditory stimulation arising from the lever presses of the partner rat. This makes sense both in general terms (e.g., sensitivity of rats to auditory stimuli), and in more specific terms (e.g., the specific behavioral history of the rats in the present study). By the time the barrier conditions were conducted in Experiment 2, the rats had extensive histories of mutual reinforcement with Plexiglas barriers that permitted correlated auditory and visual stimuli. Blocking direct visual access may have transferred stimulus control to the auditory stimuli alone. This transfer of stimulus control may be due partly to the extensive behavioral histories our rats had with the procedures. Greater sensitivity to barrier conditions may be seen in rats with less experience in the task, such as in the Łopuch and Popik

(2011) study. Exploring how such barrier effects change over time and experience with the coordination task is an important area for future research.

Coordinated behavior was not maintained in the yoked VI conditions in Experiment 1, when lever presses continued to occur but absent the mutual reinforcement contingency. This suggests that auditory feedback from a partner's lever pressing alone is not sufficient to produce coordinated responding; rather, the response-produced cues, in conjunction with the mutual reinforcement contingency, are necessary to produce coordinated behavior. That is to say, coordinated behavior was sensitive to auditory response-produced stimuli, but only when mutual behavior was reinforced. The functions of auditory stimuli (in this case, the sound of a partner's lever pressing) depend critically on the reinforcement contingencies they signal.

Such selective function of the response-produced cues is understandable in terms of the discriminative/signaling functions of stimuli, as these cues delineate situations in which coordinated behavior produces reinforcement. We recognize that some definitions of social may exclude this type of behavior, regarding it instead as a byproduct of individually motivated actions (e.g., Noë, 2006). We prefer a broader *functional* definition of social behavior, based on the contextual cues governing behavior. If these cues include those arising from the behavior of another animal, and signal when and where social behavior produces distinctive outcomes, we see no need to exclude such context-behavior relationships from the social realm.

Among the advantages of this broader definition of social is the explicit contact it makes with nonsocial associative learning mechanisms (cf. Heyes, 2012). From this point of view, the distinction between social and nonsocial behavior lies on a continuum, defined by the types and ranges of stimuli that govern behavior. One end is typified by situations in which nonsocial stimuli govern behavior (e.g., ripe fruit provides a discriminative context in which coordinated behavior will be maximally effective). Another end is typified by situations in which social stimuli govern behavior (e.g., the approach behavior of a conspecific signals when coordinated behavior will produce mutually beneficial outcomes). Between these extremes is a wide range of situations with social and nonsocial cues signaling a variety of outcomes.

Mapping out the various relationships between mutual behavior and its contextual determinants is a key part of a functional

analysis to which the present study was directed. The analysis is *functional* in two senses. First, in an evolutionary sense, mutual behavior has important *functional* consequences in the social ecology of rats; it is central to many aspects of social behavior, and may serve as a fundamental evolutionary unit of cooperative exchange. Second, the analysis is *functional* in the mechanistic sense, at the level of proximal mechanisms—the variables of which mutual behavior is a function. These two meanings of functional provide different but complementary perspectives; both are essential to an integrated approach to social behavior that combines distal questions about fitness-level outcomes with more proximal questions about underlying mechanisms (Taborsky et al., 2015).

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