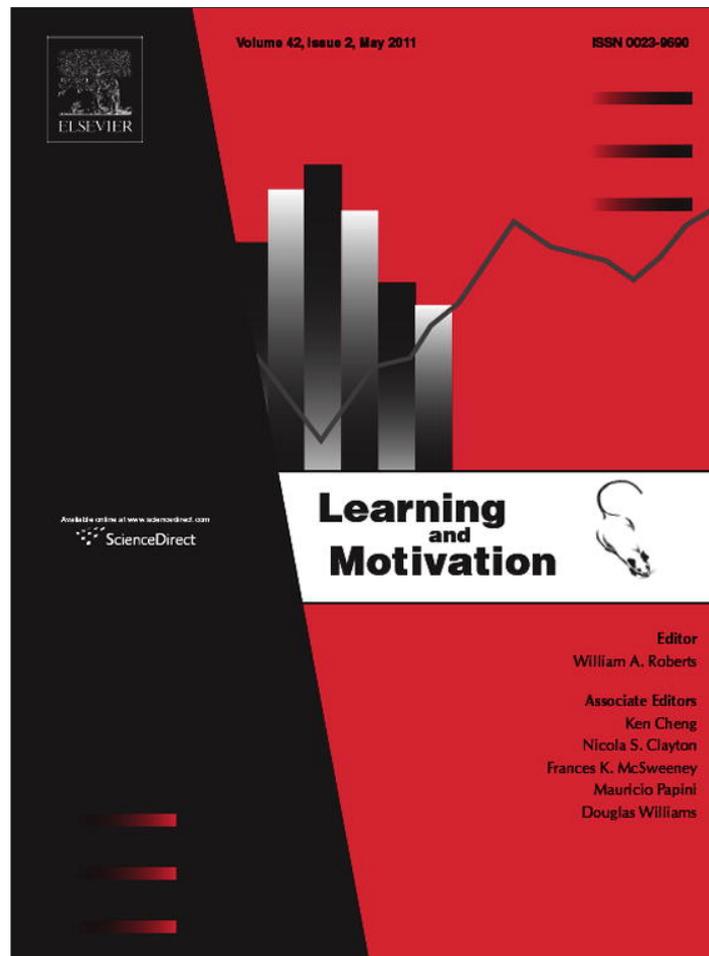


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Social effects on rat spatial choice in an open field task[☆]

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ARTICLE INFO

Article history:

Received 11 August 2010
 Received in revised form
 21 December 2010

Keywords:

Social memory
 Spatial choice

ABSTRACT

Pairs of rats foraged in trials either together or separately in an open field apparatus for pellets hidden in discreet locations in a 5×5 matrix. Trial duration was either 1 or 4 min. The tendency to choose locations that had earlier been visited by another rat was examined by comparing the choices made in the presence and absence of the other rat. Rats avoided visits to locations that had earlier been visited by the other rat, but only if they had also visited the same location earlier in a short duration trial. This pattern of results is consistent with earlier findings from experiments using the radial arm maze. Furthermore, when rats did visit locations that had earlier been visited by the other rat in a long duration trial, they tended to be locations that had been visited longer ago by the other rat than would be expected. This suggests a forgetting function for social memories. These data provide evidence that the social memory reported in earlier studies using the radial-arm maze can be found in other experimental paradigms and that at least some of its properties are common in the two paradigms.

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There is growing evidence that social learning is important for many animals (e.g., Galef & Laland, 2005; Heyes & Galef, 1996; Zentall & Galef, 1988; Zentall, 2003). For example, theories of foraging behavior and the data supporting them indicate important effects of conspecifics' behavior (e.g., Barnard & Sibly, 1981; Fretwell & Lucas, 1970; Galef & Giraldeau, 2001; Giraldeau, 2000). In addition, laboratory studies have shown that food aversions and food preferences are socially transmitted in rats (Galef, 1989; Galef, Lee, & Whiskin, 2005; Galef & Whiskin, 2003; Galef & Wigmore, 1983).

Despite this, very little is known about the existence of, properties of, or mechanisms of memory for the behavior of other animals. Social memory may involve the same processes that detect, store, and process information about physical stimuli. However, it also seems quite possible that some of the processes involved in social memory and cognition are specialized, as has been argued (primarily on theoretical grounds) to be the case in both humans (e.g., Fodor, 1983; Pinker, 2002) and non-human animals (e.g., Lefebvre, Giraldeau, Heyes, & Galef, 1996).

Surprisingly, there have been few empirical studies conducted by comparative cognitive psychologists in which the behavior of another animal served as the to-be-remembered stimulus. Although it seems clear that animals must form and use memories of the behavior of others, we need systematic evidence of the existence of memories with social content, as well as empirical analyses of their properties, in order to determine whether there are psychological systems that are specialized for such social memories.

Recent experiments conducted in our laboratory have been directed at the goal of obtaining this kind of evidence. The experiments isolate the effects that rats making choices together in a radial-arm maze have on each other and the role of social memory in producing those effects (Brown, Farley, & Lorek, 2007; Brown et al., 2008; Brown, Prince, & Doyle, 2009). These experiments demonstrate that choices made by a foraging partner affect the spatial choices made by rats. However,

[☆] The experiment reported in this paper was part of a M.S. thesis project completed by M.R.K.

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the nature of that effect varies depending on at least three factors. First, if the foraging partner is physically present, then the focal rat has a tendency to choose the location of the other rat. However, locations that were previously visited by the foraging partner, but where the partner is no longer physically present, tend to be avoided. This pattern of results was found in free choice procedures (in which both rats make choices simultaneously) used by Brown et al. (2007, 2008, 2009). In the forced choice procedures used by Brown et al. (2007), in which only one rat makes choices at a time such that the foraging partner was never physically present when the focal rat made its choices, only avoidance of locations previously visited by the other rat was found. Thus, it appears that the physical presence of the foraging partner functions as an attractant, increasing the likelihood of choosing locations just chosen by the partner. However, there is also a social memory effect that inhibits choice of locations previously visited by the partner, presumably because of the contingency between previous choices by the foraging partner and the absence of food in that location (Brown et al., 2009).

A second and a third factor appear to work together to modulate the social memory effect. Brown et al. (2008) used a maze with arms that were baited either with an undepletable amount of either a less preferred food or a more preferred food, the locations of which varied unpredictably from trial to trial. They found that the tendency to avoid locations previously visited by the other rat occurred only in the case of locations baited with the less preferred food and only if the focal rat itself had previously visited that location. They interpreted this pattern of results as indicating the rat determined the value of the food with which a location was baited during its own first visit to that location and then modulated its response to memories of the other rat's visits, avoiding visits to locations visited by the other rat only if they were known to contain the less preferred food. A directly analogous pattern of results was found by Brown et al. (2009) who, instead of varying the quality of the food with which maze arms were baited, varied the quantity of food on maze arms such that the food either was or was not depleted by the other rat's previous visit. Maze arms visited by the other rat were avoided only if they were known to contain the depletable amount of food (by virtue of the focal rat's own visit – and depletion – of the maze arm).

The present experiment was intended to explore the generality of these social effects on spatial choice and the role of social memory therein. Rats were tested in an open field apparatus in which sucrose pellets could be obtained from discrete locations in a matrix of 25 locations. Following initial training, two kinds of daily trials occurred. In half of the trials, each rat was tested individually. In the other half of the trials, rats were tested together with their cage mate. In these social trials, choice efficiency could be greatly improved by information about the choices made by the other rat, in that the locations previously visited by the other rat are depleted of pellets. As described above, however, results from the experiments involving the radial arm maze indicate that social effects on spatial choice are sometimes consistent with this contingency but can also produce a tendency that is in opposition to it.

A potentially important difference between the present task and the radial arm maze task is the extent to which rats are exposed to each other in an open field apparatus, relative to the radial maze. In a standard radial maze, rats can interact with each other only in the central arena or when they are on the same maze arm. The open field apparatus used here allows rats to be in constant perceptual contact with each other. It may thereby have more in common with the natural contexts in which social foraging occurred for the ancestors of our subjects and which occur for social foragers more generally.

The present experiment allows direct comparison of choices made in the social and individual trials, in a manner that allows any influence of choices made by the other rat to be detected. An important part of the analysis is that the data from the individual trials were treated as though the rats were tested together to allow social effects to be detected. In particular, the analysis focused on whether locations previously visited by the other rat were less (or more) likely to be chosen. Because of the many complex factors affecting (or potentially affecting) the choices made in this open field task, the tendency to choose locations visited earlier by the other rat in the social trials was compared to the tendency to choose locations visited by the other rat when the two rats were actually tested in separate trials but the data from those two separate trials were analytically yoked.

Method

Subjects

The subjects were 22 male Sprague-Dawley rats obtained from Harlan Sprague-Dawley (Indianapolis, IN). They were housed in pairs in 45 cm × 24 cm × 20 cm (tall) cages on a 12:12 h reverse light:dark cycle. The rats were tested during the dark phase of the cycle. They were food deprived to maintain them at 90% free feeding weight (in comparison to growth curves provided by the vendor) and had *ad libitum* access to water.

Apparatus

The rats were tested in a 1.17 m square area enclosed by 14 cm tall walls and painted flat black (Fig. 1). An overhead 45 W incandescent light and two fluorescent tubes illuminated the arena. A rat cage (identical to the rats' home cage) was attached to one outside wall of the arena and served as a start box; access to the maze from this start box was regulated by a guillotine door controlled by a string-and-pulley system.

A matrix of equally spaced (20.0 cm center-to-center) "pits" defined the locations that could be chosen by the rats. The pits were constructed of plastic funnels (painted flat black) and placed inside 12 oz plastic cups that were secured in the



Fig. 1. Top panel: The testing area showing the matrix of 25 pits with pit covers in place. Bottom panel: A pair of rats foraging together in the testing area. The rat in the foreground has just begun to lift the cover funnel to gain access to the pit.

floor of the maze such that the lip of the cup was flush with the floor of the arena, with the lip of the funnel directly on top (See Fig. 2). The funnels were 5.0 cm deep, 7.6 cm in diameter at the top and 1.3 cm in diameter at the bottom. The bottom of each pit was formed by nylon mesh screen, on top of which a sucrose pellet could be placed to bait the pit. Underneath the mesh floor of the pit (in the bottom of the cup) were 8–10 sucrose pellets which controlled for any effects of odor from



Fig. 2. Detail of construction of the pits. The cover (upper) funnel must be lifted to gain access to the pit. A weighted string holds the cover funnel in place and returns it to its place after a rat lifts it. The lower funnel (which functions as the bottom of the pit) is also lifted in the photograph to show the well containing the sham (odor control) pellets. However, the lower funnel is fastened in place during trials and is not moved by the rats. Pits are baited with single pellets placed inside the neck of the cover funnel and on the mesh floor inside the lower funnel.

the pellets that might be detectable by the rats (These “sham bait” pellets were present in all pits, regardless of whether an accessible pellet was present on the bottom of the pit).

As shown in Fig. 2, the pits had a second (“cover”) funnel placed inside that acted as a lid that was lifted to gain access to the pellet hidden inside the stem of the cover funnel on the bottom of the pit (if the pit was still baited). Each cover funnel was attached to a string that led through the mesh floor and a hole in the bottom of the cup extending under the platform, ending with a 6 g washer, the weight of which held the cover funnel in the bottom funnel unless the cover funnel was being pushed up by a rat’s head as the rat gained access to the pit. The cover funnel retracted back into the first funnel (because of the weight of the washer) after they were lifted so that there were no visual cues as to which pits were visited.

Procedure

Trial procedure (common to all experimental phases)

Prior to each trial, a sucrose pellet (Noyes 45-mg black sucrose pellets, Product F05480) was placed in the bottom of each pit (inside the stem of the cover funnel if it was present). The rat or pair of rats was placed in the start box. The door between the start box and arena was then raised. A timer was started when the rat’s head entered the arena (or when the first rat did so when the rats were being tested together). Trials were recorded via a camera mounted directly above the arena. Choices were coded from the resulting videotapes and were defined when there was any movement of a cover funnel caused by the rat’s head (regardless of whether a pellet was obtained). A trial ended when the scheduled trial duration expired, at which time the rat(s) were removed from the arena. Daily feeding occurred after the experimental procedures.

Training Phase 1 (14 daily trials)

In each trial of the first phase of training, the rats foraged together with their cage mate until all pellets were removed from the funnels or 20 min elapsed. During this phase, the cover funnels were not present.

Training Phase 2 (21 daily trials)

The rats foraged with their cage mates as in Training Phase 1, but a shaping procedure was used in which a third of the cover funnels were completely lifted out of the pit (and were on their side on the arena surface), a third were lifted slightly to encourage the rats to lift the funnels for access to the pellet and a third were not lifted (so that the rats had to lift them completely to obtain the pellet). The first trial of this phase was 20 min in duration, the second was 15 min, the third 10 min, and the final 18 trials were 5 min in duration. The shaping procedure was continued until each rat chose at least 20 pits during a trial. One pair of rats failed to lift the top funnel and was dropped from the experiment.

Training Phase 3 (14 daily trials)

The third phase of training involved introducing the social manipulation to be used in testing, in which the rats were tested together with their cage mate on half of the trials and they were tested separately on the other half of the trials. The trial duration remained 5 min. Three rats (from three different pairs) did not consistently lift the cover funnels, so they were returned to the shaping procedure described above for three trials. By the sixth trial of this phase, all rats were consistently lifting the cover funnel, thereby gaining access to the pellet. Training was suspended for one week due to several rats losing a substantial amount of weight for unknown reasons. During this break, all the rats were removed from their diets and given free access to food. Their weights increased to near free feeding levels, and they were then returned to their restricted diet and the training protocol.

Testing Phase (24 daily trials)

The present experiment used a 2×2 design in which the duration of trials (1 min vs. 4 min) was manipulated between groups, and social condition was manipulated within groups (together trials vs. separate trials). Five pairs of rats (randomly chosen) were assigned to each trial duration condition. Each rat was tested in one trial per day for six days in each of four trial blocks. In a randomly determined half of the trials in each trial block, the rats were tested individually in separate trials. In the remaining trials, each rat was tested together with its cage mate. These assignments to the separate and together conditions were synchronized so that each day, all 20 rats were tested in the same social condition.

Results and interpretation

Data analysis

Data from the testing phase were coded using a tracking program (locally created using Microsoft VisualBASIC™ Version 6.0). The video recording for each trial was used to specify the location of a rat in *xy* coordinates as a function of time since trial start (with a resolution of 10 Hz). This was accomplished by the coder following the rat’s path on the video recording with a computer pointing device (“mouse”) cursor. Additionally, the coder clicked the mouse button when the rat chose a pit (defined as movement of the cover funnel caused by the rat’s head) and the program identified the pit chosen based on the mouse cursor *xy* coordinates. For Together trials (in which a rat was tested with its cage mate), each trial was coded twice, once for each rat. The choices made by the two rats during a Together Trial were collated with respect to the time

of each choice since trial start (defined when one of the two rats entered the arena). Two different coders were involved in generating the data set; one (M.K.) was familiar with the goals of the experiment, and the other was naïve as to the goals and predictions. Data from two days were coded by both coders to allow determination of inter-coder agreement. M.K. coded 98% of the choices coded by the naïve coder; the naïve coder coded 95% of the choices coded by M.K. Thus, choices as operationally defined were reliably discriminated by the coders.

Of primary interest was the tendency of rats to choose pits that had been visited by the other rat earlier during the trial. That tendency was evaluated by comparing the number of choices that were to pits previously visited by the other rat in the together trials to the corresponding number of choices that were to pits visited earlier by the other rat in the separate trials. That is, the separate trials were treated analytically as though the two rats were making choices together during the same trial although they actually were not. Thus, the data from each trial allowed the choices made by each of the two rats to be analyzed with respect to the earlier choices made by the other rat. This analytical technique allowed us to evaluate the tendency to visit pits as a function of previous visits by the other rat in the Together trials in comparison to a control condition that equated numerous known and potential dynamic properties and tendencies of rats to make choices in this task. For example, rats prefer the locations in open fields tasks that are near the walls of the arena (“thigmotaxis”), and that tendency would confound any tendency to choose pits in a manner that correlates with the location chosen by the other rat. Rats also may have consistent (across rat) preferences for particular locations based on lighting, proximity to the experimenter’s station, etc. Such preferences would also confound any correlation of one rat’s choices with those of a foraging partner. However, these and other shared tendencies that are not explicitly determined by the behavior of the other rat would be equivalent in the separate and together conditions. Any differences in the tendency to visit pits that were earlier visited by the other rat, however, must be due to the presence of the other rat. Thus, the key comparisons in the analyses of the data from this experiment are comparisons of the number of pits visited by the other rat in the together condition with the corresponding number of pit visits in the separate condition.

In addition to social condition, the tendency to choose pits was evaluated in terms of three other factors. The first was whether the pit had previously been visited by the other rat. As indicated above, there might be differences in the tendency to visit pits as a function of previous visits by the other rat for reasons that do not have to do with social effects of the other rat *per se*, but instead with factors that confound previous visits by the other rat. Modulation of those differences by social condition, however, would reveal effects that must be attributed to the presence of the other rat during the trial. Thus, an interaction of effects of social condition and previous visits by the other rat would be a direct indication of social influence on choices of pits.

The second factor included in the primary data analysis was whether the pit had previously been visited by the focal rat itself. The expectation was that pits previously visited would be avoided, just as arms of the radial-arm maze that have already been visited tend to be avoided. However, the analytical techniques used in the present experiment do not allow this expectation to be directly confirmed, because the many complexities of choice dynamics in this task make it very difficult to estimate the tendency to revisit pits that would be expected on the basis of chance. This factor is included in the analysis because the work from our laboratory in the radial maze indicates that social effects of the other rat on spatial choices only occur (or are larger in magnitude) in the case of visits to locations that have previously been visited by the focal rat itself (i.e., revisits) than in the case of initial visits to locations. Inclusion of this factor allowed us to determine whether this pattern of results generalizes to the present task.

Finally, Trial Duration (1-min vs. 4-min trial group) was a factor in the analysis. This manipulation was originally motivated by an expectation on our part that shorter trials would increase the importance of information about the choices made by the other rat and that social effects would therefore be enhanced in the 1-min condition.

Findings

Fig. 3 shows the mean number of pits visited per trial as a function of trial duration group, social condition, whether the pit was visited by the focal rat earlier during the same trial, and whether the pit was visited by the other rat earlier during the trial. These results were evaluated using a 2 (trial duration group) \times 2 (social condition) \times 2 (self visited status) \times 2 (other visited status) analysis of variance (ANOVA), with the last three factors treated as repeated measures. Table 1 shows the ANOVA results. It should be noted that some effects in this analysis may not be interpreted in a meaningful manner. For example, the effect of trial duration can be attributed (at least in large part) simply to the additional time during which choices may be made. The effect of previous visits by the focal rat and by the other rat (as well as the interaction of those factors with trial duration) must be interpreted in the context of the increase in the proportion of pits previously visited as the trial progresses.

As explained above, the key factor in this analysis is the effect of social condition and, even more so, the manner in which it interacts with these other effects. Because the four-way interaction among the factors in this analysis was significant, additional ANOVAs were performed to understand the effects involving social condition. In what follows, only ANOVA factors including social condition will be reported. First, we conducted two social condition \times self visited status \times other visited status ANOVAs, one using the data from each trial duration condition (corresponding to the data from each of the two panels of Fig. 3). In the 1-min group, there was no significant effect of social condition, $F(1, 9) = 2.2$, and social condition did not interact with the visit status of the focal rat or the visit status of the other rat, both $F_s(1, 9) < 1$. The 3-way interaction among these three factors was also not significant, $F(1, 9) < 1$. In the case of the 4-min group, there was also no evidence of

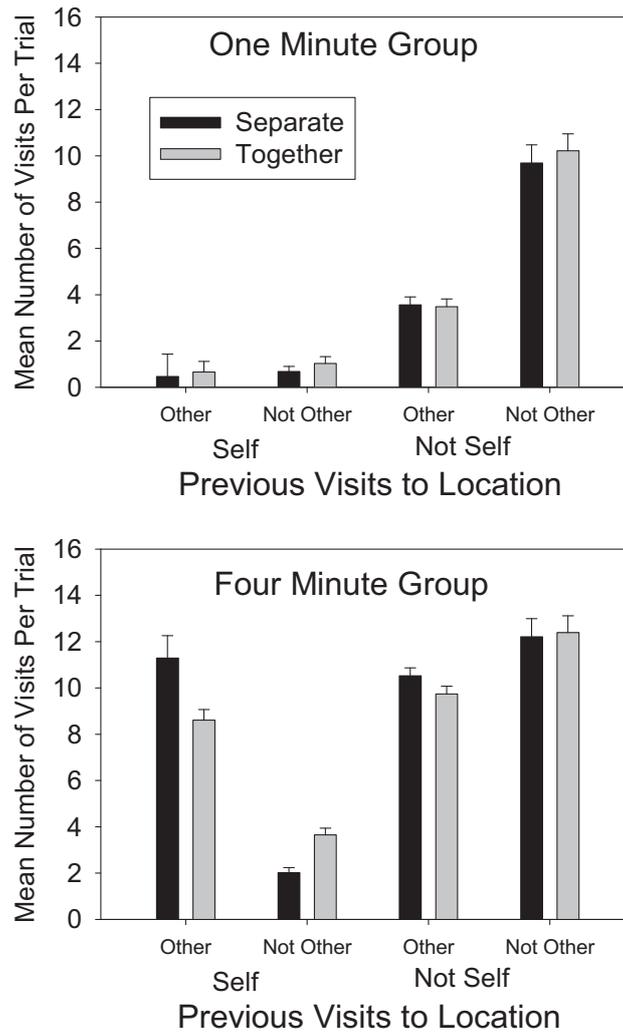


Fig. 3. The mean number of visits per trial to pits in the 1-min (top panel) and 4-min (bottom panel) groups. Visits are shown separately for the separate trials and together trials and as a function of whether the pit had been visited earlier during the trial by the focal rat and by the other rat.

a main effect of social condition, $F(1, 9) = 3.6$, and no interaction between social condition and self visit status, $F(1, 9) < 1$. However, the visit status of the other rat and social condition produced a significant interaction, $F(1, 9) = 38.6$, $p < .001$, and the three way interaction among social condition, the visit status of the other rat, and the visit status of the focal rat was also significant, $F(1, 9) = 5.6$, $p < .05$.

The latter interaction was probed with two additional ANOVAs, one for each focal rat visit status in the 4-min group. In the case of pits that had not been previously visited by the focal rat (corresponding to the two pairs of bars on the right

Table 1
ANOVA results for number of pit visits per trial.

Factor	df	F value	p Value
Trial duration group (TDG)	(1, 18)	135.5	<.001***
Social condition (SC)	(1, 18)	<1	>.05
Self visited status (SVS)	(1, 18)	251.0	<.001***
Other visited status (OVS)	(1, 18)	1.11	>.05
TDG × SC	(1, 18)	5.76	<.05*
TDG × SVS	(1, 18)	3.10	>.05
TDG × OVS	(1, 18)	47.9	<.001***
SC × SVS	(1, 18)	<1	>.05
SC × OVS	(1, 18)	24.89	<.001***
SVS × OVS	(1, 18)	237.3	<.001***
TDG × SC × SVS	(1, 18)	<1	>.05
TDG × SC × OVS	(1, 18)	13.89	<.01**
TDG × SVS × OVS	(1, 18)	9.8	<.01**
SC × SVS × OVS	(1, 18)	2.98	>.05
TDG × SC × SVS × OVS	(1, 18)	5.20	<.05*

Note: * $p < .05$, ** $p < .01$, *** $p < .001$.

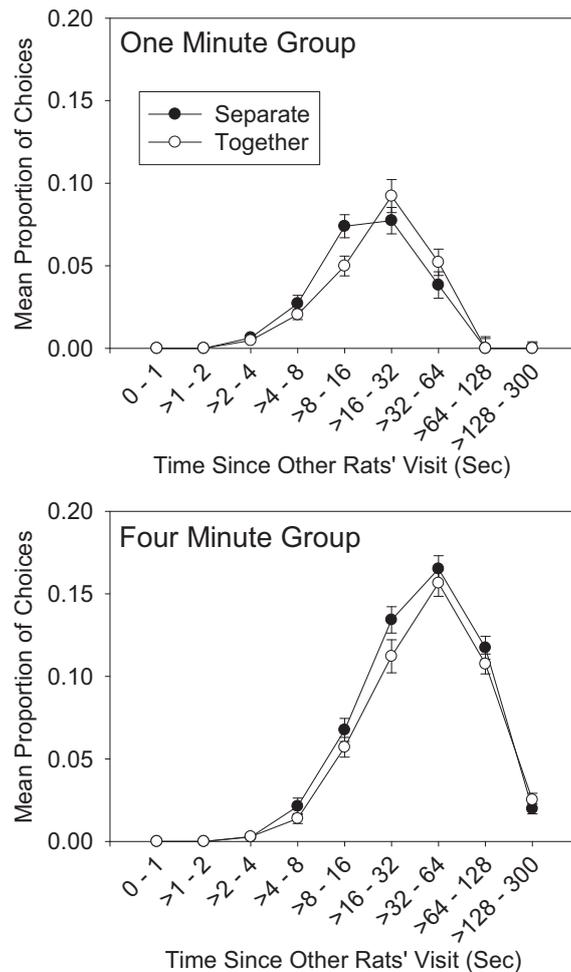


Fig. 4. Data from visits to pits that had been visited by the other rat earlier during the trial. The distributions of choices as a function of the time since the pit was visited by the other rat are shown for the 1-min (top panel) and 4-min (bottom panel) groups for the separate trials and together.

side of the lower panel of Fig. 3), there was no significant effect of social condition, $F(1, 9) = 3.8$, and no interaction between social condition and the visit status of the other rat, $F(1, 9) = 2.7$. In the case of pits that had been previously visited by the focal rat (corresponding to the two pairs of bars on the left side of the lower panel of Fig. 3), there was no significant effect of social condition, $F(1, 9) < 1$, but there was an interaction between social condition and the visit status of the other rat, $F(1, 9) = 18.4, p < .01$. The form of this interaction was revealed by the results of two t -tests, which confirmed that the number of choices of pits that had been visited by the other rat was less in the paired trials than in the separate trials, $t(9) = 2.75, p < .05$, whereas the number of choices to pits that had not been visited by the other rat was greater in the paired trials than in the separate trials, $t(9) = 6.0, p < .001$.

A second set of analyses is concerned only with choices of pits that were previously visited by the other rat. If memory is involved in the avoidance of pits visited earlier by the other rat, and if one assumes a recency effect (better memory for choices made by the other rat more recently than choices made longer ago), then visits to pits visited early by the other rat should tend to be those visited relatively longer ago. A comparison of choices as a function of the time since the other rat visited the pits that were visited by the focal rat is shown in Fig. 4. For each group, two distributions of intervals between the other rat's visit (its most recent visit, in the case of a pit visited more than once by the other rat) to a pit and the focal rat's visit to that same pit are shown; one for the separate trials and the other for the together trials. Note that the time between the two rats' choices are classified into bins defined on a logarithmic (\log_2) scale, corresponding to the scalar relationship between objective time and psychological effects of time intervals of these magnitudes (e.g., Church, 2006). The distributions are in terms of the proportion of all choices made (the proportion of choices that were to pits not visited by the other rat is not shown, but is included in calculation of these proportions). It should be noted that these distributions are affected by a number of relatively uninteresting factors; for example, the frequency of longer intervals are constrained by the trial duration (e.g., an interval of more than 60 s is not possible in the 1-min condition). However, comparison of the distributions for the together trials and separate (control) trials allows effects of the other rat to be detected. In the case of the 1-min group, the distribution for the together trials appears to be shifted to the right relative to the separate trials, indicating that when pits earlier visited by the other rat were chosen by the focal rat, they tended to be pits that had been visited longer ago by the other rat than would be expected without the presence of the other rat. For the 4-min group, on the other

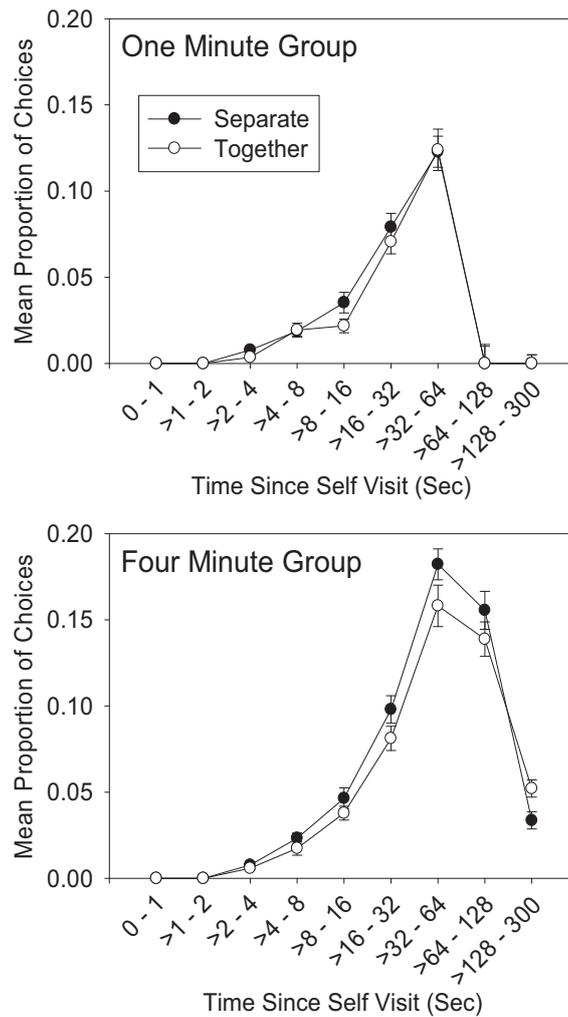


Fig. 5. Data from visits to pits that had been visited by the focal rat earlier during the trial. The distributions of the choices as a function of time since the earlier visit to the pit by the focal rat are shown for the 1-min (top panel) and 4-min (bottom panel) groups for the separate trials and together trials.

hand, there does not appear to be such a shift in the distribution. This pattern of results was confirmed by the following analyses.

A 2 (trial duration group) \times 2 (social condition) \times 9 (bin – time since other rat's visit) ANOVA, with repeated measures on the latter two factors, was performed to compare the proportions shown in Fig. 4. A significant three-way interaction among these factors was found, $F(8, 144) = 2.59, p = .01$. This interaction was probed with two social condition \times bin ANOVAs, one for each trial duration group. In the 1-min Group, there was no evidence of a main effect of social condition, $F(1, 9) < 1$, but there was a significant interaction between social condition and bin, $F(8, 72) = 3.5, p < .01$, confirming the shift in the distribution. In the 4-min group, there was a main effect of social condition, $F(1, 9) = 44.5, p < .001$, but there was no significant interaction between social condition and bin, $F(8, 72) = 1.2$. The main effect of social condition confirms the earlier conclusion that in the 4-min group, pits visited by the other rat were less likely to be visited by the focal rat.

Considered together, these results show social memory effects in both the 1-min group and the 4-min group. However, the social effect is revealed in different ways. In the 4-min group, the probability of visiting pits is lowered by the other rat's previous visits. As in the radial arm maze experiments (Brown et al., 2007, 2008, 2009), this effect of the other rat's visits is restricted to locations that had also been previously visited by the focal rat itself. In the 1-min group, however, there is no evidence that the probability of visiting pits is lowered by the other rats' visits. On the other hand, in the 1-min group the pits visited by the focal rat that were earlier visited by the other rat tend to be those visited longer ago by the other rat, indicating a (possibly more subtle) tendency to avoid locations visited by the other rat in that group as well.

A third set of analyses was conducted to examine the choices of pits that were earlier visited by the focal rat (i.e., revisits). Do previous visits by the other rat affect the ability of the focal rat to remember its own choices (and thereby avoid revisits)? Such an effect might be predicted, for example, by interference between a rat's memory for its own choices and social memory for the choices made by the other rat? Fig. 5 shows distributions that are analogous to those shown in Fig. 4, but are distributions of choices as a function of time since a chosen pit had been chosen by the focal rat itself. As before, the proportions of choices to pits that had not been previously visited is not shown, but is used in calculating the proportions. A 2 (trial duration group) \times 2 (social condition) \times 9 (bin – time since other rat's visit) ANOVA was performed to compare the

proportions shown in Fig. 5, with repeated measures on the latter two factors. There was no evidence of a triple interaction, $F(8, 144) = 1.8$. There was a significant interaction between social condition and bin, $F(1, 18) = 2.3$, $p < .05$, as well as a significant effect of social condition, $F(1, 18) = 10.0$, $p < .01$. The interaction is probably best explained in terms of the floor effect produced by bins containing small proportions of choices. The main effect of social condition indicates that rats are less likely to revisit pits (i.e., less likely to visit pits that they themselves visited earlier during the trial) when the other rat is present. The fact that this tendency is *not* modulated by the time since the earlier visit suggests the possibility that this may not be a matter of memory interference, but rather an increase in how efficiently memories for one's own choices are used. Competition from the other rat may produce a motivational effect that increases control by memory but does not affect the quality of memory.

Conclusions

Spatial choices in the present open field task were affected by the choices made earlier during the trial by the other rat, under a restricted set of conditions. There were two kinds of social effects on choice and they were obtained under different experimental conditions. Among rats with longer duration (4-min) trials (and therefore more choices per trial), a tendency to avoid pits previously visited by the other rat was found. Importantly, the restriction of social effects to locations previously visited by the focal rat replicates the pattern of results found in the radial arm maze by Brown et al. (2008, 2009). However, in those experiments, locations differed in terms of the quantity (Brown et al., 2009) or quality (Brown et al., 2008) of food available in that location, and the previous visit by the focal rat was necessary for it to identify the content (quality or quantity) of the food in the location. The food available in the pits locations in the present experiment does not differ in any way that requires a previous visit by the focal rat to identify (i.e., all the pits are baited with one sucrose pellet at the beginning of the trial). Thus, some other mechanism is required to explain the interaction of a previous visit by the other rat and a previous visit by the focal rat in modulating spatial choices. One possibility is that a visit to a pit allows the location of that pit to be better determined subsequently during the trial. Thus, when the other rat visits a pit, the location of that pit can be better discriminated (and the pit can thereby be better avoided) if the focal rat has visited that pit earlier during the trial. Obviously, additional empirical work will be required to test this possibility.

In any case, the pattern of results found for pit visits in the 4-min condition replicates the pattern of results found in the earlier radial-arm maze experiments from our laboratory. However, the corresponding pattern of results in the 1-min condition provides no evidence for social effects on spatial choice. The most reasonable explanation for that aspect of the results is the very small number of choices made to pits that were previously visited by the focal rat (i.e., revisits). This would be expected simply on the basis of the limited time available to make choices in that condition. Thus, given the modulation of social effects by previous visits by the focal rat, the lack of social effects in the 1-min condition is not surprising. When all of these factors are considered together, the pattern of results for pit visits in the present experiment is very consistent with the pattern of maze-arm visits found in the earlier experiments using the radial-arm maze.

A limitation of the pit visit data discussed above is that they do not isolate social effects due to memory from social effects that might require the physical presence of the other rat at or nearby a location it had just visited. As described above, the earlier radial maze experiments show that social effects on spatial choice are quite different when the other rat is physically present than when the other rat is no longer present at the location it previously visited. Of course, the findings and conclusions from the radial maze experiments, when applied to the present task, would predict a tendency to selectively visit (rather than avoid visiting) the locations previously visited by the other rat. So the fact that we find a tendency to avoid visits to locations previously visited by the other rat could be taken as more consistent with effects expected when the other rat is physically absent from the effective location. That conclusion must be suggested with a great deal of caution. The fact is that we have no way of determining which choices are made in the presence of the other rat and which are made in its absence, because the physical structure of the open field task does not allow clear determination of when the rats do and do not have visual access to each other.

However, the secondary data analyses involving time since the other rat's visit (for choices to locations that were previously visited by the other rat) provide a strong indication that, at least in the 1-min condition, social effects occur for locations that were chosen at least 10 s ago by the other rat. Given the rate at which choices were made in this task, it is very unlikely that a rat remained in the vicinity of a pit chosen 10 s ago. Thus, we conclude that this effect must be attributed to information about the other rat's previous visits that does not require its physical presence. The distribution of choices as a function of time since the other rat's visit is shifted to longer durations in the together condition (relative to the separate condition) because when the rat visits locations that had been earlier visited by the other rat, those locations tend to be those visited longer ago by the other rat. Thus, this effect reveals a forgetting curve for the information about the other rat's previous visits; the longer ago the other rat's visit to a location occurred, the less likely the focal rat is to avoid visiting that location.

We believe the information producing this forgetting curve is most likely to be coded in social memory for the choices made earlier during the trial by the other rat. However, we acknowledge the possibility of odor trails or other physical traces that could provide perceptual cues about the other rat's earlier visits. Social memory effects can be shown in the radial-arm maze under conditions that rule out odor or other physical traces as explanations (Brown et al., 2007; Experiments 1 and 3). Although we cannot rule out effects of physical traces in the present experiment, we favor social memory as the most likely mechanism responsible for the effects of previous choices made by the other rat.

These findings extend the earlier experiments done in our laboratory using the radial arm maze to a somewhat different task. As suggested above, the present open field task may better represent the conditions in which rats naturally forage. In relation to the radial-arm maze task used in the earlier experiments, rats can both perceive and interact with each other more readily in the open field task. Brown et al. (2008) (Experiment 2) recognized the potential importance of this issue and introduced a radial maze with transparent arms to increase visual contact between two rats as they foraged in the maze (this same apparatus was subsequently used in the experiments of Brown et al., 2009). In any case, the consistency of the social effects on spatial choice found in the present open field task with those found in the more controlled task imposed by the radial-arm maze increases the validity of the pattern of results found across these two experimental platforms.

As suggested by ideas developed in the contexts of natural foraging (e.g., Barnard & Sibly, 1981; Fretwell & Lucas, 1970; Galef & Giraldeau, 2001; Giraldeau, 2000), imitation learning (e.g., Galef & Laland, 2005; Heyes & Galef, 1996; Zentall & Galef, 1988; Zentall, 2003), and social transmission of food preferences (e.g., Galef & Wigmore, 1983; Galef, 1989), rats are affected by the presence of a foraging partner. The present experiment, along with the earlier experiments from our laboratory using the radial maze (Brown et al., 2007, 2008, 2009) provides the beginning of an understanding of those social effects and the role of memory therein. We consistently find that avoidance of choices made earlier by a foraging partner occurs only when the partner is not physically present in the location of those choices. Physical presence of the foraging partner, at least in the radial maze, elicits the opposite approach tendency and an increased probability of visiting locations previously visited by the other rat. In all of our experiments involving social effects on choice, the two rats were highly familiar with each other as cage mates. It is, of course, quite possible that different effects of the other rat's physical presence might be obtained in rats with different kinds of relationships to each other. In any case, these experiments isolate social effects caused by the previous behavior of another rat. We attribute these effects to memory for the choices made by the other rat. In several experiments, including the present one, these social memory effects are restricted to locations that were visited not only by the other rat, but also by the focal rat itself. Thus, remembered information obtained when the rat visited the location itself is combined with remembered information about the visits made by the other rat.

Although the emphasis here is on the social effects on choice that occurred, it could also be argued that the extent to which the choices made by rats in this task were affected by other rats is surprisingly small. For the most part, the choice behavior we measured was very similar when the rats were tested together and when they were tested in separate trials. Given the amount of information that is potentially available from a foraging partner, both in the natural foraging contexts relevant for omnivorous small mammals generally and in the experimental task used with these rats, the extent to which our subjects appeared to be unaffected by their cage mate foraging for the same, limited resource is interesting.

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