Social working memory:
Memory for another rat's spatial choices
can increase or decrease choice tendencies

MICHAEL F. BROWN, MARY BETH KNIGHT-GREEN, EDWARD J. LOREK, JR.,
CAROLINE PACKARD, WENDY L. SHALLCROSS, TIMOTHY WIFALL,
TOM PRICE, AND ERIK SCHUMANN
Villanova University, Villanova, Pennsylvania

In two experiments using a radial-arm maze, pairs of rats made choices among eight maze locations, each containing a large quantity of one of two food types. The choices made by 1 rat affected the choices made by the other rat. Under most conditions, visits by 1 rat increased the tendency of the other rat to subsequently choose that maze location. However, the effect depended on the quality of the food available in a particular location. When it was possible for the rats to observe each other on the maze arms and a rat had experienced that a location contained the less preferred food type, a previous visit to that location by the foraging partner decreased the tendency to visit that location. These effects are attributed to working memory for the spatial choices of another rat, and they indicate that memory produced by a rat's own visit to a maze location is integrated with memory for the behavior of another rat to determine spatial choice.

Since the report of Olton and Samuelson (1976), numerous studies using the radial-arm maze have confirmed the strong tendency of rats to avoid revisits to spatial locations (see Foreman & Ermakova, 1998, for a review). The phenomenon is reminiscent of earlier work on spontaneous alternation (Dember & Richman, 1989), but research involving the radial maze has focused on the use of a working-memory system that stores dynamic information about spatial locations, such as whether particular locations have recently been visited (Olton, 1978). The spatial locations themselves may be represented in memory as discrete items or in some kind of integrated spatial representation. There is long-standing debate about the properties and structure of spatial representations (e.g., Brown, 1992; Brown & Cook, 2006; Brown, Rish, VonCulin, & Edberg, 1993; O'Keefe & Nadel, 1978; Poucet, 1993; Tolman, 1948). Regardless of how spatial representations are structured, an important aspect of the memory used in the radial-arm maze and related tasks is the need to maintain information about the status of multiple locations as their status changes. For example, as a rat visits locations, the content of the memory used to discriminate locations not yet visited from locations yet to be visited must change in correspondence with those visits (Cook, Brown, & Riley, 1985). This dynamic quality is a core property of working memory.

Brown, Farley, and Lorek (2007) recently reported that rats also use working memory to avoid visits to locations that had been visited by another rat. The tendency to avoid locations that had already been visited by a foraging partner was not as robust as the well-known tendency of rats to avoid revisits to locations they have already visited, but it was found in several different versions of the radial-maze task. Brown et al. (2007) ruled out odor trails or other physical traces of visits made by the other rat as an explanation for this tendency and concluded that its mechanism is working memory for spatial locations chosen by the other rat.

The present experiments were designed so that we may further examine the conditions under which the spatial choices of 1 rat (the focal rat) affect the subsequent spatial choices of another rat (the nonfocal rat). Both experiments involved an eight-arm radial maze, in which 2 rats (cage mates) made choices simultaneously. It was a standard radial-arm maze, except that the maze arms were constructed of tubes, which allow 2 rats to pass each other on maze arms (Brown et al., 2007). Pairs of rats were placed in the central arena at the beginning of each trial and allowed to make choices. We examined whether the tendency to choose locations by the focal rat was affected by previous visits to that same arm by the nonfocal rat.

A focus of the present experiments was the nature of the reinforcement available at the ends of maze arms. Each location was baited with one of two types of food: grain pellets or sucrose pellets. Rats prefer the sucrose over the grain. The identity/location of the maze arms with sucrose versus grain pellets was unpredictable from trial to trial. Atypically (for procedures using the radial-arm maze), the locations were baited with a large amount of food, which was not depleted by the rats' visits.

M. F. Brown, michael.brown@villanova.edu

These features of the experimental design were intended to allow us to determine whether the locations visited by 1 rat had any effect on the locations subsequently visited by the other rat and whether any such effect was itself modulated by the type of food available in the arm visited by the first rat. In the previous experiments by Brown et al. (2007), we found that rats avoided visits to locations that they had observed being visited earlier by another rat. Part of the motivation for the present experiments was the possibility that the effect of previous choices by another rat might depend on the value of the food available at the ends of maze arms. Typically, arms in the radial-maze and similar paradigms have a small amount of food that is reliably depleted when a rat visits the arm. There is evidence that this feature of the standard radial-arm maze task is not necessary for rats to explore different maze arms and to avoid revisits to arms (FitzGerald, Isler, Rosenberg, Oettinger, & Bättig, 1985; Timberlake & White, 1990). However, we considered the possibility that providing a large amount of food (that would not be depleted during a trial) would result in the foraging partner's having an increased (rather than decreased) tendency to visit those maze arms, at least when the maze arm contained the preferred food type.

This hypothetical pattern of results would be consistent with social enhancement effects that have been reported in natural and laboratory foraging behavior (see Galef & Giraldeau, 2001; Galef & Laland, 2005, for reviews). Social effects in the context of foraging behavior include animals apparently using fellow foragers as cues to the location (and other properties) of food (Barnard & Sibly, 1981; Galef, Mischinger, & Malenfant, 1987; Galef & Wigmore, 1983). In social-enhancement experiments, rats find food in the locations that they visit after interacting with a conspecific. For example, in the Galef and Wigmore experiments, rats first learned the locations in which different kinds of food were to be found. Subsequently, interactions with conspecifics enhanced a rat's tendency to visit locations containing the food that was recently consumed by the conspecifics. In the social memory experiments involving the radial-arm maze (Brown et al., 2007), on the other hand, interactions with a conspecific decreased a rat's tendency to visit locations that were recently visited by the conspecific. There are a number of potentially important differences between the procedures and measures used in these two sets of experiments. A salient difference is the fact that food was no longer available in a maze arm following a visit in the standard radial-arm maze task, whereas food continued to be available in the locations visited by the rats in the social-facilitation experiments.

We expected that the unusual technique of baiting the arms of a radial-arm maze with a large, undepletable quantity of food would encourage rats to visit locations according to social cues (as they did in the social-facilitation experiments), rather than to avoid locations according to social cues (as they did in the Brown et al., 2007, experiments). If so, then the techniques used in these experiments would allow the rat's choices to reveal social memory effects that included information about both the locations chosen by another rat earlier in the trial (as shown by Brown

et al., 2007) and the type of food found by that other rat. This would suggest a richer, more complex kind of social memory that represents information about both the location and quality of food found by a conspecific.

EXPERIMENT 1

Method

Subjects. The subjects were 8 male Sprague Dawley rats, obtained from Harlan Sprague Dawley (Indianapolis) as weanlings. They were housed in pairs and provided with free access to water and food until they were 12 weeks old. Experimental trials occurred during the dark phase of a 12:12-h light:dark cycle. One rat in each pair was marked on its tail and back to facilitate identification.

Apparatus. The central arena of the maze was constructed of plastic 25 cm tall and 46 cm in diameter, and had a floor that consisted of a thick layer of the same wood chips used in the rats' home cages. Eight equally spaced circular holes (10 cm in diameter and centered 6.5 cm above the floor) led to the arms, which were tubes constructed of opaque white PVC 10 cm in diameter and 90 cm long. The terminal 10 cm of each tube was cut so that only the bottom half of the circumference of the tube was present. This created a platform on the end of each arm, from which visual cues were fully available and on which a small (4.5-cm-square and 0.9-cm-deep) translucent plastic dish was mounted as a food cup. It is important to emphasize that although the maze arms were enclosed, access to visual extramaze cues was available from both the central arena and the platforms at the end of each maze arm.

Maze arms were baited by filling the dishes at the ends of maze arms with approximately thirty 45-mg sucrose pellets (P. J. Noyes, Product PJFSC000045) or grain pellets (BioServe, Product F0165). Pilot work with other rats indicated that this amount of pellets would result in about half of the food being depleted by 2 rats during a 5- to 10-min trial and confirmed that rats have a strong preference for the sucrose pellets.

The maze was centered in a 36.1×35.3 m room with a variety of objects around the perimeter and illuminated by fluorescent tubes. A video camera was mounted above the central arena of the maze, which allowed the experimenter to monitor the behavior of the rats in the central arena from his or her station in one corner of the room.

Preliminary training procedure. The rats were placed on a restricted diet; their weights were monitored throughout the experiment and were maintained at 85%–95% of free-feeding weight. Beginning 3 days before their first placement in the maze, each pair of rats was given several sucrose and grain pellets in their home cage daily. Then, for three daily sessions, each pair of rats (cage mates) was placed in the maze for 10 min using the same procedure described below, except that pellets were also scattered inside the maze arms and in the central arena to facilitate exploration of the maze. Results presented below do not include behavior during these three preliminary trials.

Testing procedure. Prior to each trial, four randomly selected maze arms were baited with grain pellets and the remaining four arms were baited with sucrose pellets. The 2 rats were then placed in the central arena of the maze and allowed to choose maze arms until 10 min had elapsed. A *choice* was defined as when all four paws were on the surface of the maze arm. The experimenter recorded the sequence of arms chosen. For each pair of rats, one trial was conducted per day for 20 days.

Results

The question guiding the analysis and interpretation of the data was whether the choices made by 1 rat affected subsequent choices made by the other rat. For each trial, the number of choices among the first eight made by each rat was defined as a function of five variables: (1) the previous visit status of the focal rat (i.e., whether the location had been chosen earlier in the trial by the focal rat), (2) the pre-

vious visit status of the nonfocal rat (i.e., whether the location had not been chosen earlier in the trial by the nonfocal rat, was the nonfocal rat's most recent choice, or had been chosen by the nonfocal rat earlier in its choice sequence), (3) whether the maze arm was baited with grain pellets or sucrose pellets, (4) the serial position of the choice in the sequence, and (5) trial block (the 20 trials were structured into two blocks of 10 trials each for purposes of data analysis). Preliminary analyses failed to identify any differences in the patterns of results for the two trial blocks, so that variable is not presented in what follows.

To determine whether the tendencies to make choices in each of the categories defined by these variables differed from what would be expected on the basis of chance, the number of maze arms in each category at the time each choice was made was also determined. Revisits of maze arms occurred infrequently, although more frequently

than in a typical radial-maze procedure. The mean (over rats) proportion of choices made (during the first eight choices) that were revisits of a location by the focal rat was .162. Because of the large difference in the number of initial visits and revisits, the proportions of choices made (*obtained* proportions) and the proportions of maze locations available to choose (*expected* proportions) within the categories defined by the other variables were determined and evaluated separately for initial visits and for revisits by the focal rat (see the Appendix for details and Brown et al., 2007, for additional discussion of the analysis approach).

Figure 1 shows the mean (over rats) obtained and expected proportions in the visit-status and food-type categories. The expected proportions (at the time choices were made) provided an estimate of the proportions of choices expected on the basis of chance. The critical comparisons in the primary
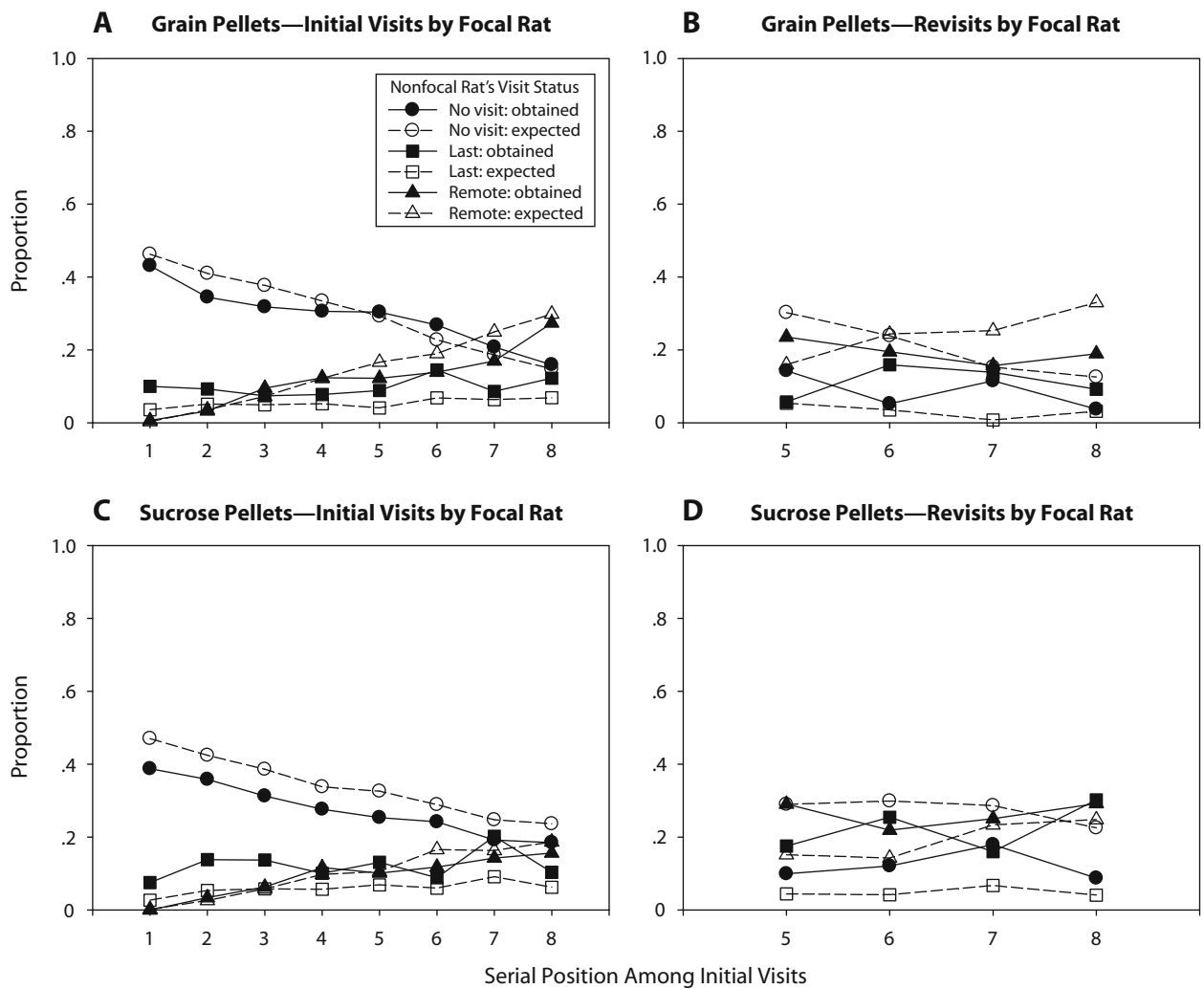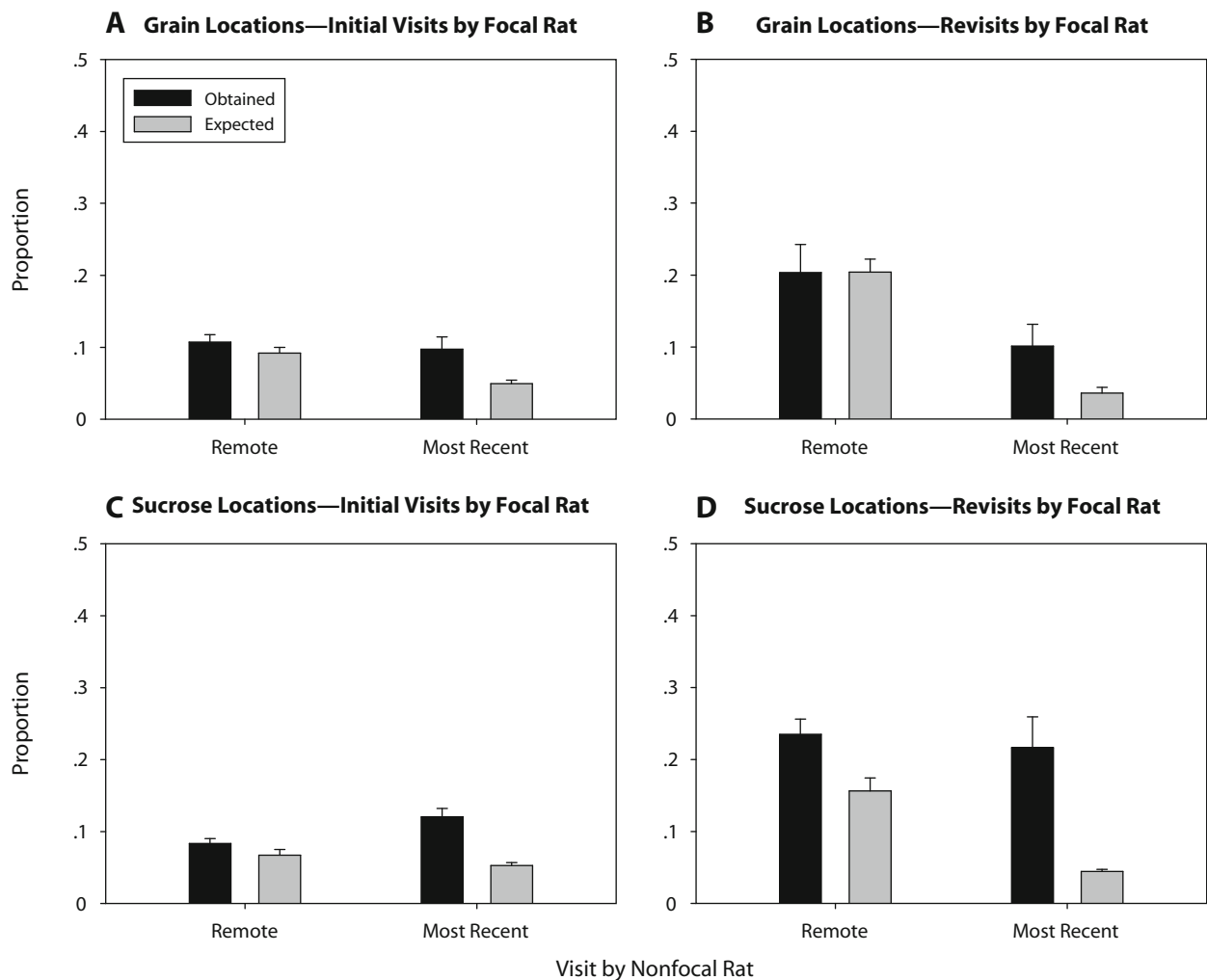

Figure 1. Mean proportions of maze locations chosen by the focal rat (obtained proportions) and proportions of maze locations available at the time those choices were made (expected proportions) during Experiment 1. Proportions were calculated and analyzed separately for initial visits and for revisits to maze locations. Within each visit type, proportions were determined for choices made by each rat at each serial position, as a function of the bait type and whether the location had not been visited by the nonfocal rat (circles), was the most recent location visited by the nonfocal rat (squares), or had been visited earlier in the nonfocal rat's choice sequence (triangles). The means (over rats) of these proportions are shown.

data analyses presented below are the differences between these obtained and expected proportions for each category of maze location. Panels A and C of Figure 1 show the proportions over the first eight choices for the focal rat's initial choices (i.e., the first visit to a particular maze location). Because revisits to maze locations are rare during early choices (impossible, in the case of the first choice), revisit proportions are shown (in panels B and D of Figure 1) only for Serial Positions 5–8 of the focal rat's choice sequence. (In the case of all earlier serial positions, there was at least 1 rat that made no revisits at that serial position.) Note that because obtained and expected proportions were determined separately for initial visits and for revisits, the obtained and expected proportions sum to 1.0 at each serial position within each of those two types. As is clear from Figure 1, the expected tendency of visits by the focal rat to locations that had been visited by the nonfocal rat changed substantially as the trial progressed and as the nonfocal rat visited additional

locations. This dynamic is among the reasons why detection of effects of visits by the nonfocal rat requires comparison of the obtained proportion with the expected proportion.

Locations that were the most recent visit of the nonfocal rat and locations visited more remotely in the nonfocal rat's choice sequence are analyzed separately, because the nonfocal rat may have still been physically present in or near the maze arm that it chose most recently. Separation of the effects of more remote choices made by the nonfocal rat allows effects requiring memory to be isolated from effects that can be partially attributed to the physical presence of the nonfocal rat.

In order to allow statistical evaluation, the data were collapsed over the first eight choices of each trial, resulting in the obtained and expected proportions shown in Figure 2. Note that Figure 2 and the ANOVA used to evaluate differences among these proportions do not include the obtained or expected proportions of visits to maze locations not

Figure 2. Mean proportions of maze locations chosen by the focal rat (obtained proportions) and proportions of maze locations available at the time those choices were made (expected proportions) during Experiment 1. These proportions are based on the same counts of choices and maze locations available as the proportions shown in Figure 1, but the counts are collapsed over the first eight choices of each trial. The values shown are the means (over rats) of the resulting proportions for maze locations previously visited by the nonfocal rat. Error bars show one standard error of the mean.

visited by the nonfocal rat (i.e., the data depicted by the circles in Figure 1). The nonindependence of the proportions requires that those proportions not be included in the statistical analyses, because the proportions of locations not visited by the nonfocal rat are complements of the proportions of locations that were visited by the nonfocal rat. The ANOVA compared the obtained proportions with the expected proportion as a function of whether the nonfocal rat's choice was its most recent (or a more remote choice), whether the focal rat had previously chosen the location, and the bait type—that is, a 2 (nonfocal visit status: most recent vs. remote) × 2 (focal visit status: initial visit vs. revisit) × 2 (food type: grain vs. sucrose) × 2 (proportion type: obtained vs. expected) ANOVA. Note that only the factors involving comparisons of the obtained proportion of choices (obtained proportion) and proportion of maze locations (expected proportion) have any theoretical or interpretive meaning, and so only those factors are reported in this article.

The overall proportion of the focal rat's visits to locations previously visited by the nonfocal rat (.146) was greater than the expected proportion [.088; proportion type, $F(1,7) = 27.44$; $p < .05$ is the statistical decision criterion used throughout this article]. There was also a proportion type × focal visit status interaction [$F(1,7) = 10.9$]. The difference between the proportion of locations visited by the nonfocal rat and the proportion of locations available was smaller in the case of the focal rat's initial visits (.102 and .065, respectively) than in the case of its revisits (.189 and .110, respectively). No other significant effects were revealed by the ANOVA.

For the reasons explained below, we also determined the mean serial position of the initial visit to each of the eight maze locations in the sequence of initial visits of each rat. In the (rare) case of a trial in which a rat did not visit all eight locations, the location(s) not visited were assigned a serial position that was the mean of the remaining positions (e.g., if a rat visited only six different locations, the two not visited were both assigned serial positions of 7.5). The mean serial position of each location for each rat is shown in Table 1. Note that a lack of any tendency to choose particular locations would result in mean serial positions of 4.5 for each location. We also determined the

correlations between the mean serial positions of locations for the members of each pair of rats, which are shown in the rightmost column of the table. None of the four correlations is significant, and only one of them is positive.

Discussion

The results of this experiment demonstrate a relationship between visits to locations by 1 rat and the subsequent choices made by another rat during the same trial. Specifically, there was a tendency for the focal rat to selectively visit locations that had been visited earlier in the trial by the nonfocal rat. This is the same tendency that Brown et al. (2007) found for maze locations that were the nonfocal rat's most recent choice. However, Brown et al. (2007) found the opposite tendency: The focal rat avoided visits to maze locations that had been visited more remotely (earlier in the nonfocal rat's choice sequence). A trend in the same direction is suggested by the present pattern of results, in that the tendency for the focal rat to visit locations visited by the nonfocal rat appears to be greater for the most recent choice of the nonfocal rat than for its more remote choices. However, the interaction corresponding to that difference was not significant. There were no significant effects indicating any differences as a function of the type of bait.

Our interest here is in the effect of choices made by 1 rat on those made by the other rat. The tendency of the focal rat to visit locations that had been visited earlier in the trial by the nonfocal rat is consistent with such an effect. However, there is an alternative explanation. It could be that rats in this experiment had similar preferences for the eight maze locations. If so, the tendency of 1 rat to choose locations that had been visited earlier in the trial by the other rat may not have been caused by those visits but, rather, by the common preferences. The serial position of the rats' first visit to each location provides a measure of the relevant preferences. No evidence of correlations between the preferences of the rats tested together was found. Thus, the primary effect cannot be explained in terms of common preferences and, instead, must be a result of the particular choices made by the other rat during each trial.

There is at least one feature of the present experiment that may have limited its ability to detect social memory

Table 1
Mean Serial Order of Initial Visit to Maze Locations in Experiment 1,
and Correlations Between Mean Serial Positions of Locations for Members of Each Pair of Rats

Rat	Maze Location								r
	Arm 1	Arm 2	Arm 3	Arm 4	Arm 5	Arm 6	Arm 7	Arm 8	
1A	2.50	4.35	5.35	4.75	4.75	4.90	4.05	5.35	−.339, n.s.
1B	3.35	4.65	4.90	4.60	5.20	4.75	4.95	3.60	
2A	4.10	5.35	5.65	4.60	4.55	4.60	4.05	3.10	−.330, n.s.
2B	2.20	5.55	4.25	4.60	4.50	5.45	3.95	5.50	
3A	4.90	4.75	5.60	4.50	4.65	2.85	4.40	4.30	.095, n.s.
3B	4.25	3.35	4.90	4.85	4.90	5.65	4.95	4.15	
4A	4.85	4.35	4.45	4.05	4.50	4.20	4.75	4.85	−.444, n.s.
4B	4.70	4.55	3.65	5.25	4.70	4.20	5.30	3.65	
Mean	3.90	4.60	4.80	4.65	4.70	4.45	4.55	4.30	

Note—Correlations were calculated for each pair of rats on the eight maze locations ($n = 8$).

effects. It seems likely that any social effects on spatial choices involve visual observation of the foraging partner. However, the apparatus used in this experiment was not ideal for allowing a rat visual access to the other rat and its choices. Because of the opaque, enclosed maze arms, the rats may have been limited to observing only some of the choices made by their foraging partner, most likely the ones made while the focal rat happened to be in the central arena of the maze. Experiment 2 was designed to overcome this limitation.

EXPERIMENT 2

Experiment 2 involved a maze that was identical to that used in Experiment 1, with one important exception. Specifically, the maze arms were constructed of transparent plastic tubes. Although we do not have independent confirmation, we assume that this material was not only transparent to the human visual system, but also allowed the rats to observe their foraging partners in the maze to a greater extent than was possible in Experiment 1. In Experiment 2, we used the same logic and techniques as we did in Experiment 1, with this modified apparatus and a larger number of subjects.

Method

Subjects. The subjects were 14 experimentally naive, male Sprague Dawley rats, obtained from the same source and maintained in the same manner as were the rats in Experiment 1.

Apparatus. The apparatus was the same as that used in Experiment 1, except that the PVC maze arms were replaced by transparent plastic tubes. These tubes were of the same diameter (10.0 cm) as those used in Experiment 1, but were constructed of 0.9-mm-thick PETG plastic tubing. In addition, the food cups mounted inside the ends of the arms were replaced during testing (see below) by plastic food cups that were mounted on pedestals just beyond the ends of the maze arms. These food cups were constructed of translucent plastic and were 10 cm in diameter and 6.5 cm deep. They included an opaque white plastic lid, in which a 3.5-cm-diameter hole was cut to allow access to the food pellets inside. The cups were baited with a very large number of pellets so that there were always pellets available at the end of every maze arm, even after the rats had visited a maze arm several times.

Procedure. The procedure was the same as that of Experiment 1, except that the trial duration was shortened to 6 min. Testing was conducted in two phases. Each phase consisted of one trial per day for 20 days. During Phase 1, the same food cups that had been used in Experiment 1 were used. We became concerned, however, because the rats tended to scatter food pellets down the length of the maze arms. In response to this concern, the food cups were replaced by the larger food cups described above during Phase 2 of the experiment.

Results

For the data analysis, we followed the same fundamental techniques, logic, and plan as we did in Experiment 1. Data from Phases 1 and 2 were analyzed separately. The pattern of results over the focal rats' choice sequences was similar to that found in Experiment 1. The data are presented below, collapsed over the first eight choices of the focal rat.

Phase 1. Figure 3 shows the data from Phase 1 in the same terms that Figure 2 did for Experiment 1. The (obtained) proportions of the focal rat's visits and the (expected) maze locations available to visit that had been vis-

ited by the nonfocal rat were analyzed using a 2 (nonfocal visit status: most recent vs. remote) $\times$ 2 (focal visit status: initial visit vs. revisit) $\times$ 2 (food type: grain vs. sucrose) $\times$ 2 (proportion type: obtained vs. expected) ANOVA, identical in design to the one used in Experiment 1. As in Experiment 1, the overall proportion of the focal rat's visits to locations previously visited by the nonfocal rat (.151) was greater than the expected proportion of locations that had been visited by the nonfocal rat (.093) [proportion type, $F(1,7) = 65.5$]. The significant interactions involving proportion type were proportion type $\times$ focal visit status [$F(1,13) = 29.5$], proportion type $\times$ food type [$F(1,13) = 32.6$], proportion type $\times$ focal visit status $\times$ food type [$F(1,13) = 35.0$], proportion type $\times$ nonfocal visit status [$F(1,13) = 36.6$], and proportion type $\times$ nonfocal visit status $\times$ focal visit status [$F(1,13) = 33.8$]. The proportion type $\times$ nonfocal visit status $\times$ food type [$F(1,13) = 3.6$] and the proportion type $\times$ nonfocal visit status $\times$ focal visit status $\times$ food type [$F(1,13) = 2.3$] interactions were not significant.
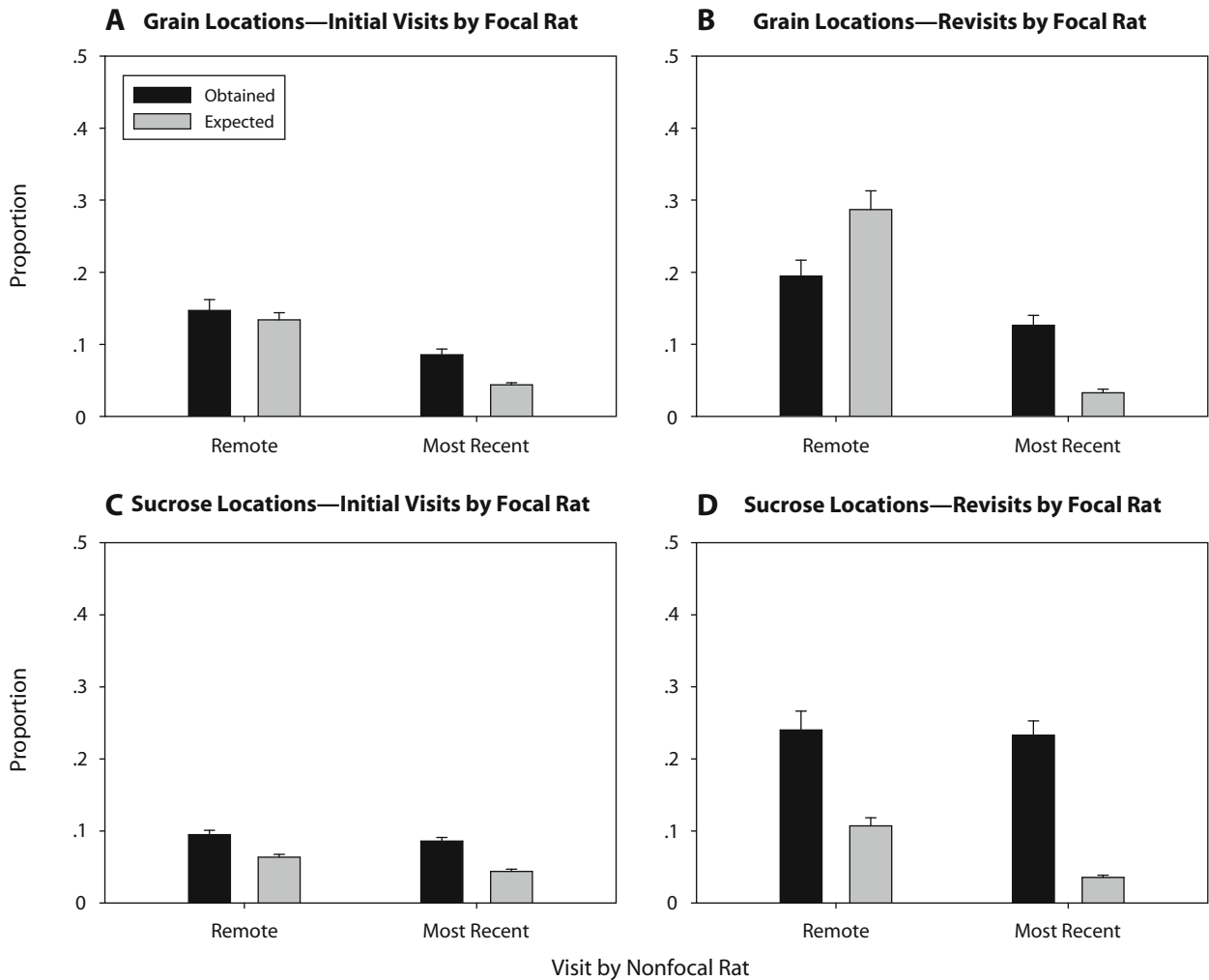
To understand the nature of these interactions, four nonfocal visit status $\times$ proportion type ANOVAs were performed, each corresponding to the results shown in a panel of Figure 3. In the case of the focal rat's initial visits to maze locations that had been previously visited by the nonfocal rat and had been baited with grain pellets (Figure 3A), the obtained proportion was greater than the expected proportion [proportion type, $F(1,13) = 77.5$]. The tendency for the focal rat to visit maze arms that had been visited by the nonfocal rat was greater if the location was the most recent choice of the nonfocal rat, as indicated by a proportion type $\times$ nonfocal visit status interaction [$F(1,13) = 9.8$].

In the case of the focal rat's revisits to maze locations that had been previously visited by the nonfocal rat and had been baited with grain pellets (Figure 3B), the obtained proportion and the expected proportion did not differ significantly [proportion type, $F(1,13) < 1$]. However, there was a proportion type $\times$ nonfocal visit status interaction [$F(1,13) = 18.4$]. The most recent obtained proportion was greater than the most recent expected proportion [$t(1,13) = 5.6$]. On the other hand, the more remote obtained proportion was less than the corresponding expected proportion [$t(1,13) = 3.1$].

In the case of the focal rat's initial visits to maze locations that had been previously visited by the nonfocal rat and had been baited with sucrose pellets (Figure 3C), the obtained proportion was greater than the expected proportion [proportion type, $F(1,13) = 46.0$]. There was no evidence of a difference between most recent and more remote obtained proportions [proportion type $\times$ nonfocal visit status, $F(1,13) < 1$].

In the case of the focal rat's revisits to maze locations that had been previously visited by the nonfocal rat and had been baited with sucrose pellets (Figure 3D), the obtained proportion was greater than the expected proportion [proportion type, $F(1,13) = 49.9$]. The proportion type $\times$ nonfocal visit status interaction was not significant [$F(1,13) = 3.2, p = .10$].

As for Experiment 1, the mean serial position of the initial visit to each of the eight maze locations in the se-

A Grain Locations—Initial Visits by Focal Rat

B Grain Locations—Revisits by Focal Rat

C Sucrose Locations—Initial Visits by Focal Rat

D Sucrose Locations—Revisits by Focal Rat

Visit by Nonfocal Rat

Figure 3. Mean proportions of maze locations chosen by the focal rat (obtained proportions) and proportions of maze locations available at the time those choices were made (expected proportions) during Phase 1 of Experiment 2. These proportions are based on counts of choices and maze locations collapsed over the first eight choices of each trial. The values shown are the means (over rats) of the resulting proportions for maze locations previously visited by the nonfocal rat. Error bars show one standard error of the mean.

quence of initial visits was determined for each rat. Those values are shown in Table 2, as are the correlations between the mean serial positions for the rats in each pair. The mean serial positions were significantly correlated for two pairs of rats. The r value was positive for six of the seven pairs of rats.

Phase 2. Figure 4 shows the mean obtained and expected proportions during Phase 2. The same analyses used for the data from Phase 1 were used for that from Phase 2, and the pattern of results obtained was very similar.

The overall obtained proportion (.157) was greater than the expected proportion for locations that had been previously visited by the nonfocal rat (.091) [proportion type, $F(1,7) = 172.0$]. The significant interactions involving proportion type were proportion type $\times$ focal visit status [$F(1,13) = 54.5$], proportion type $\times$ food type [$F(1,13) = 62.9$], proportion type $\times$ focal visit status $\times$ food type [$F(1,13) = 87.2$], proportion type $\times$ nonfocal visit status

[$F(1,13) = 27.5$], proportion type $\times$ nonfocal visit status $\times$ focal visit status [$F(1,13) = 39.3$], and proportion type $\times$ nonfocal visit status $\times$ focal visit status $\times$ food type [$F(1,13) = 6.0$]. The proportion type $\times$ nonfocal visit status $\times$ food type interaction did not reach significance [$F(1,13) = 3.9, p = .07$].

To understand the nature of these interactions, four nonfocal visit status $\times$ proportion type ANOVAs were performed, each corresponding to the results shown in a panel of Figure 4. In the case of initial visits to maze locations baited with grain pellets (Figure 4A), the obtained proportion was greater than the expected proportion for maze locations that had been visited by the nonfocal rat [proportion type, $F(1,13) = 51.8$]. There was no evidence of a difference between the most recent and more remote obtained proportions [proportion type $\times$ nonfocal visit status, $F(1,13) < 1$].

In the case of the focal rat's revisits to maze locations that had been previously visited by the nonfocal rat and

Table 2
Mean Serial Order of Initial Visit to Maze Locations in Experiment 2, Phase 1,
and Correlations Between Mean Serial Positions of Locations for Members of Each Pair of Rats

| Rat | Maze Location | | | | | | | | r |
	Arm 1	Arm 2	Arm 3	Arm 4	Arm 5	Arm 6	Arm 7	Arm 8	
1A	2.50	4.00	4.80	3.52	4.28	2.04	3.60	4.12	.277, n.s.
1B	3.72	4.12	3.88	3.04	3.44	3.36	3.80	3.44	
2A	2.84	3.88	3.44	3.22	3.96	3.56	4.02	3.88	−.208, n.s.
2B	3.92	4.24	3.44	3.60	2.80	3.52	3.88	3.40	
3A	3.16	4.52	3.68	2.32	2.92	3.36	4.36	4.48	.672, n.s.
3B	2.60	4.04	3.92	2.96	4.00	2.84	4.40	4.04	
4A	3.32	3.04	3.08	3.04	3.64	3.60	4.20	4.88	.483, n.s.
4B	2.64	3.58	3.04	3.96	4.20	3.36	4.00	4.06	
5A	2.16	4.50	4.10	4.00	3.54	2.08	3.94	4.48	.542, n.s.
5B	3.86	3.92	3.80	2.88	3.78	2.34	3.68	4.54	
6A	3.08	3.76	3.64	3.36	3.44	2.24	4.24	5.04	.815, $p < .05$
6B	2.32	4.68	3.36	2.60	3.68	2.80	4.16	5.20	
7A	2.36	3.76	4.40	2.88	3.96	2.16	4.20	5.08	.857, $p < .01$
7B	3.20	3.60	3.64	3.20	4.28	2.92	3.60	4.36	
Mean	2.98	3.97	3.73	3.18	3.71	2.87	4.01	4.36	

Note—Correlations were calculated for each pair of rats on the eight maze locations ($n = 8$).

had been baited with grain pellets (Figure 4B), the obtained proportion and the expected proportion did not differ significantly [proportion type, $F(1,13) = 2.0$]. However, there was a proportion type × nonfocal visit status interaction [$F(1,13) = 29.2$]. The most recent obtained proportion was greater than the most recent expected proportion [$t(1,13) = 5.4$]. On the other hand, the more remote obtained proportion was less than the corresponding expected proportion [$t(1,13) = 4.0$].

In the case of the focal rat's initial visits to maze locations that had been previously visited by the nonfocal rat and had been baited with sucrose pellets (Figure 4C), the obtained proportion was greater than the expected proportion [proportion type, $F(1,13) = 51.5$]. There was no evidence of a difference between the most recent and more remote obtained proportions [proportion type × nonfocal visit status, $F(1,13) < 1$].

In the case of the focal rat's revisits to maze locations that had been previously visited by the nonfocal rat and had been baited with sucrose pellets (Figure 4D), the obtained proportion was greater than the expected proportion [proportion type, $F(1,13) = 177.4$]. The proportion type × nonfocal visit status interaction was not significant [$F(1,13) = 3.4$, $p = .09$].

The mean serial positions of the initial visit to each of the eight maze locations are shown in Table 3, as are the correlations between the mean serial positions for the rats in each pair. The mean serial positions were significantly correlated for one pair of rats. The r value was positive for six of the seven pairs of rats.

Discussion

As in Experiment 1, there was a general tendency for the focal rat to visit maze locations that had been visited earlier in the trial by the nonfocal rat. However, for maze locations that had been visited earlier in the trial by the focal rat (i.e., revisits), this tendency was jointly modulated by the recency of the nonfocal rat's visit and by the type of food available in the location.

The most critical and telling result is that, in the case of maze arms baited with grain pellets revisited by the focal rat, there was a tendency for the focal rat to visit such a location if it was the most recent choice of the nonfocal rat, but there was a tendency for the focal rat to avoid visiting such a location if it had been visited by the nonfocal rat more remotely in the nonfocal rat's choice sequence. Thus, the general tendency that was revealed in both experiments for rats to visit locations that had been visited by the foraging partner was violated in the case of a previously visited arm that contained the less preferred food.

In contrast to the results of Experiment 1, there was some indication in the present experiment that the rats in each pair had similar preferences for particular maze arms, as revealed by the mean serial positions of their initial visits to the maze arms. Although the correlation of mean serial positions of initial visits was significant for only two of the seven pairs of rats during Phase 1 and for one pair of rats during Phase 2, the correlations had a positive value in both phases for all but one pair. Thus, it may be that part of the overall tendency for the focal rat to visit locations that had been visited earlier in the trial by the nonfocal rat resulted from the commonality of these preferences. However, it is difficult to interpret the meaning of this correlation, because it could be produced either by similar preferences for maze locations or by preferences on the part of 1 rat that influenced the choices made by its foraging partner. In any case, the tendency for the focal rat to avoid locations that had been visited earlier in the trial by the nonfocal rat cannot be explained in this manner (and, in fact, must overcome any commonality of location preferences in order to be expressed and detected). This tendency to avoid the locations visited by the other rat was found by Brown et al. (2007) and was also found—under a particular set of conditions—in the present experiment.
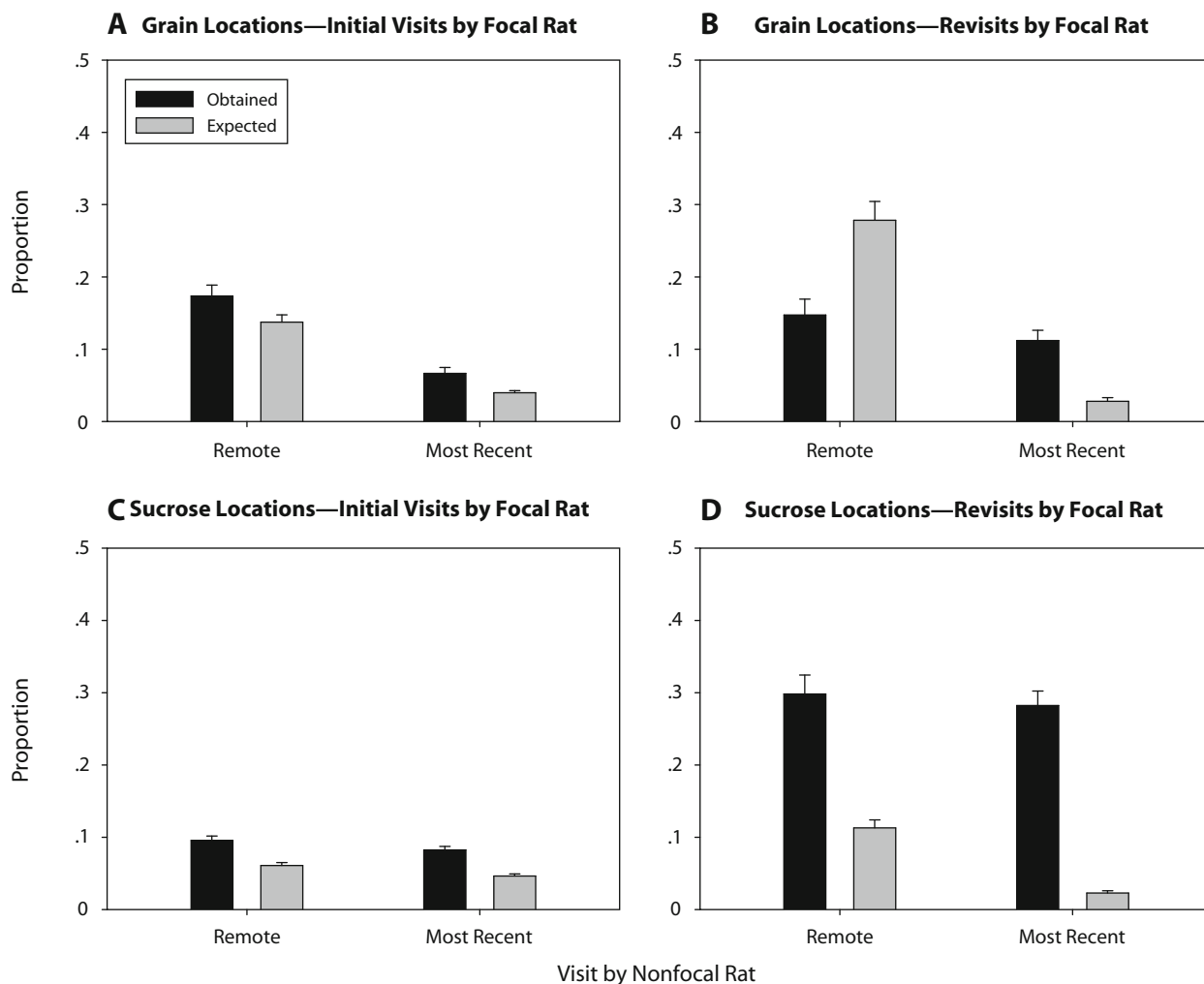
Figure 4. Mean proportions of maze locations chosen by the focal rat (obtained proportions) and proportions of maze locations available at the time those choices were made (expected proportions) during Phase 2 of Experiment 2. These proportions are based on counts of choices and maze locations collapsed over the first eight choices of each trial. The values shown are the means (over rats) of the resulting proportions for maze locations previously visited by the nonfocal rat. Error bars show one standard error of the mean.

GENERAL DISCUSSION

Brown et al. (2007) found a tendency for focal rats to visit the maze location most recently visited by the other rat. Because the nonfocal rat is often physically present in or near the maze arm it most recently visited, this can be attributed to an attractive effect of the foraging partner as a social stimulus. Brown et al. (2007) also found a tendency for rats to avoid maze locations that were visited earlier in the other rat's choice sequence. They argued that an effect of the nonfocal rat's earlier choices requires social working memory. A tendency for a rat to avoid locations chosen by the other rat was supported by the contingencies in their experiment. In particular, locations visited by the nonfocal rat were no longer baited. Under most conditions in the present experiment, there was a tendency for the focal rat to visit locations that had been visited by the nonfocal rat, regardless of whether they were the nonfocal rat's most recent choice or had been chosen by the nonfocal rat ear-

lier in the trial. This difference between the results of the present experiments and those of Brown et al. (2007) can be understood in terms of the different contingencies between previous visits and the presence of food in the two cases. In the present experiments, food was not depleted by visits to maze locations and so revisits to locations (that had been previously visited either by the focal rat or by the nonfocal rat) resulted in food reinforcement.

A tendency for a rat to visit locations that were previously visited by a foraging partner could be due to common preferences for locations, rather than to social effects. This possibility was examined in both experiments by determining the order in which the eight maze locations were first chosen by each rat and comparing the maze-arm preferences indicated thereby. Generally, there were not strong preferences for particular maze locations on the part of individual rats in either experiment (most of the mean ranks were close to the chance value of 4.5). In Experiment 1, there was no evidence that the preferences of the pairs of

Table 3
Mean Serial Order of Initial Visit to Maze Locations in Experiment 2, Phase 2,
and Correlations Between Mean Serial Positions of Locations for Members of Each Pair of Rats

Rat	Maze Location								
	Arm 1	Arm 2	Arm 3	Arm 4	Arm 5	Arm 6	Arm 7	Arm 8	r
1A	3.50	5.70	5.60	5.00	3.90	3.80	3.95	4.40	.465, n.s.
1B	3.45	5.30	5.55	3.45	3.60	5.25	4.70	4.75	
2A	3.80	5.80	4.20	3.90	4.60	5.10	4.00	4.50	$-.063$, n.s.
2B	4.90	6.00	4.70	4.10	3.50	1.70	5.20	5.90	
3A	3.40	5.30	4.60	3.00	5.55	4.40	4.85	5.00	.565, n.s.
3B	3.60	5.95	4.80	4.25	5.10	4.20	3.10	5.00	
4A	4.05	4.10	3.85	4.40	5.00	4.60	5.05	4.95	.494, n.s.
4B	3.60	4.30	4.65	4.85	5.20	4.15	4.80	4.45	
5A	3.65	5.70	4.95	4.70	4.70	2.85	3.90	5.50	.867, $p < .05$
5B	3.40	5.20	5.60	4.20	4.60	2.70	4.80	5.50	
6A	3.80	5.30	6.30	4.50	3.95	3.40	4.25	4.50	.690, $p = .06$
6B	3.20	5.75	5.20	4.25	3.35	3.55	5.05	5.70	
7A	3.20	5.60	4.90	3.50	4.40	3.00	5.10	6.30	.627, $p = .10$
7B	3.55	5.20	5.50	4.60	4.45	3.50	4.85	4.35	
Mean	3.60	5.40	5.00	4.20	4.40	3.70	4.50	5.00	

Note—Correlations were calculated for each pair of rats on the eight maze locations ($n = 8$).

rats tested together corresponded. In Experiment 2, there was some correspondence between the preferences exhibited by the rats tested together. Thus, at least part of the tendency for the focal rat to choose locations visited by the nonfocal rat in Experiment 2 can be attributed to common preferences for particular maze locations.

Although there was a general tendency for the focal rat to visit maze locations that had been visited by the nonfocal rat, there was also a clear exception. In Experiment 2, earlier visits by the nonfocal rat to locations containing grain pellets resulted in a reduced tendency for the focal rat to revisit that location. Each of the four factors involved in this exception is revealing. First, avoidance was produced by the nonfocal rat's visits only if the maze location contained grain pellets. Given that grain pellets are the less preferred of the two food types available in the experiment, this suggests that rats were avoiding visits to maze locations on the basis of the value of the food type available there. Related to this is the fact that the focal rat's avoidance of grain locations visited by the nonfocal rat was found only for maze locations that had also been visited earlier in the trial by the focal rat. This restriction of the avoidance tendency can be understood if a previous visit by the focal rat is necessary to determine which of the two food types is present there. The restriction indicates that the focal rat is controlled by the nature of the food present on an arm in addition to the location of the arm. Third, comparison of the results of Experiments 1 and 2 indicates that the additional visibility afforded by the transparent arms allowed the rats to acquire information about the choices of their foraging partner that allowed maze arms chosen by the foraging partner to be later avoided. There was no indication of the critical result under consideration in Experiment 1. Finally, the focal rat did not avoid the nonfocal rat's most recently visited location, but only the location visited more remotely in the nonfocal rat's choice sequence. This is consistent with Brown et al.'s (2007) conclusion that the physical pres-

ence of the nonfocal rat produces a social facilitation effect, regardless of other factors determining the effects of social memories.

These results show that the spatial choices made by 1 rat in a radial-arm maze affect the spatial choices subsequently made by a second rat. This finding replicates the earlier ones of Brown et al. (2007). The form of the effect varied across the experiments. In Brown et al.'s (2007) experiments, rats consistently tended to visit the maze location more recently visited by the other rat but to avoid maze locations visited earlier in the trial by that other rat. In both of the present experiments, there was the same tendency for the focal rat to visit the location most recently visited by the nonfocal rat. Because the nonfocal rat was often still physically present in or near its most recent choice, this effect can be explained as social facilitation by the presence of the nonfocal rat (Galef et al., 1987; Galef & Wigmore, 1983). The focal rat's choices were also consistently influenced by temporally remote observations of the nonfocal rat's choices, but the direction of the effect varied for reasons that we do not yet fully understand.

Consider the possible roles of odor cues in the present experiments. Odor cues cannot provide information about the presence of food on maze arms in these experiments, because food was always present on every arm. It is possible a priori that odor from the food pellets might provide information about the type of food present on each maze arm. However, there is no indication in the data from either experiment that initial choices were more likely to be directed to sucrose locations than to grain locations. Different tendencies to visit grain and sucrose locations occurred only when the focal rat had previously visited the location (during these visits, it almost always consumed pellets from that location). Odor cues provided by the rats should also be considered. That rats avoided revisits to arms that they had visited themselves using odor cues is extremely unlikely, given the numerous experiments that

have ruled out the use of such odor trails in the radial maze (Foreman & Ermakova, 1998). The use of odor left by the other rat was carefully evaluated by Brown et al. (2007) as an alternative to social memory for providing information about the location of maze arms chosen earlier in the trial by the nonfocal rat. Brown et al. (2007) ruled out that possibility by rotating the maze either during a short break while two rats chose freely among the arms of the maze (Brown et al., 2007, Experiment 1) or between the time that a focal rat observed the choices of another rat and the time it made choices itself (Brown et al., 2007, Experiment 3). In both cases, choices were controlled by the spatial location that had been chosen by the nonfocal rat and not by the presence of odor from the nonfocal rat (on maze arms rotated into new spatial locations).

One remaining possibility is that odor cues produced by the nonfocal rat might provide information about the type of food available in different maze locations. This possibility is encouraged by the earlier findings of Galef and Wigmore (1983), who showed that odor cues produced by food eaten by 1 rat served as a cue to a second rat that the corresponding food was available. If the second rat had previously learned the location of that food (by visiting it), the odor cues provided by the first rat increased the tendency of the second rat to revisit that location. A corresponding use of odor information about the identity of food available in maze locations in the present experiments would be more challenging, because the rats visited maze arms containing both kinds of food (and ate both kinds of food) during each trial. Furthermore, the results of Experiment 2 showed that the type of food in a maze location affected the tendency to visit that location only if the focal rat had already visited the maze location (i.e., the data from revisits shown in panels B and D of Figures 3 and 4). As detailed below, this strongly suggests that information about the type of food available in maze locations comes not from the nonfocal rat but, rather, from information obtained by the focal rat when it visited the location earlier during the trial.

Consideration of the present results, together with those reported by Brown et al. (2007), indicates that there are at least two factors involved in determining the effects of social memories on spatial choices. The first is the outcome of a visit to an arm location. In the earlier experiments of Brown et al. (2007), the typical win–shift contingency was in force. In the present experiments, there was no contingency between visits and presence of food on maze arms (neither win–shift nor win–stay; Gaffan & Davies, 1981; Olton & Schlosberg, 1978). Rats are known to have a tendency to avoid revisits to maze locations, despite nondifferential reinforcement of arm choices when food is not provided on any arms (FitzGerald et al., 1985; Timberlake & White, 1990) or when the food available in maze arms is devalued (Sage & Knowlton, 2000). Similarly, rats in the present experiments tended to avoid revisits to maze arms when food was available on all maze arms, regardless of previous visits. The nondifferential presence of food in maze locations, regardless of previous visits, may be responsible, at least in part, for the facilitation of the focal rat's choice tendencies by remembered visits of the nonfocal rat.

The second factor that appears to be involved in determining the effect of social memories of spatial choice is the hedonic properties of the food available in particular maze locations. Because the locations baited with grain and sucrose pellets varied unpredictably from trial to trial, information about the type of food available in maze locations had to be obtained within each trial. There are two possible sources of such information: previous visits by the focal rat itself and information obtained socially following visits by the nonfocal rat. Critically, maze locations previously visited and containing the less preferred grain pellets were the one case in which a visit by the nonfocal rat resulted in a decreased tendency for the focal rat to subsequently revisit that maze location. Thus, the focal rat's choices were affected both by the location of choices previously made by the other rat and by the identity of the food in that location. The fact that the focal rat's avoidance of locations visited by the nonfocal rat and containing the less preferred food occurs only in the case of locations visited earlier in the trial by the focal rat indicates that this choice is based on the focal rat's own previous visit to that location, rather than on information obtained socially. In turn, this indicates that information from the memory of the focal rat's own previous visit (the type of food) is combined with information obtained from the memory for the nonfocal rat's visit (the location).

The mechanism producing this interaction between memories for the focal rat's own behavior and memories for the nonfocal rat's behavior is unclear. One possibility is that the observed visit by the nonfocal rat to a maze location reactivates (Spear & Parsons, 1976) memory of the focal rat's own visit to that location, which includes the identity of the food. Another is that memory of the nonfocal rat's visits, combined with information about the identity of food in specific maze arms, may modulate tendencies to visit maze locations via social enhancement processes of the sort described by Galef and colleagues (e.g., Galef & Whiskin, 2003; Galef, Whiskin, & Bielavska, 1997).

The present work extends Brown et al.'s (2007) demonstration of working memory for the spatial choices of familiar conspecifics in two primary directions. First, these experiments show that memory for the spatial choices of a familiar conspecific can either decrease or increase the tendency to visit spatial locations. The present experiments provide information about the factors involved in determining which effect occurs; however, the mechanisms involved remain to be resolved. Second, information in a rat's working memory about the spatial choices of another rat is combined with information in working memory obtained during the focal rat's own visits to the same location. It seems reasonable to expect that information in working memory about the behavior of others would commonly need to be combined with other kinds of dynamic information. The present pattern of results is a starting point for examining such processes. In this context, we think that the study of social working memory may lead to important insights about the mechanisms, function, and evolution of memory processes and the relations between memory and social behavior.

REFERENCES

Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, **29**, 543-550.

Brown, M. F. (1992). Does a cognitive map guide choices in the radial-arm maze? *Journal of Experimental Psychology: Animal Behavior Processes*, **18**, 56-66.

Brown, M. F., & Cook, R. G. (Eds.) (2006). *Animal spatial cognition: Comparative, neural, and computational approaches* [On-line]. Available: www.pigeon.psy.tufts.edu/asc/.

Brown, M. F., Farley, R. F., & Lorek, E. J. (2007). Remembrance of places you passed: Social spatial working memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, **33**, 213-224.

Brown, M. F., Rish, P. A., VonCulin, J. E., & Edberg, J. A. (1993). Spatial guidance of choice behavior in the radial-arm maze. *Journal of Experimental Psychology: Animal Behavior Processes*, **19**, 195-214.

Cook, R. G., Brown, M. F., & Riley, D. A. (1985). Flexible memory processing by rats: Use of prospective and retrospective information in the radial maze. *Journal of Experimental Psychology: Animal Behavior Processes*, **11**, 453-469.

Dember, W. N., & Richman, C. L. (1989). *Spontaneous alternation behavior*. New York: Springer.

FitzGerald, R. E., Isler, R., Rosenberg, E., Oettinger, R., & Bättig, K. (1985). Maze patrolling by rats with and without food reward. *Animal Learning & Behavior*, **13**, 451-462.

Foreman, N., & Ermakova, I. (1998). The radial arm maze: Twenty years on. In N. Foreman & R. Gillett (Eds.), *Handbook of spatial research paradigms and methodologies* (Vol. 2, pp. 87-143). Hove, U.K.: Psychology Press.

Gaffan, E. A., & Davies, J. (1981). The role of exploration in win–shift and win–stay performance on a radial maze. *Learning & Motivation*, **12**, 282-299.

Galef, B. G., Jr., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour*, **61**, 3-15.

Galef, B. G., Jr., & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *Bioscience*, **55**, 489-500.

Galef, B. G. [Jr.], Mischinger, A., & Malenfant, S. A. (1987). Hungry rats' following of conspecifics to food depends on the diets eaten by potential leaders. *Animal Behaviour*, **35**, 1234-1239.

Galef, B. G., Jr., & Whiskin, E. E. (2003). Socially transmitted food preferences can be used to study long-term memory in rats. *Learning & Behavior*, **31**, 160-164.

Galef, B. G., Jr., Whiskin, E. E., & Bielavska, E. (1997). Interaction with demonstrator rats changes observer rats' affective responses to flavors. *Journal of Comparative Psychology*, **111**, 393-398.

Galef, B. G., Jr., & Wigmore, S. W. (1983). Transfer of information concerning distant foods: A laboratory investigation of the "information-centre" hypothesis. *Animal Behaviour*, **31**, 748-758.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Oxford University Press.

Olton, D. S. (1978). Characteristics of spatial memory. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior* (pp. 341-374). Hillsdale, NJ: Erlbaum.

Olton, D. S., & Samuelson, R. J. (1976). Remembrance of places passed: Spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, **2**, 97-116.

Olton, D. S., & Schlosberg, P. (1978). Food-searching strategies in young rats: Win–shift predominates over win–stay. *Journal of Comparative & Physiological Psychology*, **92**, 609-618.

Poucet, B. (1993). Spatial cognitive maps in animals: New hypotheses on their structure and neural mechanisms. *Psychological Review*, **100**, 163-182.

Sage, J. R., & Knowlton, B. J. (2000). Effects of US devaluation on win–stay and win–shift radial maze performance in rats. *Behavioral Neuroscience*, **114**, 295-306.

Spear, N. E., & Parsons, P. J. (1976). Analysis of a reactivation treatment: Ontogenetic determinants of alleviated forgetting. In D. L. Medin, W. A. Roberts, & R. T. Davis (Eds.), *Processes of animal memory* (pp. 135-166). Hillsdale, NJ: Erlbaum.

Timberlake, W., & White, W. (1990). Winning isn't everything: Rats need only food deprivation and not food reward to efficiently traverse a radial arm maze. *Learning & Motivation*, **21**, 153-163.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, **55**, 189-208.

APPENDIX
Calculation of Obtained and Expected Proportions

For each rat, each of the first eight choices made was categorized in terms of choice number, whether it was the focal rat's first visit to that location (initial visit) or was a revisit to a location visited earlier during the trial, whether it was a location containing grain or sucrose pellets, and in terms of the visit status of the nonfocal rat (not visited by the nonfocal rat, the location most recently visited, or a location that was visited earlier [remotely] in the nonfocal rat's choice sequence). Each of these categories corresponds to a cell in Table A1. Furthermore, for each choice made, each of the eight locations in the maze was categorized (in terms of the same variables) into the corresponding categories shown in Table A2. Thus, each choice made by the focal rat resulted in one addition to one of the categories in Table A1 and eight additions to categories in Table A2.

Table A1
Categories of Choices Made by Focal Rat

| | Initial Visit to Location | | | | | | Revisit of Location | | | | | |
| | Grain Locations | | | Sucrose Locations | | | Grain Locations | | | Sucrose Locations | | |
Choice Number	Not Visited by Nonfocal Rat	Most Recent Visit of Nonfocal Rat	More Remote Visit of Nonfocal Rat	Not Visited by Nonfocal Rat	Most Recent Visit of Nonfocal Rat	More Remote Visit of Nonfocal Rat	Not Visited by Nonfocal Rat	Most Recent Visit of Nonfocal Rat	More Remote Visit of Nonfocal Rat	Not Visited by Nonfocal Rat	Most Recent Visit of Nonfocal Rat	More Remote Visit of Nonfocal Rat
1	IGN_1	IGM_1	IGE_1	ISN_1	ISM_1	ISE_1	*	*	*	*	*	*
2	IGN_2	IGM_2	IGE_2	ISN_2	ISM_2	ISE_2	RGN_2	RGM_2	RGE_2	RSN_2	RSM_2	RSE_2
3	IGN_3	IGM_3	IGE_3	ISN_3	ISM_3	ISE_3	RGN_3	RGM_3	RGE_3	RSN_3	RSM_3	RSE_3
4	IGN_4	IGM_4	IGE_4	ISN_4	ISM_4	ISE_4	RGN_4	RGM_4	RGE_4	RSN_4	RSM_4	RSE_4
5	IGN_5	IGM_5	IGE_5	ISN_5	ISM_5	ISE_5	RGN_5	RGM_5	RGE_5	RSN_5	RSM_5	RSE_5
6	IGN_6	IGM_6	IGE_6	ISN_6	ISM_6	ISE_6	RGN_6	RGM_6	RGE_6	RSN_6	RSM_6	RSE_6
7	IGN_7	IGM_7	IGE_7	ISN_7	ISM_7	ISE_7	RGN_7	RGM_7	RGE_7	RSN_7	RSM_7	RSE_7
8	IGN_8	IGM_8	IGE_8	ISN_8	ISM_8	ISE_8	RGN_8	RGM_8	RGE_8	RSN_8	RSM_8	RSE_8

Note—I, initial visits by focal rat; R, revisits by focal rat; G, visits to grain locations; S, visits to sucrose locations; N, visits by focal rat to locations not previously visited by other rat; M, visits by focal rat to locations most recently visited by other rat; E, visits by focal rat to locations visited earlier in other rat's choice sequence (i.e., not its most recent choice).   *Revisits are not possible for first choice. Analysis did not include choices beyond eighth choice.

Table A2
Categories of Locations Available When Choices Made by Focal Rat

| | Locations Not Visited by Focal Rat | | | | | | Locations Previously Visited by Focal Rat | | | | | |
| | Grain Locations | | | Sucrose Locations | | | Grain Locations | | | Sucrose Locations | | |
Choice Number	Not Visited by Nonfocal Rat	Most Recent Visit of Nonfocal Rat	More Remote Visit of Nonfocal Rat	Not Visited by Nonfocal Rat	Most Recent Visit of Nonfocal Rat	More Remote Visit of Nonfocal Rat	Not Visited by Nonfocal Rat	Most Recent Visit of Nonfocal Rat	More Remote Visit of Nonfocal Rat	Not Visited by Nonfocal Rat	Most Recent Visit of Nonfocal Rat	More Remote Visit of Nonfocal Rat
1	ign_1	igm_1	ige_1	isn_1	ism_1	ise_1	*	*	*	*	*	*
2	ign_2	igm_2	ige_2	isn_2	ism_2	ise_2	rgn_2	rgm_2	rge_2	rsn_2	rsm_2	rse_2
3	ign_3	igm_3	ige_3	isn_3	ism_3	ise_3	rgn_3	rgm_3	rge_3	rsn_3	rsm_3	rse_3
4	ign_4	igm_4	ige_4	isn_4	ism_4	ise_4	rgn_4	rgm_4	rge_4	rsn_4	rsm_4	rse_4
5	ign_5	igm_5	ige_5	isn_5	ism_5	ise_5	rgn_5	rgm_5	rge_5	rsn_5	rsm_5	rse_5
6	ign_6	igm_6	ige_6	isn_6	ism_6	ise_6	rgn_6	rgm_6	rge_6	rsn_6	rsm_6	rse_6
7	ign_7	igm_7	ige_7	isn_7	ism_7	ise_7	rgn_7	rgm_7	rge_7	rsn_7	rsm_7	rse_7
8	ign_8	igm_8	ige_8	isn_8	ism_8	ise_8	rgn_8	rgm_8	rge_8	rsn_8	rsm_8	rse_8

Note—i, locations not previously visited by focal rat; r, locations previously visited by focal rat; g, grain locations; s, sucrose locations; n, locations not previously visited by other rat; m, locations most recently visited by other rat; e, locations visited earlier in other rat's choice sequence (i.e., not its most recent choice).   *Locations previously visited do not exist during first choice. Analysis did not include choices beyond eighth choice.

The obtained empirical proportions of the focal rat's visits to locations that had been visited by the nonfocal rat were determined using the counts in the categories in Table A1. Equation A1 is an example; specifically, the proportion of initial choices to grain locations that were in the location most recently visited by the nonfocal rat. For each category represented by the cells of Table A1, a corresponding proportion was calculated. Note that the proportions are determined separately for initial choices (the first visit to a particular location by the focal rat) and for revisits.

$$p(IGM_n) = IGM_n/(IGN_n + IGM_n + IGE_n + ISN_n + ISM_n + ISE_n) \tag{A1}$$

In addition, a corresponding proportion of the maze locations available when choices were made (the expected proportion) was calculated. Equation A2 is the example corresponding to Equation A1. The proportions represented by Equations A1 and A2 were calculated separately for each serial position in the focal rat's choice sequence. The means (over rats) shown in Figure 1 are based

APPENDIX (Continued)

on these proportions, which provide an estimate of the values expected, assuming that the focal rat's choices are not controlled by the behavior of the nonfocal rat.

$$p(\text{igm}_n) = \text{igm}_n/(\text{ign}_n + \text{igm}_n + \text{ige}_n + \text{isn}_n + \text{ism}_n + \text{ise}_n) \tag{A2}$$

Equations A3 and A4 are examples of the obtained and expected proportions, respectively, collapsed over the focal rat's first eight choices (the examples are for the proportion of revisits that are to sucrose locations visited earlier in the nonfocal rat's choice sequence). The means (over rats) shown in Figures 2, 3, and 4 and used in all of the statistical analyses are based on these proportions.

$$P(\text{RSM}) = \frac{\sum_{i=1}^{8} \text{RSM}_i}{\left(\sum_{i=1}^{8} \text{RGN}_i + \sum_{i=1}^{8} \text{RGM}_i + \sum_{i=1}^{8} \text{RGE}_i + \sum_{i=1}^{8} \text{RSN}_i + \sum_{i=1}^{8} \text{RSM}_i + \sum_{i=1}^{8} \text{RSE}_i \right)} \tag{A3}$$

$$P(\text{rsm}) = \frac{\sum_{i=1}^{8} \text{rsm}_i}{\left(\sum_{i=1}^{8} \text{rgn}_i + \sum_{i=1}^{8} \text{rgm}_i + \sum_{i=1}^{8} \text{rge}_i + \sum_{i=1}^{8} \text{rsn}_i + \sum_{i=1}^{8} \text{rsm}_i + \sum_{i=1}^{8} \text{rse}_i \right)} \tag{A4}$$