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Social Influences on Rat Spatial Choice

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Although there is abundant evidence for social learning and other forms of social influence on behavior, relatively little experimental analysis of the mechanisms involved is available. The present paper reviews a line of research examining social influences on spatial choice in the context of spatial working memory paradigms using pairs of laboratory rats foraging together for food. There is a social affiliation effect – rats are attracted to spatial locations if a familiar conspecific is there. However, there is a countervailing tendency to avoid visits to spatial locations that were previously depleted of food by the other rat. The latter effect is based on working memory for the choices made previously by the other rat. The memories for the previous choices of another rat can affect subsequent choices flexibly, either increasing or decreasing choice tendencies depending on working memory for the contents of spatial locations resulting from the rat's own visits to the location.

Keywords: social memory; social learning; working memory; spatial memory

The ability to navigate in space is critical to the survival of most animals and it has therefore received much attention in biology and psychology. The means by which animals navigate and represent spatial properties of the world have been investigated from several perspectives, including behavioral ecology (e.g., Boinski & Garber, 2000; Dyer, 1998) and neuroscience (e.g., Thinus-Blanc, 1996; Jeffery, 2003) as well as comparative cognition. The work of psychologists studying spatial cognition in animals has been concerned almost exclusively with memories corresponding to physical stimuli (goal locations, spatial cues) or memories produced by the subject animal's own behavior (Gallistel, 1990). Much of the work on spatial memory, for example, involves memory for previous visits to goal locations (Olton, 1978), routes taken to find a goal location or explore a space (Collett, Collett, Bisch, & Wehner, 1998), or anticipated movements through (or choices to be made in) space (Cook, Brown, & Riley, 1985). Psychological analyses of other (i.e., non-spatial) forms of animal memory have also been concerned with memories of either physical stimuli or the animal's own behavior.

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Important elements of most animals' world, it would seem, include the existence, characteristics, and behavior of conspecifics. Although many animals live in relative isolation, many others often interact with members of their own species in critically important ways. Given the importance of social interaction, one would expect that the behavior of others serves as the content of many memories and that such social memory would be an important part of our investigations of animal memory. However, despite increasing evidence that learning from other individuals is important for many animals (e.g., Galef & Laland, 2005), very little is known about the properties or mechanisms of memory for the behavior of others.

Many animals forage in groups, including the rats and pigeons that are the most common non-human subjects in psychology laboratories. Researchers concerned with natural foraging behavior have developed a variety of ideas about the adaptive function of social foraging and the variables that affect it (for reviews, see Galef & Giraldeau, 2001; Kendal, Galef, & van Schaik, 2010). For example, group foraging is generally believed to produce a fundamental trade off. It provides the benefit of increasing the chances that new sources of food will be discovered and/or successfully procured, but at the cost of having to compete with others for access to that food. Many models of social foraging make predictions about the tendency of species to forage socially and the size

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of foraging groups based on this trade off (Giraldeau, 2000). Other theoretical models suggest that animals will adopt different strategies for foraging successfully, depending on social conditions. For example, the "Producer-Scrounger" model (Barnard & Sibly, 1981) predicts that animals distribute themselves between two behavioral modes. Some individuals focus their efforts on food procurement ("producers") while others focus on finding other animals who are feeding, thereby locating patches of food ("scroungers"). According to the model, an individual will engage in producer or scrounger behavior, depending on the proportion of producers and scroungers currently foraging and the concentration of food sources in the environment. Other models predict the spatial or temporal distribution of foragers in a group. The dominant model of this type is the "Ideal Free Distribution" (Fretwell & Lucas, 1970) which predicts that animals will distribute themselves among patches of a resource in proportion to the relative amount (or rate) of the resource available in particular patches. This prediction is based on the fact that the amount of food that can be obtained from a particular patch is a function of the number of foragers currently in the patch, as well as the amount of food in the patch.

These and other ideas about the ecological factors affecting social foraging clearly suggest the use of cognitive processes used to detect, remember, and process information about the behavior of others. Such cognitive processes may be the same ones involved in detecting, remembering, and processing information about physical stimuli, which have been the subject of much empirical and theoretical attention from comparative cognitive psychologists. However, it also seems quite possible that some of the processes involved in social memory & cognition are unique, as has been argued to be the case in both humans (e.g., Fodor, 1983; Pinker, 1997) and non-human animals (e.g., Lefebvre & Giraldeau, 1996). Surprisingly, there have been very few empirical studies conducted by comparative cognitive psychologists in which the behavior of another animal served as the to-be-remembered stimulus. Thus, we do not have the information necessary to determine whether there are learning and memory systems that are specialized for such social memories. Although it seems clear that animals must form and use memories of the behavior of others, there is very little systematic evidence that provides confirmation of the existence of memories with social content, let alone empirical analyses of their properties.

One important exception to the lack of knowledge regarding social aspects of animal cognition is an extensive literature on imitative learning (for reviews, see Heyes & Galef, 1996; Zentall, 2003; Zentall & Galef, 1988). It is clear from this literature that animals learn from the observation of the behavior of other animals, including where food is located (e.g., McQuoid & Galef, 1992), which food items are palatable (e.g., Galef, 1989; Laland & Plotkin, 1993), and behaviors used to obtain food (e.g., Laland & Plotkin, 1990; Lefebvre, Whittle, & Finkelstein, 1997). It seems likely that such imitative learning involves memory for the observed behaviors (but see Zentall's (2003) analysis of data presented by Gallese, Fadiga, Fogassi, and Rizzolatti (1996)). The work on imitative learning has focused on the conditions that produce imitation and the nature of the learning process(es) involved. But there has been little or no analysis of the content or mechanism of memories involved in imitation.

In addition, Galef and his colleagues have shown that food aversions and food preferences are socially transmitted in rats (e.g., Galef, 1989; Galef & Wigmore, 1983). They have shown that food preferences acquired socially are retained for at least one month (Galef & Whiskin, 2003) and are retained despite a variety of intervening food-related experiences (Galef, Lee, & Whiskin, 2005). These findings clearly suggest the involvement of a long-term memory system which stores information obtained from conspecifics (for reviews, see Galef, 2005; 2007).

Goals and Rationale of our Laboratory Analyses of Social Influences on Spatial Choice

The project reviewed in this paper began as an investigation of short-term social memory for spatial locations. A critical property of the memory we will examine is that its content changes flexibly – i.e., it is memory of the short-term ("working") variety that allows information to be temporarily stored, perhaps while it is processed by other cognitive systems. Working memory is a central concept in cognitive psychology, including comparative cognitive psychology (see Olton, 1978 for a classic treatment of the topic). The goal was to examine some basic properties of short-term memory that has social content (i.e., the memory appears to be *of* another animal's behavior) and functions in a social foraging context. In the tasks we use, the memories with social content are the several locations visited by a foraging partner during each of many daily trials. Because those locations vary unpredictable from trial to trial, a flexible working memory system must be used to code the locations visited by the foraging partner.

All of the empirical work reviewed in this chapter involves male Sprague-Dawley laboratory rats. Rats are a good choice of study species not only because of the massive database of information available about the behavior of laboratory rats, but also because many species of rats forage socially, including the wild Norway rat (*Rattus norvegicus*) from which our laboratory rat is derived (Barnett, 1963). There is very clear evidence that laboratory rats transfer information about the identity and quality of food sources socially (Galef & Wig-

more, 1983; Laland & Plotkin, 1993). There is also evidence that laboratory-reared rats released and living in natural settings exhibit social foraging behaviors as well as many other components of the their ancestors' natural foraging behavior (Berdoy, 2002). Spatial navigation and spatial short-term memory have been very well studied in laboratory studies using rats. Thus, rats have the combined advantage of being ecologically appropriate for studies of social foraging and very well understood from a psychological perspective.

Although we know a great deal about animal working memory for inanimate physical stimuli, virtually nothing is known about working memory for social information. The experiments reviewed below provide evidence that rats code the behavior of a conspecific in working memory and that these memories allow locations visited (and thereby depleted of food) by a foraging partner to be avoided. However, there are two important complications. First, the behaviors controlled by memory of locations chosen by another rat turn out to have effects that are, at least under many of the conditions we have used, in opposition to the social affiliation produced by the physical presence of the other rat. Second, it appears that information in memory about the spatial choices made by another rat interacts with information in memory about the spatial choices made by the focal rat to determine choices made by the focal rat. The findings that support these conclusions will be reviewed below.

Evidence for Social Spatial Memory

Preliminary Evidence. A student research project completed in my laboratory provided the initial evidence that rats remember spatial choices made by another rat (the project was by Haley Solodky and reported by Brown, Farley, Solodky, & Bachrach, 2005). The experiment involved the Pole Box Maze, an experimental paradigm developed in my laboratory in the context of our studies of spatial pattern learning (e.g., Brown & Terrinoni, 1996). In this paradigm, rats search for sucrose pellets that are hidden on top of vertical poles. After learning to rear up on their hind limbs in order to obtain pellets from the tops of the poles, ten rats were given a series of trials in which they were allowed to search the poles until the pellet had been obtained from all 25 poles (see Figure 1). There were a total of 60 trials (2 per day) for each rat. During half of them the rat was tested by itself and during the other half the rat was tested along with its cage mate. Thus, under the "social foraging" condition, the two rats had to compete for access to the same 25 pellets.

Results from the trials in which rats were tested separately showed that rats learned to avoid revisiting locations over the course of the experiment (Figure 2, top panel). Surprisingly, they showed no evidence of the pre-experimental tendency to avoid revisits to spatial locations that exists in the radial-arm maze (Timberlake & White, 1990). In the social trials (Figure 2, bottom panel) there are two findings. First, during Trial Block 1, the rats were slightly more likely to visit locations that had been visited by the other rat earlier during the trial (the red data points are slightly above chance and the black data points are correspondingly below chance). After experience foraging with their cage mate, however, the rats preferentially visited the poles that had *not* been visited by their cage mate earlier in the trial (Figure 2; during Block 3, poles earlier visited by the other rat (red symbols) are less likely than those not earlier visited by the other rat (corresponding black symbols). Poles already visited by the other rat did not contain a pellet. It appears that, over the course of the experiment, rats learned that no food was to be found in places already visited by the other rat and were able to avoid such locations. This tendency indicates the existence of social spatial memory for the locations visited by the other rat.

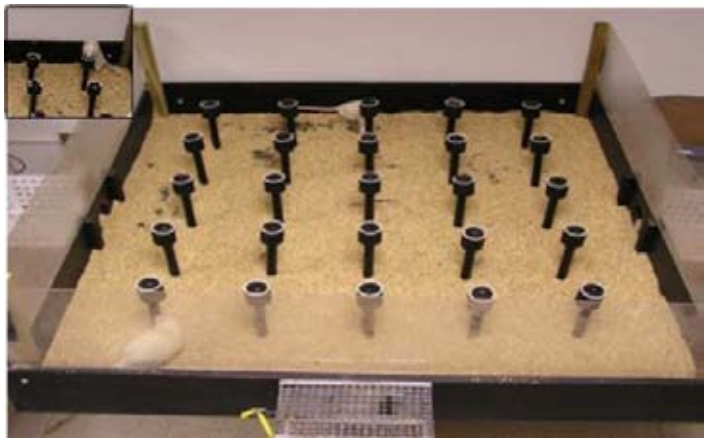

Figure 1. *Pole Box Maze used by Brown, Farley, Solodky, & Bachrach (2005). Inset in upper-left shows rat choosing pole to locate food pellet hidden on top. Photograph by the author.*

These results are intriguing but they have a number of limitations. First, part of the behavioral tendency to visit or avoid visits to poles visited earlier by the other rat may not depend on memory. The other rat may still be present in the area of the poles it recently visited. Thus, the presence of the other rat (as a physically-present stimulus) may be controlling behavior rather than a memory for its earlier choices. In addition, the tendency to avoid visits to poles visited by the other rat was relatively small in magnitude (although statistically reliable). In this experiment, as in earlier experiments using the Pole Box apparatus (e.g., Brown & Wintersteen, 2004; Lebowitz & Brown, 1999), there is only a mild tendency for rats to avoid revisits to poles that they had visited earlier in the trial. Thus, it should not be surprising that there is only a weak ability to avoid poles visited by another rat.

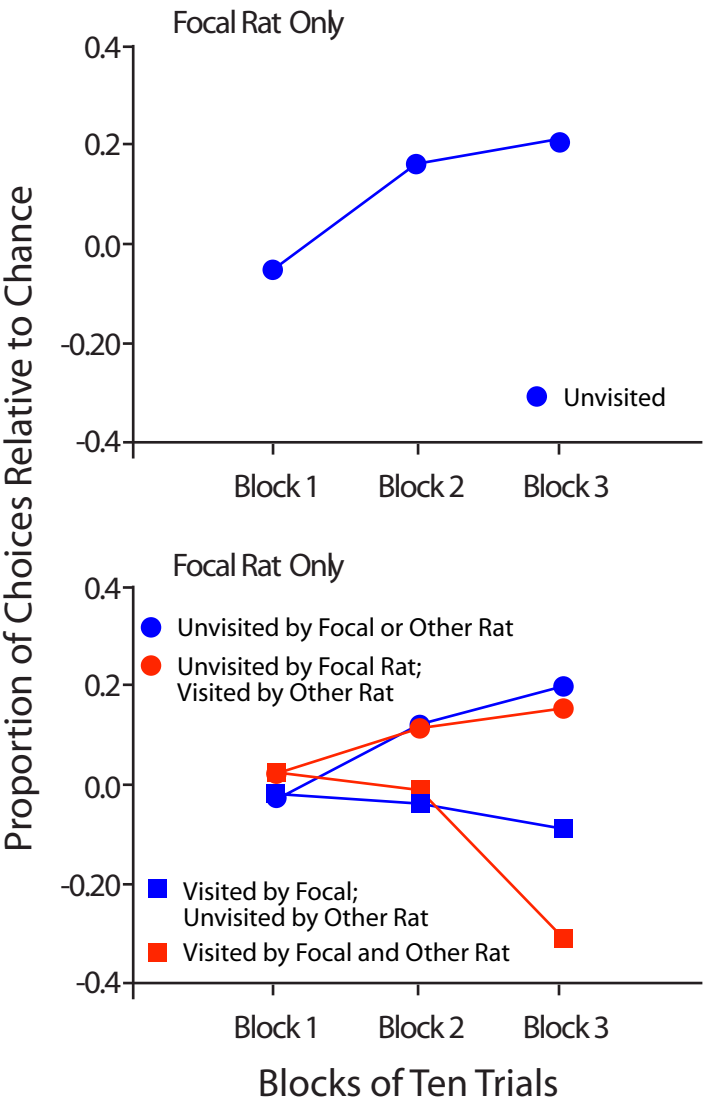

Figure 2. *Performance in Pole Box experiment of Brown et al (2005) when rats were tested separately (Top Panel) and together (Bottom Panel). The difference between the mean proportions of choices made and the proportions of poles available as choice alternatives are shown as a function of whether the focal rat did (Squares) or did not (Circles) previously visit the pole and (in the case of the bottom panel) according to whether the foraging partner did (Red) or did not (Black) previously visit the pole. Note: Data are previously unpublished.*

Advantages of Radial-arm Maze for the Study of Social Spatial Memory

In response to these considerations, most of our subsequent experiments have used the radial-arm maze paradigm which, we believe, better isolates memory-based social effects from effects of the physical presence of the other rat. In addition, the radial-arm maze clearly supports a strong tendency for rats to avoid revisits to locations that they previously visited and so may better support a parallel social memory effect. Introduced by Olton and Samuelson (1976), the radial maze has been a dominant laboratory paradigm for the study of spatial memory for several decades (for a review of early work, see Foreman & Ermakova, 1998). In the standard version of this task, rats experience a large number of daily trials in which they forage for food in a maze with a central hub and a number of arms (usually eight or twelve) approximately 1 meter long, configured as shown in Figure 3. A small amount of preferred food (in my laboratory, two 45 mg sucrose pellets) is placed at the end of each arm, and the rat is allowed to choose arms until all of the food has been collected. A critical feature of performance in this spatial task is an exceptional ability to avoid visiting locations that have already been depleted of food during an earlier choice. In the 12 arm maze shown in Figure 3, for example, we and others have repeatedly found that rats revisit an average of approximately one maze arm in the process of gathering all of the food. It is very clear that rats use memories that code the visual features of the 12 locations to discriminate the locations and avoid revisits – they do not do so on the basis of odor trails or learned response algorithms (e.g., Olton, 1978; Olton & Collison, 1979; Suzuki, Augerinos, & Black, 1980; Zoladek & Roberts, 1978). The ability of rats to perform so accurately in the radial-arm maze task has encouraged the view that this task emulates features of the natural foraging behavior of rats. It may therefore involve a specialized (or particularly effective) spatial memory system that is adapted to the selective forces operating on animals that gather food from small patches that are spatially scattered in familiar territory (e.g., Bond, Cook, & Lamb, 1982; Olton & Schlosberg, 1978; Timberlake & Hoffman, 2002). Given that rats forage socially and that the radial-arm maze mimics at least some aspects of that ecology, this view also encourages the use of the radial-arm maze to look for social memory used in the context of foraging.

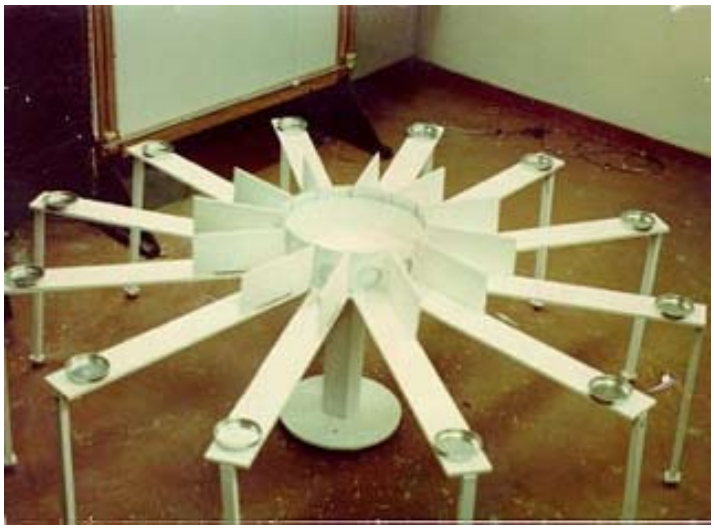

Figure 3. *Standard Radial-arm Maze. Photograph by the author.*

We have tested rats in experiments using a radial-arm maze in an attempt to determine whether the choices made by one rat in the maze affect choices made by a second rat foraging in the same maze and, if so, whether spatial memory is involved. The standard version of the radial-arm maze (shown in Figure 3) will not accommodate two rats on the same maze arm. the rats cannot pass each other on the narrow arms. I suspected that a modified apparatus, similar to one that I have used in several earlier experiments (e.g., Brown & Moore, 1997), would allow two rats to visit the same arm simultaneously. The key feature of this modified apparatus is that the arms are constructed of PVC tubes (Figure 4). Relative to more typical radial-arm mazes, this design feature decreases access to the visual cues known to provide the primary spatial information used by rats to navigate in the maze and code spatial locations (e.g., Olton, 1978; Suzuki et al., 1980; Brown, Rish, VonCulin, & Edberg, 1993). However, previous work using mazes constructed in the same fashion clearly shows that choices in mazes with enclosed arms are also controlled by visual spatial cues (Brown & Drew, 1998) as long as visual cues are available from the ends of the maze arms (Brown et al., 1997).

Figure 4. *Eight-arm maze used in the experiments of Brown, Farley and Lorek (2007) and Experiment 1 of Brown, et al. (2008). Photograph by the author.*

Free Choices in the Radial-arm Maze. Brown, Farley, & Lorek (2007, Experiment 1) investigated social effects on choices in the radial-arm maze when two rats were allowed to freely choose from among the eight arms of the maze. Ten male Sprague-Dawley (SD) rats (five sets of cage mates) were first shaped to visit the ends of the arms of the maze shown in Figure 4 to obtain sucrose pellets (two 45 mg pellets on each arm). Shaping required approximately four daily sessions of 10 minutes for each subject. They were then tested once per day with their cage mate for 30 days. During each of these daily trials, the two rats were allowed to choose from among the eight maze arms for six minutes.

Our analyses of the data focused on the relationship between choices made by a rat and choices that had been made earlier during the same trial by its foraging partner. The data from each trial were analyzed twice, once from the perspective of each of the two rats. The choices made by a rat (referred to as the "focal rat") were classified according to whether the maze arm chosen had been or had not been visited earlier during the trial by its foraging partner (the "other rat"). We discovered, however, that this binomial classification procedure occluded a key aspect of the results. Specifically, it turned out that the location most recently visited by the other rat produced a very different pattern of results than did the locations visited earlier in the trial by the other rat. In addition, the pattern of results was different for "correct" choices (choices of maze arms that had not previously been visited by the focal rat itself, referred to below as "initial choices") and "incorrect" choices (choices of maze arms that had already been visited by the focal rat, referred to below as "revisits"). Thus, in what follows the location visited most recently by the other rat is considered separately from the location(s) that the other rat visited earlier during the trial. Note that, in the case of the "most recent" choice of the other rat, the other rat may currently be visiting that maze location or may have already completed that visit. Regardless, it is likely to be in proximity to its most recently chosen location.

The red bars in Figure 5 show the mean distribution of choices made by the rats in this experiment, when the choices are classified according to whether the choice was an initial visit to the location for the focal rat ("correct" choice; left panel) or was a revisit of a location that the focal rat had visited earlier during the same trial ("incorrect" choice; right panel). These means are calculated over proportions for each of the 10 rats during each of three blocks of 10 trials each. Interpreting the relationship between the choices made by the focal rat and the choices made by the other rat requires an estimate of the proportions expected on the basis of chance. The blue bars in Figure 5 show the mean values of the estimate of chance that we use for comparison. These values represent the proportions of maze-arms in each of the six categories that were available to be chosen at the time the focal rat made its choice. In other words, the blue bars show the distribution of choice alternatives available to the rat. These values are empirically determined for each rat during each of the three trial blocks in the following manner. The algorithm that evaluates the choices made by a focal rat classifies each choice made by the focal rat in terms of the six categories shown in Figure 5 (the means of those values are shown as the red bars) and then, for each choice, classifies each of the eight maze arms at the time the choice was

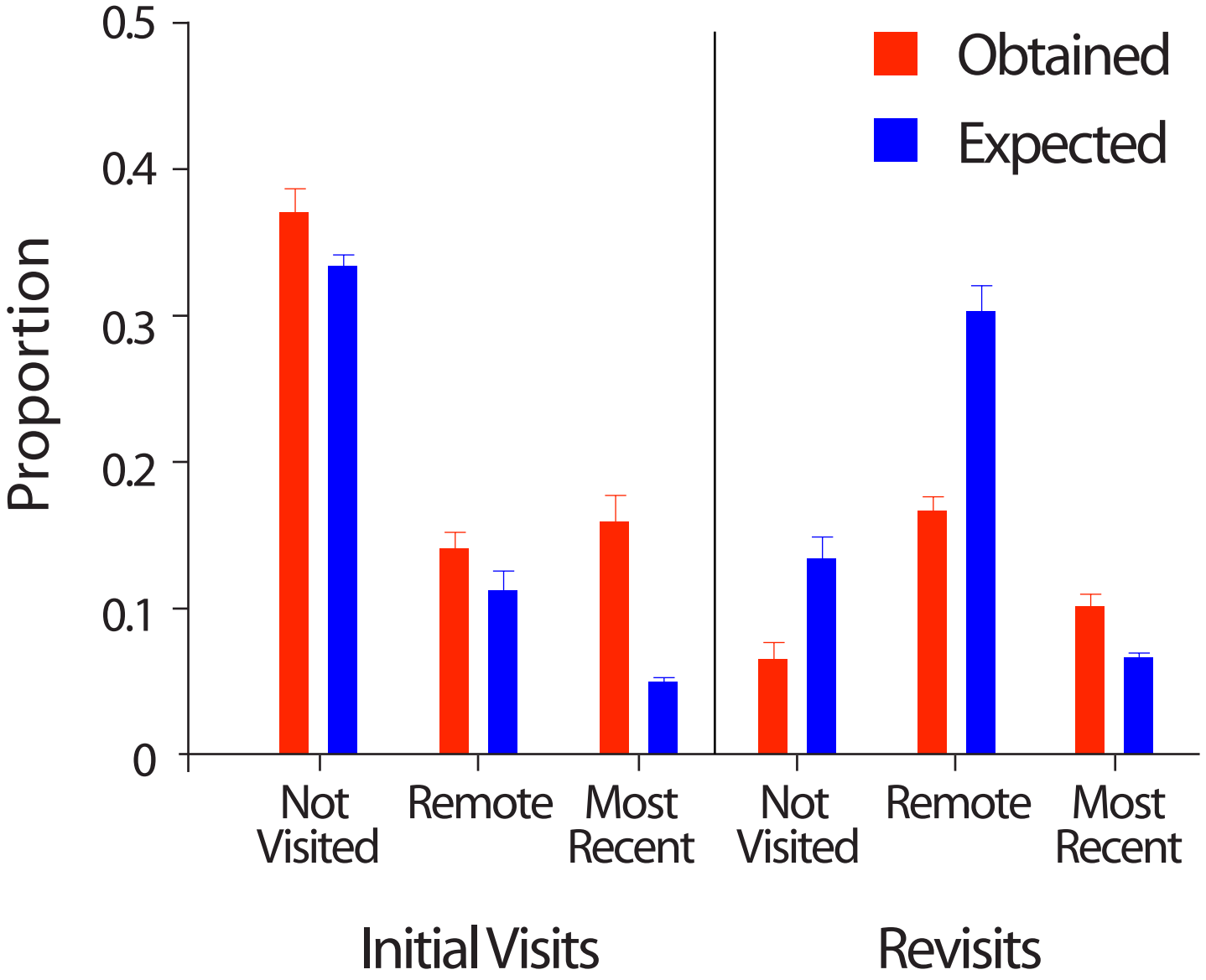

Figure 5. *Figure 5. Distributions of choices made and expected during the free choices of Brown, Farley, & Lorek (2007; Experiment 1). Choices expected are determined based on the distribution of maze arms available at the time choices were made. Based on data shown in Figure 1 of Brown, Farley, & Lorek (2007) and shown here with permission.*

made in terms of the six categories. The mean distribution of the latter values is shown by the blue bars.

A preliminary point about the data in Figure 5 concerns the effect of the focal rat's own previous choices. As expected on the basis of numerous experiments using the radial-arm maze, the rats tended not to revisit maze arms. That is, the overall probability of an initial visit was greater than expected (and, thus, the probability of a revisit was necessarily less than expected). This tendency appears not to be as strong as is typically the case in the radial maze. This is due in part to our procedure of allowing the rats to make choices beyond the point at which all locations have been visited (for a total of six minutes). However, as results described below also indicate, this is just part of the explanation. Rats making choices in the presence of another rat do not have the strong tendency to avoid revisits that is typically seen in the radial maze.

The primary issue here is the relationship between the choices of the focal rat and earlier choices of the other rat. There was clearly a relationship between earlier choices made by the other rat and the choices made by the focal rat. However, as already mentioned, the relationship was complex. First, the location that was most recently visited by the other rat was more likely to be chosen than expected. This tendency was stronger in the case of the focal rat's initial visits to maze locations, but there was a significantly larger proportion of choices made to the other rat's most recent choice for both initial choices and revisits by the focal rat. Second,

in the case of revisits by the focal rat, those locations that had been visited earlier by the other rat were *less* likely to be chosen than expected. However, this was true only for the choices made earlier during the trial (not for the location chosen most recently by the other rat; in that case there was no difference between the proportion of choices made and the proportion expected).

This pattern of results suggests that the processes in force when another rat is physically present and those engendered by memory for another rat's choices need to be considered separately. Specifically, when the other rat is physically present, the focal rat is attracted to its location and, therefore, tends to choose it. It should be pointed out that this tendency is in contradiction to the contingencies in place relating a location visited by the other rat and the presence of food in that location; there is no reinforcement for choice of the location that was earlier chosen by the other rat. The other rat is an attractant despite this contingency. Keep in mind that the rats tested in this experiment are cage mates and therefore highly familiar with each other. We do not yet know whether this familiarity is important, but at least in some cases, rats are attracted to locations occupied by another rat. This is consistent with the strong impression one gets observing the rats in these experiments that they tend to "follow each other". In any case, when the other rat is no longer physically present in a location, but had visited the location earlier during the trial, then there is an opposite tendency to avoid choice of the location. This result indicates that rats remember the locations of maze arms chosen by a conspecific (and thereby depleted of food) and avoid those locations on the basis of those memories.

This interpretation of the data shown in Figure 5 implies that two processes work against each other to modulate choice tendencies in relation to locations chosen by a foraging partner in the radial maze. The physical presence of another rat (at least in the case of a familiar, male cage mate) elicits social affiliation and thereby increases the likelihood of choosing the same location that was just chosen by the other rat. On the other hand, information about the locations previously chosen by the other rat allows those locations to be avoided, which is the adaptive or "correct" response given that such locations have been depleted by the other rat.

Forced Choice Tests of Working Memory for Social Information. Two additional sets of results reported by Brown, Farley and Lorek (2007) support this interpretation. First, the same rats tested in the experiment described above were given a series of five daily trials, each of which had two phases. In the first, *forced choice* phase of each trial, only a randomly chosen set of four maze-arms was available to be chosen. Access to the remaining arms was blocked as illustrated in Figure 6. Then the two rats were allowed to make choices until each of the four accessible maze arms had been chosen (by at least one of the rats). The rats were then removed from the maze briefly (2 min) while the doors blocking access to arms were removed, the maze was rotated such that different maze-arms were in the eight maze locations, and the *locations* (not maze-arms) that had not been visited during the forced choice phase were baited. Both rats were then returned to the maze and allowed to make choices from among all eight locations until all four baited locations were chosen by one (or both) of them.

Figure 6. *Technique used to determine forced choices by Brown, Farley, & Lorek (2007, Experiments 1 & 2). Photograph by the author.*

Figure 7 shows the probability of visiting maze locations during the second phase of the trials as a function of whether that location had been visited by the focal rat during the first phase of the trial and whether it had been visited by the other rat during the first phase of the trial. As would be expected

on the basis of numerous previous experiments using the radial maze, rats tended to avoid locations that they had visited. They also avoided locations that the other rat had visited. There are two important implications of these results. First, because the procedure allowed us to rotate the maze during the delay between the two trial phases, we can rule out the possibility that odor trails left by the other rat are responsible for its effect on the focal rat's choice. There are numerous previous experiments indicating the odor is not responsible for rats' ability to avoid returning to location it chose earlier. However, in our earlier free choice experiment it remained possible that the odor of another rat could have been used a cue to its previous choices, particularly given the importance of odor in other domains of social influence known to exist in rats (Galef, 2005; 2007). The avoidance of the other rat's choices seen in Figure 7 is in terms of the *locations* the other rat chose, regardless of whether the maze-arm rotated into that location had been chosen. When the choices are coded in terms of the maze-arm chosen by the other rat (regardless of the location into which they were rotated), then there is no evidence of an effect of previous choices. Thus, what matters is which locations were visited by the other rat, not which maze-arms (hypothetically) have its odor.

The second important point to be made about these results is that they were obtained in a situation in which the other rat is no longer physically present at the location of its most recent choice (except, of course, by chance). Thus, given the interpretation of the data presented above, one would not expect to find a tendency to choose the location most recently visited by the other rat. Instead, the locations previously visited by the other rat were systematically avoided. Thus, the procedure of this experiment appears to have isolated the memory-based process involved in avoiding locations visited by the other from the social affiliation tendency that occurs when the other rat is present.

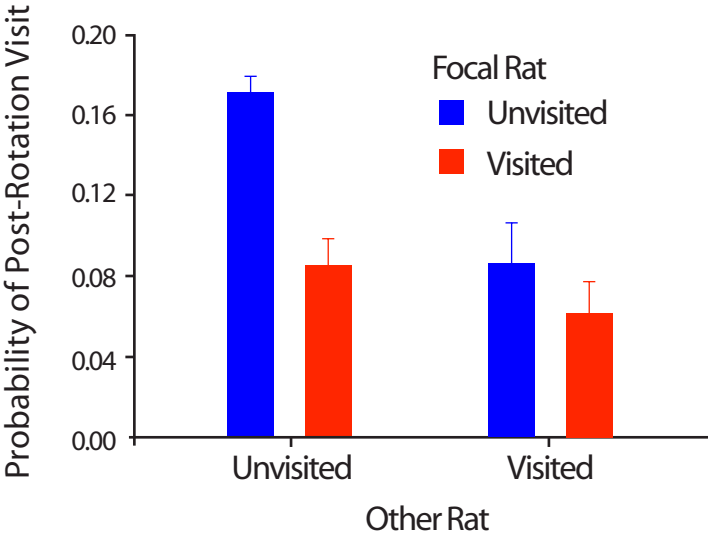

Figure 7. *Probability of visiting spatial locations in Brown, Farley and Lorek (2007, Experiment 1, Forced Choice Trials) as a function of visits by the focal rat and its foraging partner. Adapted from Figure 2, "Remembrance of places you passed: Social spatial working memory in rats". Journal of Experimental Psychology: Animal Behavior Processes, 33, 218. Copyright 2007 by the American Psychological Association. Adapted with permission.*

Brown, Farley and Lorek (2007; Experiments 2 & 3) took this strategy of isolating social memory effects from social affiliation effects a step further in two additional experiments. One rat of each pair was assigned as the model rat for each trial and the other served as the subject. During the first ("study") phase of each trial, the model rat made choices from among four randomly selected maze-arms (access to the other four arms were blocked as described above). The subject rat had an opportunity to observe the choices made by the model rat during the study phase but could not make choices itself because it was kept inside the observation chamber shown in Figure 8. After the model rat made its choices of the four available maze arms, the model rat was removed from the maze, the maze-arms were unblocked, and four locations not visited by the model rat were baited. The subject rat was then released from the observation chamber and allowed to make choices until it visited all eight baited arms (or 5 min elapsed).

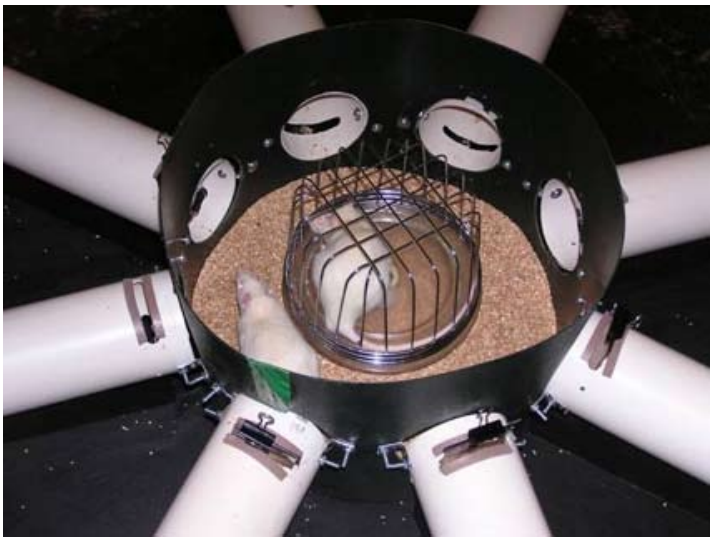

Figure 8. *Subject rat in observation chamber while model rat makes choices in the first phase of trials in Brown, Farley and Lorek (Experiments 2 and 3). Click on Photo (or here) for video of example trial. Photograph from Figure 3, "Remembrance of places You passed: Social spatial working memory in rats". Journal of Experimental Psychology: Animal Behavior Processes, 33, 217. Copyright 2007 by the American Psychological Association. Adapted with permission. Video by the author. Thanks to Jenna Brown for video editing.*

With rare exceptions, subject rats choose all eight maze arms within the five minutes allotted. We determined the effect of the model rat's previous choices by considering the *order* in which the location were chosen by the subject rat. A preference for locations not chosen by the model rat would be indicated by a tendency to choose those locations relative early in the subject rat's choice sequence. Thus, the serial position of each location in the subject rat's choice was noted. The mean serial position (in the subject rat's choice sequence) of the locations visited by the model rat were determined are shown in Figure 9 over the course of the six blocks of five trials each that comprised the experiment. A value of 4.5 represents chance performance and 6.5 represents maximum preference for locations not visited by the model rat, given eight serial positions. Although the tendency to visit locations that had not been visited by the model rat was not strong, it was significantly above chance by the third trial block.

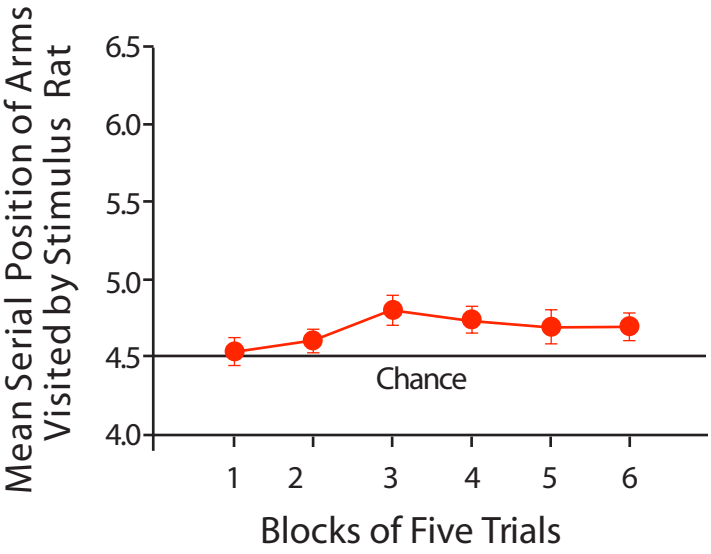

Figure 9. *Mean serial position of choices made by subject rat to arms previously visited by stimulus rat – shown across trial blocks. Adapted from Figure 5, "Remembrance of places you passed: Social spatial working memory in rats". Journal of Experimental Psychology: Animal Behavior Processes, 33, 220. Copyright 2007 by the American Psychological Association. Adapted with permission.*

In addition, we looked at the preference for locations not visited by the model rat as a function of the location's serial position in the *model rat's choice sequence*. Given the existence of recency effects in radial maze performance (e.g., Cook, Brown, & Riley, 1985), one might expect the choices made relatively late in the model rat's choice sequence to be better remembered than the model rat's earlier choices. Figure 10 shows the same data that are depicted in Figure 9, but collapsed over trial blocks and shown in terms of the location's serial position in the model rat's choice sequence. The tendency to avoid locations previously visited by the model rat was limited to the two locations visited last by the model rat. This can be understood in terms of a recency effect.

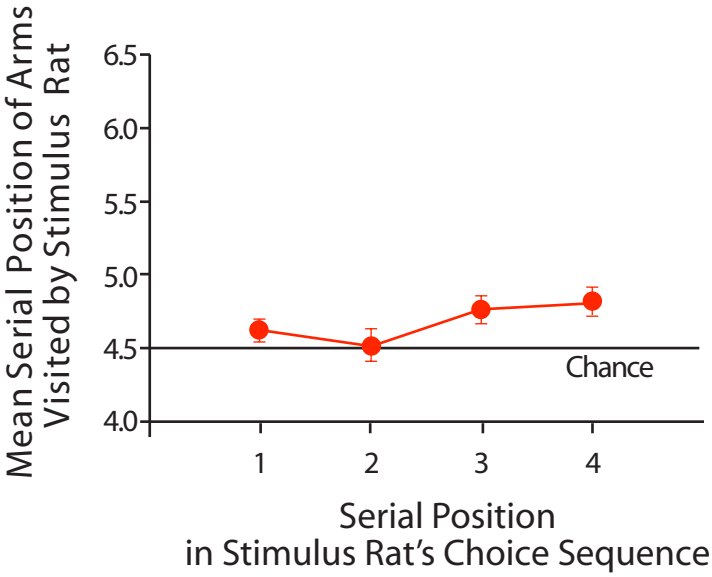

Figure 10. *Mean serial position of choices made by subject rat to arms previously visited by stimulus rat, shown as a function of the serial position of choice of that location by the model rat. Adapted from Figure 6, "Remembrance of places you passed: Social spatial working memory in rats". Journal of Experimental Psychology: Animal Behavior Processes, 33, 220. Copyright 2007 by the American Psychological Association. Adapted with permission.*

The data from this procedure in which one rat makes forced choices to randomly selected maze locations while being observed by the subject rat provides the clearest support for the idea that memory for another rat's choices control the choices subsequently made by a rat in the radial-arm maze. Again, it is important to note that this procedure removes the other rat as a physically present stimulus at the time the subject rat makes its choices. Thus, any effect of another rat that depends on its presence – as we propose the social affiliation effect does – is removed and the subject rat's choices can be modulated only by information in memory about the choices previously made by its foraging partner. The model/observer technique also allows experimental control over the identity of the maze locations chosen by the other rat. The experiments described above show that spatial choices are affected by the choices made by a foraging partner in at least two ways. First, there is a social affiliation tendency that results in increased choice of the location chosen most recently by the other rat. This effect appears to depend on the physical presence of the other rat. The choices made earlier by the other rat have a different effect on choices.

However, the magnitude of the social memory effects

found under these circumstances is somewhat limited. The tendency to avoid locations chosen by the model rat is significantly greater than that expected on the basis of chance, but by an amount that is about 15% of the range between chance and the maximum possible tendency. In contrast, when the two rats make choices together during the "study" phase of the trial, the tendency to avoid locations earlier chosen by the other rat is much stronger; in the data shown in Figure 7, a visit by the other rat reduces the likelihood of choice by the focal rat by about 50%. We do not know what differences between the procedures of these experiments are responsible for the difference in the magnitude of the tendency to avoid locations previously chosen by another rat. Two straightforward possibilities are 1) the extended temporal delay between the choices made by the other rat and the choices made by the focal rat and 2) the reduced scope of social interaction between the two rats.

In any case, we have chosen to give up the increased experimental control of the model/observer paradigm in our more recent investigations in order to test rats in situations that allow them to freely interact and make choices simultaneously. As will be seen below, this requires some relatively complex analytic techniques for measuring social effects. However, it allows us to test the rats in a more natural social context that seems to better reveal social memory effects.

Social Memory for "What" as well as "Where"? Given that radial maze choices are determined by spatial location, information about the *location* of the other rat's choices must be coded. We have also explored the possibility that other information is obtained from the foraging partner and subsequently affects spatial choices. Exposure to a social partner that has recently eaten a novel food is known to increase preferences for the food eaten by the partner (Galef & Wigmore, 1983; Laland & Plotkin, 1993). But would working memory for the type of food found in particular locations of the maze by a foraging partner allow a rat to selectively choose locations with a preferred food type?

In two experiments, Brown et al (2008) used a free choice radial maze procedure very similar to the one described above; two rats (cage mates) were simply allowed to make choices together during each daily trial and choose from among the eight maze locations. However, there were two kinds of food available in maze arms. Half of the arms provided grain pellets and the other half provided sucrose pellets. The grain pellets are very similar in content to the maintenance diet eaten by our rats but the sucrose pellets are much preferred. Furthermore, there was an unlimited supply of food available in maze arms (see Figure 11). This is an unusual procedure for the radial maze that eliminates the contingency between choice of a location and depletion of food in that location. Thus, a revisit to a maze arm is not an "error" in the typical sense because food will be available on any maze-arm chosen, regardless of previous visits by the rat itself or by a foraging partner. One might expect that this situation would result in rats simply visiting a maze arm and consuming food there to satiation. However, as first described by Timberlake and White (1990), rats' discrimination of visited and unvisited locations does not depend on a contingency between maze-arm visits and depletion of food in those locations. In Timberlake and White's experiment, choice accuracy and other aspects of performance were similar regardless of whether food reward was or was not present at the ends of maze-arms. In our experiments, it turns out that rats continue to choose spatial locations and consume small amounts of food from those locations even when large, undepletable caches of food are available.

Figure 11. *Food cup with undepletable supply food pellets at the end of a maze arm. Photograph by the author.*

Critically, the location of the grain pellets and the sucrose pellets varied unpredictably from trial to trial. Thus, the rats could not learn the locations of the two food types over trials. These procedures were designed to create a situation in

which the rats could benefit from coding not just *where* the other rat had visited maze-arms but also what the other rat found there. In fact, it would not increase efficiency to know where the other rat's choices were without knowing what it found there (because the food supply on each arm was undepletable). But coding both what food type the other rat found and where it found that food would allow choices to be made to locations that contain the preferred sucrose pellets.

Brown et al (2008) reported two very similar experiments that used this basic design and logic. The first involved the same radial maze described above and shown in Figure 4. The second involved a radial maze that was similar but modified such that the maze arms were transparent (shown in Figure 12). The transparent arms were intended to allow the rats to have greater visual contact with each other, thereby enhancing the opportunity for social effects on choice. The results of the two experiments were consistent with each other, but the effects were enhanced in the second experiment and the description here will be limited to that experiment.

Figure 12. *Radial arm maze used by Brown et al (2008; Experiment 2) and Brown, Prince, Doyle (2009). Photograph by the author*

The data were analyzed in a manner very similar to that described above for the data in Figure 5. Each choice was categorized according to whether the focal rat had previously visited the location chosen, whether the other rat had previously visited it (and, if so, whether the location was the other rat's most recent choice or had been visited earlier in the choice sequence) and which of the two food types was available on the maze arm. In addition, for each choice made, all eight of the maze arms were categorized according to the same three dimensions. These counts of choices and choice alternatives, respectively, were calculated separately for each choice in the focal rat's choice sequence. The resulting data, shown in Figure 13, are collapsed across choice number and come from 20 trials (see Brown, et al, 2008, Experiment 2, Phase 2 for details). For ease of presentation, Figure 13 does not show the categories of locations that had not been visited by the other rat (which are complementary sets in relation to the locations that had been visited by the other rat).

As for the data from free choice experiment described above, tendencies to visit or avoid visiting locations can be detected by comparing the proportions of choices to the various categories of locations (filled bars in Figure 13) to the proportions expected on the basis of the distributions of choice alternatives available (unfilled bars in Figure 13). In the case of locations that were the most recent choice of the other rat (blue bars in Figure 13) there is a consistent tendency to visit those locations regardless of the other variables. This is in agreement with our earlier conclusion that the physical presence of the other rat elicits a social facilitation effect, attracting the focal rat to the location just chosen by the other rat.

In the case of maze locations visited more remotely (earlier in the other rats choice sequence; red bars in Figure 13), the effect of those visits by the other depends jointly on the other two variables. For locations that had not been visited earlier by the focal rat (left panels of Figure 13), there is a small (but significant) tendency to visit locations earlier visited by the focal rat and this is the case for both grain locations and sucrose locations. However, in the case of locations that had earlier been visited by the other rat (right panels of Figure 13), the effect of the other rats earlier visit depends of the food type with which the location is baited. There is a tendency to visit those locations if they contain sucrose pellets but a tendency to avoid visiting those locations if they contain grain pellets. (Note. this most critical aspect of the results is circled in Figure 13 for emphasis.)

Brown et al (2008) report two additional data sets that are consistent with pattern described above. The previous (remote) visits made by the other rat affect the choices made by the focal rat and they affect it positively or negatively depending on whether the location contains the more-preferred or less-preferred food, respectively. But this is the case only if the focal rat itself has also previously visited the location. This indicates that rats are *not* controlled by information about *what* the other rat found during its visits. Rather they must have visited the location themselves to determine and code that information, but apparently they do code the hedonic value of the food type found in the locations visited earlier during a trial. This information is apparently combined with information about *where* the other rat has been. A combination of both kinds of information is necessary to explain the pattern of results just described.

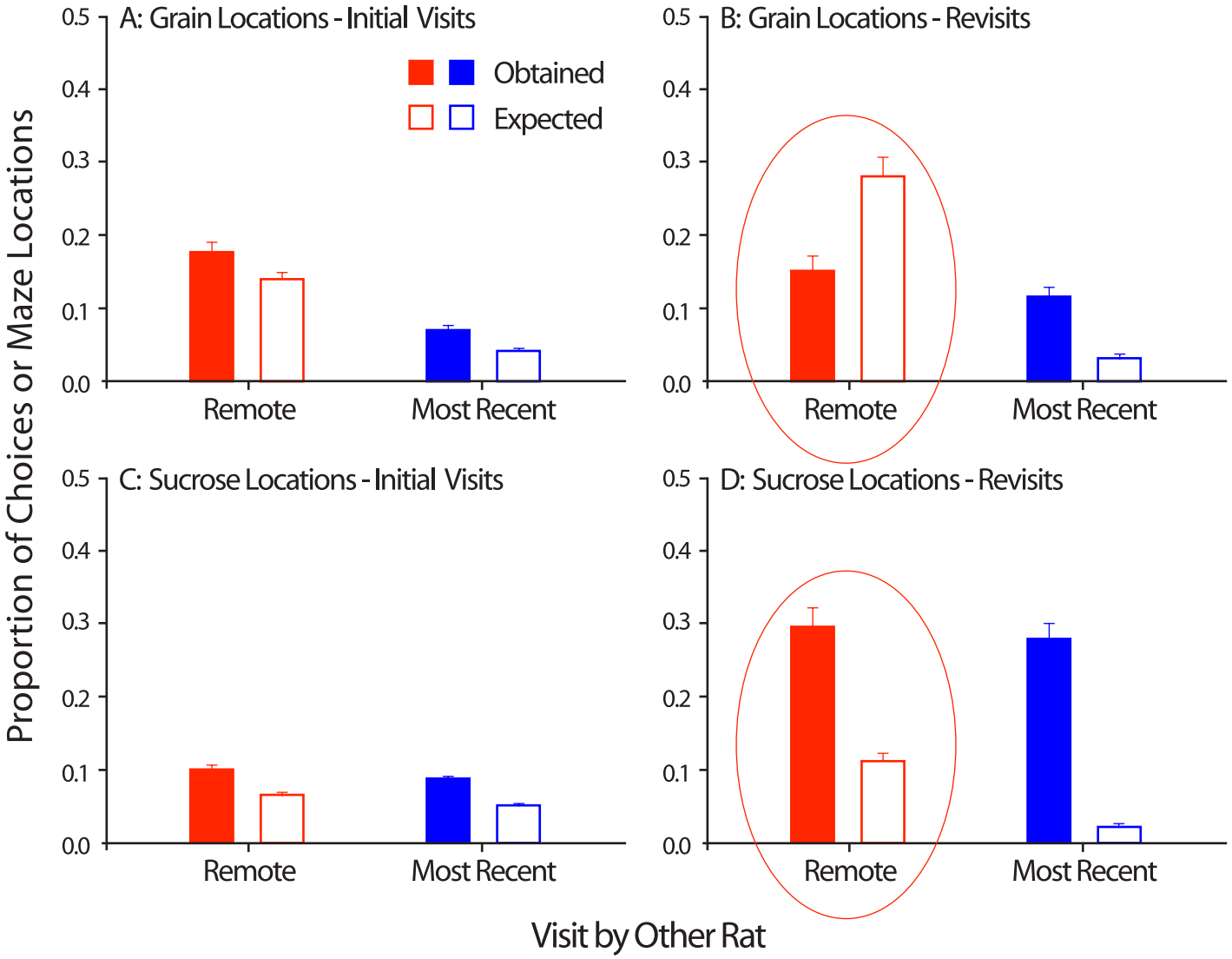

Figure 13. *Proportions of choices and choice alternatives in Brown et al (2008; Experiment 2). The proportions are calculated separately for the focal rat's initial visits and revisits. Adapted from Figure 2, "Social working memory: Memory for another rat's spatial choices can increase or decrease choice tendencies". Learning and Behavior, 36, 333. Copyright 2008 by the Psychonomic Society. Adapted with permission.*

This is in contrast to longer-term social influences on food preferences (e.g., Galef & Wigmore, 1983) which appear to require social transmission about what another has eaten. A possibly critical difference between the two situations is that, in our working memory paradigms, the identity of different foods found in multiple places by the other rat must be discriminated.

Brown, Prince and Doyle (2009) reported a series of similar experiments, with the primary difference being that the quantity of food, rather than the qualitative value of the food, differed among the maze locations. In two experiments using the maze as shown in Figure 12, no tendency to avoid visits to locations previously visited by the other rat was found under any conditions (Brown et al, 2009; Experiments 2 & 3). However, in one experiment, Brown et al (2009; Experiment 4) varied the extent to which the rats had visual access to each other. The rationale was that the transparent maze arms may allow sufficient visual access to the other rat that a social affiliation tendency might dominate choice tendencies. So the degree of visual access was varied using opaque sleeves that reduced visual access between the rats such that they could only see each other when they were in the central arena (or, just as in a standard radial maze, when one was in the central arena oriented toward a maze arm being visited by the other). The sleeves restricting visual access were present on half of the trials and absent (allowing visual access) on the other half of the trials (see Figure 14). When the sleeves were absent (allowing full visual access), there was no evidence for a tendency to avoid visits to locations previously visited by the other rat. However, when the sleeves were present and visual access thereby restricted, a pattern of results emerged that was parallel to that found by Brown et al (2008).

Figure 14. *Maze-arms covered by sleeves to occlude access to visual cues (Brown, Prince, & Doyle, 2009; Experiment 4). Photograph by the author.*

In Brown, Prince, and Doyle's experiments, there were two groups of rats. For one group, each maze location was baited with two 45-mg sucrose pellets. For the other group, each maze location was baited with an unlimited supply of sucrose pellets. Thus, the former group was exposed to the standard contingency between a previous visit to the maze location and the absence of food on the maze arm. But, for the latter group, there was no contingency between previous visits and food being in the location.

Again, there was a consistent tendency to visit the maze location most recently visited by the other rat (the means shown by all the filled blue bars in Figure 15 are greater than the corresponding expected values). As in the experiments of Brown, et al (2008), there was a small (but significant) tendency to visit maze locations visited remotely by the other rat if the location had not been visited previously by the focal rat (the blue bars in the left panels of Figure 15). The results of most interest are those highlighted by the circles in Figure 15. For locations previously visited by the focal rats (Revisits shown in right panels of Figure 15), choice tendencies depended on the amount of food available in that maze location. There was a tendency to visit locations with an undepletable supply of pellets but a tendency to avoid visiting locations that had been baited with two pellets.

Thus, as was the case for quality of food available, the behavioral reaction to quantity of food available in a maze location depended jointly on previous visits by the focal rat and previous visits by the other rat. The interaction between effects of the focal and other rat's previous visits again indicates that information from those two events is combined to determine choice tendencies. Information about the quantity of food available in a location apparently requires a previous visit by the focal rat itself (because the quantity of food only affects choice tendencies if the location has been previously visited by the focal rat). Therefore, the tendency to avoid revisits to maze locations previously visited by the other rat only if the location was baited with the small quantity of food depends on combining information about *where* the other rat's choices were made with information about *what* quantity of food was found when the focal rat visited the location. This combination of information about where and what from socially-generated and self-generated memory, respectively, parallels the conclusions regarding food quality found in the experiments of Brown, et al (2008).

Limitations of Social Influence on Spatial Choice. Considered together, these results clearly indicate social influences on spatial choice. However, it should be pointed out that the magnitude of these social influences is limited and there are circumstances under which rats show little or no control by the choices of a foraging partner even when there are strong contingencies between the other rat's choice and the outcome of choices by the focal rat. A clear illustration of this point comes from a recent experiment reported by Keller and Brown (2011). In this experiment, we returned to an open field task like the one in which we began our investigations of social memory. The task involved rats searching for pellets hidden in a matrix of "pits" (Figure 16, top panel). At the beginning of each trial, a single pellet was hidden at the bottom of each pit and the rat had to lift a retractable cover in order to determine whether a pellet was hidden in the pit (and obtain it if so). On half of the trials ("Separate" trials), rats were tested individually and on the

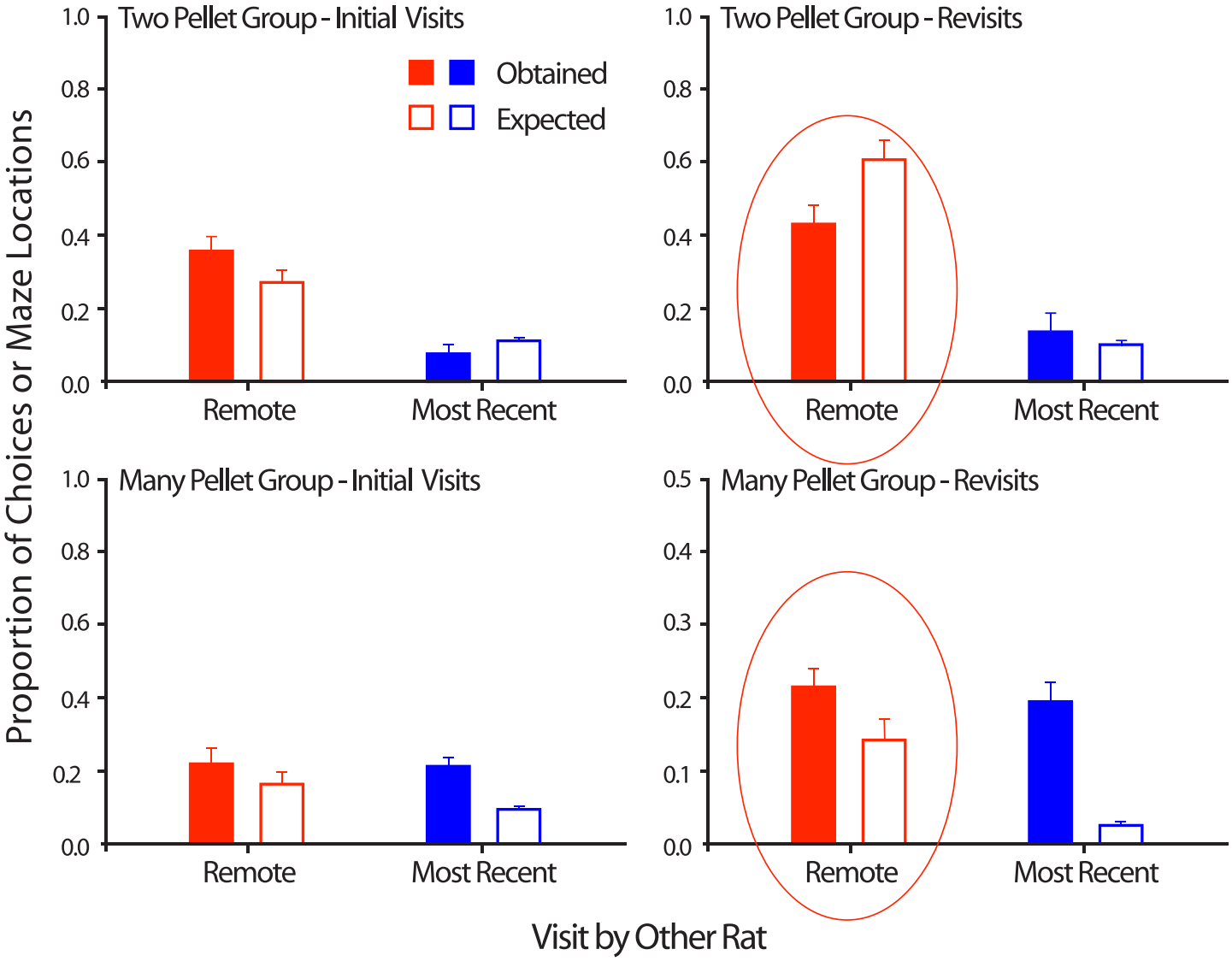

Figure 15. *Proportions of choices and choice alternatives in Brown, Prince, & Doyle (2009; Experiment 4) in the conditions with visual access restricted by sleeves covering the maze arms. The proportions are calculated separately for the focal rat's initial visits and revisits. Adapted from Figure 4, "Social effects on spatial choice in the radial arm maze, Learning and Behavior, 37, 277. Copyright 2009 by the Psychonomic Society. Adapted with permission.*

other half ("Together" trials) they were tested together with their cage mate (Figure 16, bottom panel). There were two groups of rat pairs; one group had trials that were one minute in duration (enough time to check about half of the pits) and the second group had trials that were four minutes in duration (more than enough time to check all the pits).

We compared performance in the Together trials and Separate trials by treating the separate trials as if the rats were tested together and then determining the probability of choosing a pit as a function of 1) whether the pit had been previously visited during the trial by the focal rat (i.e., was a revisit) and 2) whether the pit had been previously visited during the trial by the focal rat. In the case of the Separate trials, the two trials of the focal and other rat were temporally collated and treated as if the rats were making choices during the same trial. This was a means of controlling for any choice tendencies that might confound visits by the other rat, thus comparison of the distributions of choices in these categories for the Together trials to the distribution for the Separate trials allows effects of the other rat's choices on choices by the focal rat to by isolated.

Figure 17 shows the distribution of choices for the two groups of rats. In the case of the rats with short (one minute) trials (Top Panel of Figure 17), there was no evidence that being tested together with its cage mate had any effect on the pits chosen. In the case of rats with the long (four minute) trials (Bottom Panel of Figure 17), a pattern of results was obtained like that found in the radial-arm maze. Specifi-

Figure 16. *The Pit Maze used by Keller and Brown (2011). Each pit is covered with a retractable cover which the rat can lift to obtain access to a single sucrose pellet hidden in unvisited pits (Top Panel). A pair of rats engaged in the task (Bottom Panel). Rat in foreground is lifting cover to search for the pellet that may be hidden in the pit. A choice is defined when a pit cover is moved. Photographs from Figure 1, "Social effects on spatial choice in an open field task", Learning and Motivation, 42, 125. Copyright 2011 by Elsevier Inc. Used with permission.*

cally, there were effects of choice made by the other rat only for choices to pits that were previously visited by the focal rat (i.e., revisits; left half of bottom panel of Figure 17). For those choices, there was a systematic tendency to avoid pits visited by the other rat and a corresponding tendency to selectively visit pits that had not been visited by the other rat. It is puzzling that this effect occurs for rats with long duration trials but not for rats with short trials. We expected that shorter trials would set up a more competitive situation in which information about the choices made by the other rat would be particularly important. There was a more subtle social memory effect in the One Minute group (described in Keller & Brown, 2011), but the lack of modulation of choices by the other rat's choices more severely reduced the number of pellets obtained by each rat in the One Minute group (relative to what was possible if pits chosen by the other rat were avoided). A closer look at the data indicated that modulation of choices by the other rat's choices in the Four Minute group only occurred for choices made relatively later during the four minute trials. Thus, it may simply be that rats are not controlled by social information until after a number of choices have been made and, perhaps, control by other processes wanes.

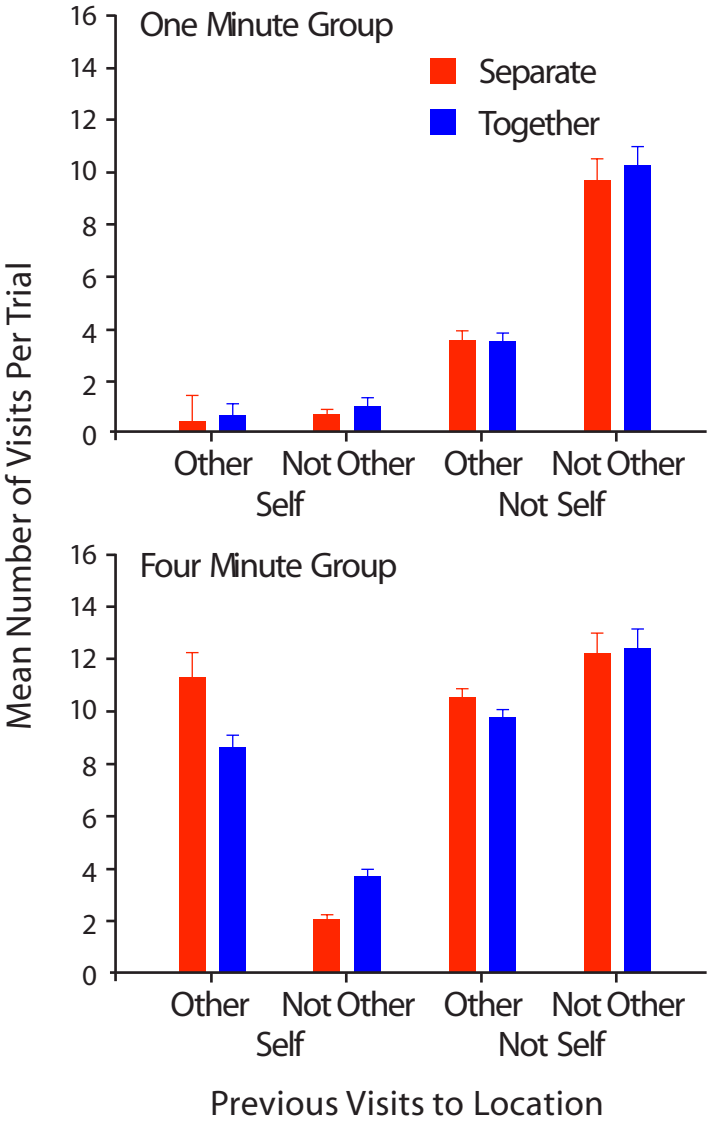

Figure 17. *Distributions of choices made by rats that experienced short (top panel) or long (bottom panel) trials in the study of Keller & Brown (2011). Distributions for Separate and Together trials are shown separately in terms of whether pits were previously visited by the focal rat and whether they were previously visited by the other rat. Adapted from Figure 3, "Social effects on spatial choice in an open field task". Learning and Motivation, 42, 128. Copyright 2011 by Elsevier Inc. Adapted with permission.*

Summary of Social Effects on Rats' Spatial Choices

Considered together, our research on social effects in laboratory spatial choice paradigms with rats provides two sets of insights into the mechanisms of social influences on spatial choice.

Opposing Forces. Social Affiliation and Social Memory Effects. Two countervailing social effects are revealed by these experiments. First, the subjects that we have used in these experiments – male Sprague-Dawley cage mates – demonstrate social affiliation in response to their cage mate and this produces a robust tendency to visit locations that are currently being, or have very recently been, visited by their cage mate. In the experiments using the radial-arm maze and a procedure in which both rats simultaneously made choices, this social affiliation effect consistently occurred for the most recent choice of the other rat (Brown, Farley, & Lorek, 2007; Brown, et al., 2008; Brown, Prince, & Doyle, 2009). In the open field task used by Brown, Farley, Solodky, and Bachrach (2005; "pole box maze") a small social affiliation effect was found during the first of three trial blocks. No evidence of a social affiliation effect was found in the open field task used by Keller and Brown (2011). In the radial-arm maze, a rat is likely to be spatially proximal to its most recent choice but much less likely to be spatially proximal to choices made earlier (more remotely). In the open field tasks there is a substantially weaker correspondence between the recency of a rat's previous spatial choices and its current location in relation to those choices. This is because a return to a central location between each choice is required in the radial arm maze, whereas in the open field tasks multiple choices can be made in succession in the same area of the apparatus. Because of this, we were able to distinguish between choices made to locations where the other rat is physically present and locations made to locations where the rat had made choices but was not physically present only in the radial-arm maze experiments. Thus, we were able to dissociate effects of the other rat as a physically present stimulus from social memory effects on in the radial-arm maze experiments.

Locations visited earlier by the other rat, but where the other rat is not (or is unlikely to be) physically present, on the other hand, are either avoided or selectively visited, depending on their hedonic value. If a previous (remote) visit by the other rat results in depletion of food in that location, then those locations are avoided in the radial-arm maze (Brown, Farley, & Lorek, 2007, Experiment 1; Brown, Prince, & Doyle, 2009, Experiment 4, 2-pellet condition) or come to be avoided with experience in the pole maze task (Brown, Farley, Solodky, and Bachrach, 2005). The effect of remote choices by the other rat when its visit does not deplete the resource in that location, however, depends on the information *available to the focal rat* about the properties of the resource in that location (see next section for explanation of the *italicized qualifier*). Remote visits by the other rat to locations not depleted of pellets (when visits to other locations do result in depletion) increase the tendency to visit those locations whereas remote visits by the other rat to the depleted locations decrease the tendency to visit those locations (Brown, Prince, & Doyle, 2009; Experiment 4). Likewise, remote visits by the other rat to locations containing a preferred food type increase the tendency to visit those locations whereas remote visits by the other rat to locations containing the unpreferred food type (Brown, et al., 2008). Thus, remembered spatial choices by a foraging partner provide information that can guide spatial choices in a flexible manner, depending on other information available about the spatial choice alternatives. This is in contrast to the social affiliation effect produced by a physically present rat, which is less flexible. We find no evidence that the social affiliation tendency is modulated by the outcome of visiting spatial locations in which the other rat is present.

Synthesis of Social and Self Egocentric Information. A second general conclusion to be drawn from these experiments is that information from memories of a rat's own visits to a spatial location is combined with information from social memory for the locations visited by another rat to determine subsequent choices. In the experiments of Brown et al (2008) and those of Brown, Prince, and Doyle (2009) locations visited by the other rat were avoided by the focal rat only if. 1) the focal rat had itself earlier visited that same location and 2) the location contained an outcome of relatively lesser value (grain rather than sucrose pellets in the case of Brown et al, 2008; no more pellets rather than additional pellets in the case of Brown, Prince, & Doyle, 2009). We infer that information about the value of the reinforcement is obtained when the focal rat visits the location and either encounters the lower value grain pellets or depletes the two-sucrose pellets. The remembered value of the location can then modulate the response to a location that is remembered to have been visited by the other rat.

Difficulties Inherent in Experimental Studies of Social Influence and Social Memory. One of the advantages of studying behavioral phenomena in laboratory paradigms is the control one has of the variable of interest. A difficulty inherent in the study of social phenomena, however, is that the stimuli of interest cannot be controlled like a physical stimulus can be. In fact, our experience with the model/observer paradigm (Figures 8 – 10) suggests that getting experimental control of the social stimuli of interest greatly reduces the psychological control that social stimuli have on behavior. The free choice paradigms in which two rats are allowed to full interact and make choices simultaneously have the advantage of maximizing the opportunity for social

influence and interaction but relinquish experimental control of the social stimulus. The forced choice procedures used by Brown, Farley, & Lorek (2007), on the other hand, allow better experimental control but result in lower levels of social influence, apparently because of the reduced social interaction between the two rats. Progress in understanding the mechanisms of social learning and memory is probably going to require that this trade-off be accommodated with the kind of converging operations represented by work reviewed in this paper.

Future Directions for Experimental Studies of Social Influence and Social Memory. A wide variety of examples of social learning in natural settings have been well documented (e.g., Kendal, Galef, & van Schaik, 2010; Reader & Biro, 2010). Several lines of laboratory research using rats provide detailed information about examples of social learning, such as food preference learning (e.g., Galef, 1989; 2005; 2007; Galef & Wigmore, 1983) and imitation (Heyes & Galef, 1996; Zentall, 2003; Zentall & Galef, 1988). A recent line of experimental research using female laboratory rats suggests memory for the behavior of specific individuals that is used in the context of cooperative behavior (Rutte & Taborsky, 2008). These examples all require that information about the behavior of a conspecific be represented in memory. The work described here shows that memory for social information can be isolated from other effects of social stimuli and that memory for the behavior of others can be used to flexibly guide subsequent behavior in combination with other kinds of remembered information. These conclusions and the techniques that guided them can be applied to a wide range of social phenomena.

However, the experiments reviewed here also provide a cautionary note for analyses of complex social behavior like the natural foraging behavior, imitative behavior and social influences on food preference reviewed above. There are multiple influences of social partners on behavior and choice. They interact in complex and sometimes counter-intuitive ways even in the context of the relatively simple social situations examined in these experiments. Any complete understanding of complex social influences is going to require that those influences first be experimentally isolated in the manner described here. Only then will we be in a position to begin understanding how those influences interact to produce natural behavior.

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