

Factors Modulating Social Influence on Spatial Choice in Rats

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Three experiments examined the conditions under which the spatial choices of rats searching for food are influenced by the choices made by other rats. Model rats learned a consistent set of baited locations in a 5×5 matrix of locations, some of which contained food. In Experiment 1, subject rats could determine the baited locations after choosing 1 location because all of the baited locations were on the same side of the matrix during each trial (the baited side varied over trials). Under these conditions, the social cues provided by the model rats had little or no effect on the choices made by the subject rats. The lack of social influence on choices occurred despite a simultaneous social influence on rats' location in the testing arena (Experiment 2). When the outcome of the subject rats' own choices provided no information about the positions of other baited locations, on the other hand, social cues strongly controlled spatial choices (Experiment 3). These results indicate that social information about the location of food influences spatial choices only when those cues provide valid information that is not redundant with the information provided by other cues. This suggests that social information is learned about, processed, and controls behavior via the same mechanisms as other kinds of stimuli.

Keywords: social cognition, spatial cognition

The information processed and used by animals includes the behavior of conspecifics. There is, of course, tremendous variation in the degree of sociality among animals, but virtually all of them interact to some degree with others of their species. Many animals, including most mammals, interact with conspecifics quite extensively, and social interaction is ubiquitous in human behavior. Given this, the principles and processes related to social effects on behavior and social cognition are, a priori, extremely important. Social learning and cognition may have been a central force in the evolutionary history of our species (Cosmides & Tooby, 1992; Trivers, 1985). Although empirical work on social learning and cognition has been limited until recently, a wide range of social behaviors has been studied in the past few decades using a variety of species and from a variety of theoretical perspectives (e.g., Box & Gibson, 1999; Byrne & Whiten, 1988; Giraldeau & Caraco, 2000; Heyes & Galef, 1996; Zentall & Galef, 1988).

The present work is about social influences on spatial choice in laboratory rats. The rat, of course, is a standard laboratory model for studies of learning, memory, and other cognitive processes. Furthermore, the recent ancestors of laboratory rats, like many small mammals, likely foraged socially and had moderate levels of sociality more generally (Barnett, 1963; Hanson, 2004). In fact, laboratory rats, when released into seminaturalistic environments,

are found to exhibit the same social foraging tendencies found in most wild rats (Berdy, 2002). Thus, laboratory rats are a reasonable choice for studies of social learning and cognition as representative mammals and are an excellent choice given their role as model organisms in studies of learning and cognition.

Galef and colleagues have explored social influences on food choice in rats (for a review, see Galef, 2012). Food aversions and food preferences are socially transmitted in rats (Galef, 1989; Galef & Wigmore, 1983). Food preferences acquired socially are retained for at least 1 month (Galef & Whiskin, 2003) and are retained despite a variety of intervening food-related experiences (Galef, Lee, & Whiskin, 2005). Rats and other animals learn from observing the behavior of other animals, including where food is located (McQuoid & Galef, 1992), which food items are palatable (Galef, 1989; Laland & Plotkin, 1993), and behaviors used to obtain food (e.g., Laland & Plotkin, 1990; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997).

An important distinction emphasized in several theoretical contexts in the study of natural foraging behavior is between information that an animal acquires directly from its own experience with the environment ("personal" information) and "social" or "public" information that an animal acquires from another animal, generally a conspecific (Danchin, Giraldeau, Valone, & Wagner, 2004; Templeton & Giraldeau, 1996). The present experiments are concerned with social information about the location of food and with the relationship between social information and personal information.

In our laboratory, social influences on spatial choices have been studied in two laboratory paradigms using male rats (see Brown, 2011, for a review). In the radial-arm maze, two countervailing social influences have been found (Brown, Farley, & Lorek, 2007). The physical presence of a familiar (cage mate) rat results in approach toward the other rat and a corresponding increase in the tendency to choose a spatial location (maze arm) that was just

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chosen by the other rat. At the same time, locations that had been visited by the conspecific (and were therefore depleted of food) earlier in the trial are avoided.

Two additional studies show that memories of spatial choices made by another rat can be incorporated with information about the content of the locations to modulate the tendency to make subsequent choices of those locations. Specifically, [Brown, Prince, and Doyle \(2009\)](#) found that maze arms previously visited by another rat were avoided if they were baited with only two small food pellets (and therefore depleted when the other rat visited the arm) but were more likely to be chosen if maze arms were baited with an undepletable supply of pellets. Similarly, [Brown et al. \(2008\)](#) found that when maze arms were baited with a large amount of a less preferred food type, previous visits by the other rat decreased choice of that arm. However, the tendency to choose maze arms baited with a more preferred food type was increased when the maze arm had been previously visited by the other rat. This modulation of the social influence of the other rat's choices by the value of the food to be found in the maze arm was dependent on the maze arm having been previously visited by the focal rat itself, indicating that information about the content of the location experienced by the rat ("personal information") was integrated with social information about the choices made by the other rat.

More recently, social influences on spatial search and choice were examined in an open-field spatial choice task dubbed the "pit maze" ([Keller & Brown, 2011](#)). Similar to apparatus that have been used to study spatial memory (e.g., [van der Staay, van Nies, & Raaijmakers, 1990](#)), pattern learning ([Brown, 2006](#)), and object memory ([Cohen et al., 2010](#)), the pit maze is an arena with a matrix of spatial choice alternatives arranged in a 5×5 grid. The rats lift a cover to determine whether a pit is baited with sucrose pellets. We suspected that an open arena is more likely to support social influences on spatial choices than the radial-arm maze because rats are exposed to each other continuously and have the opportunity to spend more time in close proximity.

[Keller and Brown \(2011\)](#) studied the spatial choices made when two rats were tested together in the pit maze. At the beginning of each trial, all 25 pit locations were baited with a single 45-mg sucrose pellet. Choice of a pit location virtually always resulted in depletion of the pellet, so it would be advantageous for rats to avoid choosing pit locations that were visited by the other rat earlier in the trial. By comparing choices made when the rats were tested together with choices made when the same rats were tested alone in the pit maze, [Keller and Brown \(2011\)](#) were able to show that the rats did, in fact, avoid choosing pit locations that had been visited by the other rat. The effect was small in magnitude, however. A reduction in the tendency to choose a pit location as a result of its being previously chosen by the other rat was detected only when the focal rat had itself previously visited the same pit location, perhaps because its own previous visit allowed it to better discriminate the locations chosen by the other rat. A more sensitive measure—the relative likelihood of visiting pit locations as a function of how long ago the other rat had visited them—revealed an effect of the other rat's choices regardless of previous visits by the focal rat. So, although [Keller and Brown's \(2011\)](#) data show social influences in the pit maze, those influences appear not to strongly control choices.

The present experiments were designed to explore several factors that might be important in modulating social influences on spatial choices. We used the same pit maze apparatus introduced by [Keller and Brown \(2011\)](#). Rats were trained such that some of them (termed "model rats" in what follows) learned the locations of consistently baited pits. The model rats were tested together with rats for which the location of baited pits was not consistent over trials (termed "subject rats"). The focus was on whether the choices made by the (informed) model rat had any effect on the choices made by the uninformed subject rat.

Experiment 1

In Experiment 1, the baited locations were always on one side of the arena. Model rats always found baited locations on the same side of the arena over trials. Subject rats also found baited locations on only one side of the arena, but the side varied over trials. On half of the trials, a subject rat and a model rat were tested together, and on the remaining trials they were tested separately. Assuming that the model rats learned to preferentially choose locations on the baited side of the arena, the subject rats could benefit from choosing locations that were on the side chosen by the model rats. The goal of the experiment was to determine whether choices made by the subject rats were in fact influenced by the model rats. To this end, we compared the subject rats' tendency to choose locations on the baited side of the arena in the presence of a model rat (together trials) to the same tendency in the absence of a model rat (separate trials).

Method

Subjects. Twenty male Sprague–Dawley rats were obtained from Harlan Sprague Dawley (Indianapolis, Indiana). They were housed in pairs in $45 \times 24 \times 20$ cm (tall) cages on a 12:12-hr reversed light:dark cycle. The rats were tested during the dark phase of the cycle. They were food deprived to maintain them at approximately 90% of free feeding weight (in comparison to growth curves provided by the vendor) and had ad libitum access to water. Assignment of rats to cage mate pairs occurred when the rats were received from the vendor at approximately 4 weeks of age. The experiment began when the rats were approximately 15 weeks old.

Apparatus. The rats were tested in a 1.17-m-square arena enclosed by 14-cm-tall walls and painted flat black (see [Figure 1](#) and [Keller & Brown, 2011](#), for photographs of the apparatus). Two fluorescent tubes illuminated the room. 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 drinking cups that were secured in the floor of the maze such that the lip of the cup was flush with the floor of the arena, with the funnel directly on top of the cup (see [Keller & Brown, 2011](#), for an illustration). 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

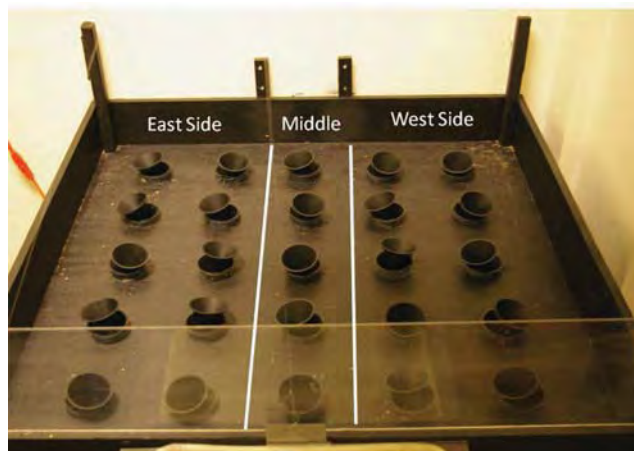


Figure 1. Top view of the testing arena. The edge of the start box and the door from the start box to the arena are visible at the bottom. Pit covers were lifted by the rats to get access to the pellets that were hidden in the bottom of each pit. The white boundaries and labels indicating the three areas of the arena are superimposed on the photo for illustration (no boundaries or labels were present for the rats). See Keller and Brown (2011) for additional photos of the apparatus. See the online article for the color version of this figure.

of which a sucrose pellet could be placed to bait the pit. Underneath the mesh floor of every pit (in the bottom of the cup) were eight to 10 sucrose pellets that controlled for any odor effects from the pellets.

The pits had a second (“cover”) funnel placed inside that acted as a lid that was lifted to gain access to the pellet that might be hidden inside the stem of the cover funnel on the bottom of the pit. 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 14-g weight. The weight 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 after it was lifted so that there were no visual cues as to which pits had been visited.

Procedure. Prior to each trial, a sucrose pellet (BioServe 45-mg sucrose pellets, Product F0042) was placed in 15 of the 25 pits (inside the stem of the cover funnel). The rat or pair of rats was placed in the start box. The door between the start box and the arena was then raised. A timer was started when the rat(s) entered the arena (when the rat’s tail cleared the doorway or when the second rat’s tail did so during trials in which the rats were being tested together). The door closed after the rat (or both rats) had entered the arena. Trials were recorded via a camera mounted directly above the arena. Choices were coded from the resulting video 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 after 1 min, at which time the rat(s) were removed from the arena. Daily feeding occurred after the experimental procedures.

One member of each cage mate pair was randomly assigned to be a model rat, and its cage mate was assigned to be a subject rat. Model and subject rats were differently marked on their tails for identification. For the model rats, the locations of the 15 pits baited

prior to each trial were consistent from trial to trial. Specifically, five of them were randomly assigned to have the 10 pits on the east side of the arena baited prior to each trial (as well as the five pits in the middle section of the arena). The remaining half were assigned to have the 10 pits on the west side of the arena baited prior to each trial (as well as the five pits in the middle section of the arena). As illustrated in Figure 1, this corresponds to three columns being baited for each model rat, with the middle column baited for all model rats. The 15 pits baited prior to each trial for the subject rats varied over trials but always consisted of the five pits in the middle section of the arena as well as the 10 pits on either the east or west side.

Each rat experienced two trials per day (typically 5 days per week). Trials were structured in blocks of 20 trials each. Three trial blocks were conducted. During each trial block, each rat was tested by itself during 10 trials (separate trials) and with another rat during 10 trials (together trials). There was one separate trial and one together trial each day (ordered randomly over days and separated by at least 1 hr). During together trials, the 15 pits baited at the beginning of the trial were determined by the east-versus-west assignment of the model rat. During separate trials, the pits baited for a model rat were determined by its east-versus-west assignment, whereas the pits baited for a subject rat were on the east side of the arena for a randomly determined half of the trials and on the west side during the other half of the trials. The pairings of model and subject rats on days when together trials occurred were randomly determined within each trial block. Within each trial block, each subject rat was tested in five trials with the pits on the east side of the arena baited and five with the pits on the west side of the arena baited (randomly ordered).

During a session of testing rats in either separate trials or together trials, the order of testing rats (or pairs of rats) was such that those with pits baited on one side of arena were tested first, followed by the rats for which the other side was baited. This ensured that any effects of odor left over from rats tested during earlier trials were as consistent as possible, allowing the comparison of performance during separate and together trials to better isolate social effects produced by the model rat’s behavior (i.e., any effects of odors from rats tested during earlier trials would be similarly present in separate and together trials and consistent with other cues in both cases).

Results

Data were coded using a tracking program (locally created using Microsoft Visual Basic Version 6.0). The video recording of 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, 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. In this and all of the experiments reported in this paper, only the first choice made to a particular pit

during a trial was included in the data analyses (i.e., revisits to a location visited earlier in the trial were ignored).

Figure 2 shows the number of pits chosen per trial by the model rats (top panels) and subject rats (bottom panels) during the separate and together trials over the three trial blocks. Choices of pits in the middle column of the arena are not shown and were not included in the data analyses.¹ Choices were classified according to whether they were to pits on the assigned (baited) side of the arena or the unassigned (not baited) side. The results shown in the figure indicate that a strong tendency to choose pits on the baited side of the arena is acquired by both model and subject rats, but there is no indication that the subject rats' choices are affected by the choices made by the model rats (i.e., no evidence for a difference between the pattern of results in separate and together trials).

This apparent pattern of results is supported by the results of two analyses of variance (ANOVAs). The first was a 3 (Trial Block) $\times$ 2 (Social Condition: Separate vs. Together Trials) $\times$ 2 (Arena Side: Assigned vs. Unassigned) within-subject ANOVA performed on the number of choices per trial made by the model rats. The goal of this first analysis was to confirm that the model rats modeled choices to the assigned side of the arena. Because the focus of this experiment was differences in the tendency to visit pits on the assigned and unassigned sides of the arena, only factors

involving the arena side are reported here (comparisons collapsing over the arena side factor provide no theoretically meaningful information). The model rats chose pits on the assigned (baited) side more than pits on the unassigned (unbaited) side, as shown by an effect of arena side, $F(1, 9) = 90.57, p < .001, \eta_p^2 = .910$, 95% confidence interval (CI) = [.64, .95]. There was a significant Arena Side $\times$ Trial Block interaction, $F(2, 18) = 112.08, p < .001, \eta_p^2 = .926$, 95% CI = [.82, .95]. Neither of the other two interaction effects involving the arena side was significant.

To better understand the lack of evidence for an effect of social condition in the model rats, we determined the proportion of choices that were to the assigned side for each rat during each trial block and the Bayes factors for an effect of social condition on those proportions in each of the three trial blocks (Table 1, left columns). For all three blocks, the Bayes factor was in favor of the null model; however, only in the case of Block 3 was the evidence for the null model substantial by the conventionally accepted threshold of 3:1.

The second ANOVA had the same structure as the one reported above but was performed on the number of choices per trial made by the subject rats. Again, only those factors involving the arena side are reported. All four factors involving the arena side produced significant effects: arena side, $F(1, 9) = 245.58, p < .001, \eta_p^2 = .965$, 95% CI = [.84, .98]; Arena Side $\times$ Trial Block, $F(2, 18) = 53.26, p < .01, \eta_p^2 = .855$, 95% CI = [.66, .90]; Arena Side $\times$ Social Condition, $F(2, 18) = 6.22, p < .05, \eta_p^2 = .409$, 95% CI = [.04, .60]; and Arena Side $\times$ Block $\times$ Social Condition, $F(2, 18) = 8.21, p < .01, \eta_p^2 = .477$, 95% CI = [.09, .65]. Like the model rats, the subject rats tended to choose pits on the assigned side of the arena, and this tendency increased over the course of the trial blocks.

To better understand the interactions involving social condition, we compared the proportion of choices made to the assigned side by the subject rats during each of the three trial blocks for the separate and together trials (Table 1, right columns). The t tests failed to provide evidence for an effect of social condition in any of the trial blocks. The Bayes factors favored the null model for all trial blocks, substantially so for Blocks 1 and 2.

Figure 3 shows an analysis of the first choice made by each rat during each trial (referred to here as "initial choices"). As will be discussed below, the first choice of each trial is diagnostically special because it cannot be affected by feedback that the rat has from its own choices made earlier during the trial (because it has not yet made any choices). The proportion of initial choices that were made to pits on the assigned side (from among the initial choices made to either side; choices made to pits in the middle column were again not included in the analysis) was determined for each rat during each trial block for each of the two social conditions. These proportions were analyzed in terms of the same

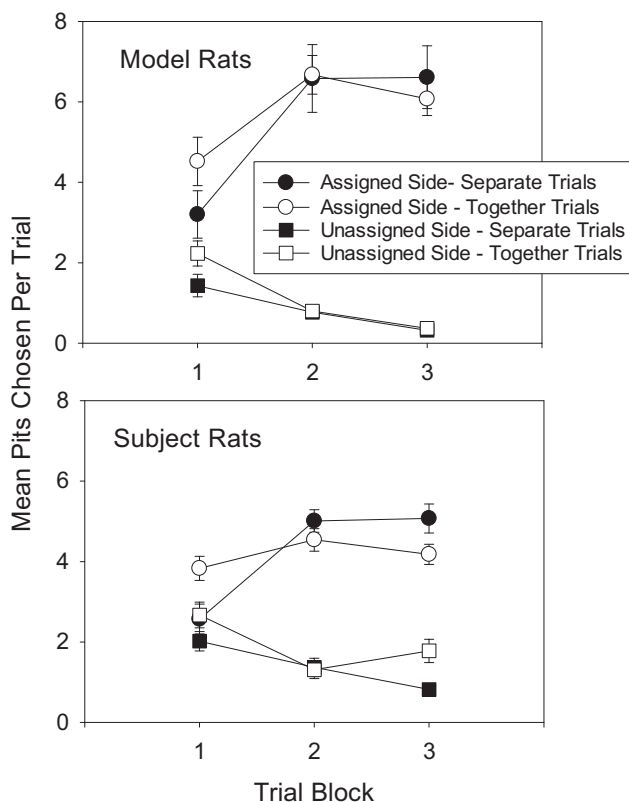


Figure 2. Experiment 1. Mean number of pits chosen per trial from among the 10 pits on the baited side of the arena (Side+) and the 10 pits on the unbaited side (Side-). Data are shown separately for the model rats (top panel) and subject rats (bottom panel) as a function of trial block and trial type. Error bars indicate 1 standard error of the mean.

¹ Because the middle column of the pits is baited as part of both sides of the arena, choices to the pits in the middle cannot be classified in terms of arena side. Choices to the middle pits are difficult to interpret because of a tendency to avoid the pit in the middle of the arena as well as the proximity of the middle column to the start box door. The intention of including the middle column in both arena sides was to make discrimination of arena side relatively more difficult by producing overlap in the locations corresponding to the two sides.

Table 1
Proportions of Choices to Assigned Side Over Trial Blocks in Experiment 1 With Pairwise Comparisons of Separate and Together Trials

	Model rat			Subject rat		
	Block 1	Block 2	Block 3	Block 1	Block 2	Block 3
Separate trials	.63	.895	.865	.57	.79	.87
Together trials	.69	.89	.96	.60	.79	.82
<i>t</i> test	$t(9) < 1$	$t(9) < 1$	$t(9) = 1.11, p > .05$	$t(9) < 1$	$t(9) < 1$	$t(9) = 1.11, p > .05$
Bayes factor	2.60 in favor of null	1.36 in favor of null	3.68 in favor of null	3.67 in favor of null	3.22 in favor of null	1.96 in favor of null

Note. Bayes factors are calculated using the Jeffreys-Zellner-Siow priors and technique described by Rouder, Speckman, Sun, Morey, and Iverson (2009).

factors involved in the analyses of all choices reported above using two ANOVAs.

The first of these was a 3 (Trial Block) $\times$ 2 (Social Condition: Separate vs. Together Trials) ANOVA performed on the proportion of initial choices made by the model rats that were to pits on the assigned side (Figure 3, top panel). None of the factors in this ANOVA produced significant effects.

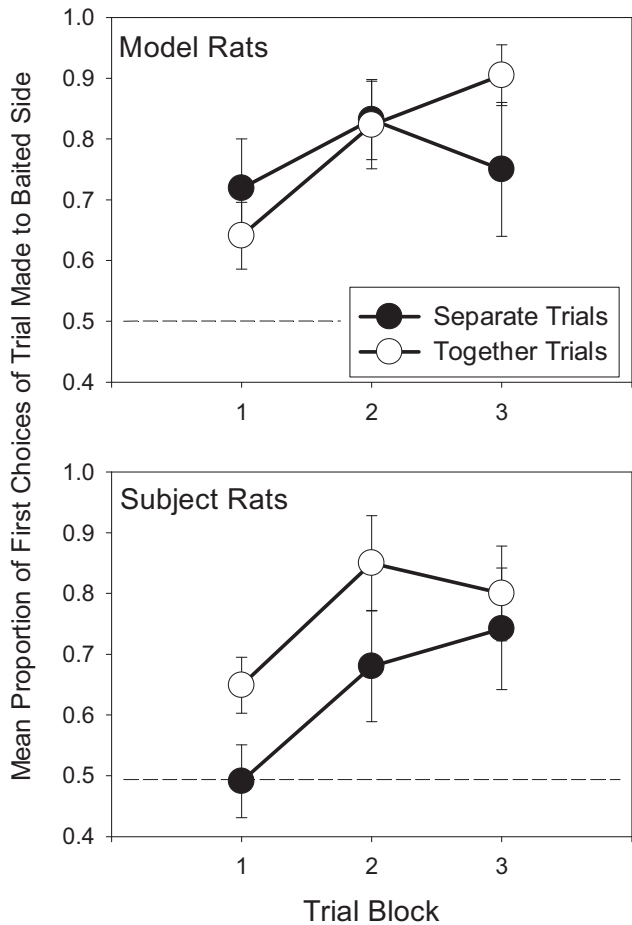


Figure 3. Experiment 1. Mean proportion of pits chosen as the FIRST pit chosen during a trial that were to the baited side of the arena rather than to the unbaited side. Data are shown separately for the model rats (top panel) and subject rats (bottom panel) as a function of trial block and trial type. Error bars indicate 1 standard error of the mean.

Table 2 shows sets of comparisons using *t* tests and Bayes factors to examine which of the mean proportions shown in Figure 3 are above chance (0.5 choices to the assigned side of the arena) and to contrast proportions for separate and together trials. For the model rat, these comparisons generally confirmed that the first choice of each trial tended to be to a pit on the assigned side. There was no evidence that this tendency differed in separate and together trials, but the Bayes factors provided substantial evidence for the null model only in the case of Block 2.

The same analyses were applied to the data of the subject rats (Figure 3, bottom panel). The ANOVA revealed a significant effect of trial block, $F(2, 18) = 5.77, p < .05, \eta_p^2 = .391, 95\% \text{ CI} = [.03, .59]$. The effect of social condition did not reach the criterion for significance, $F(1, 9) = 3.5, p = .09, \eta_p^2 = .280, 95\% \text{ CI} = [.00, .59]$, nor did the Trial Block $\times$ Social Condition interaction, $F(2, 18) < 1, \eta_p^2 = .08, 95\% \text{ CI} = [.00, .30]$. Four of the six mean proportions shown in Figure 3 (bottom panel) were significantly greater than the chance level of 0.5 (see Table 2). The exceptions were the mean proportions for separate trials during Blocks 1 and 2, and the Bayes factor indicated substantial evidence for the null hypothesis in the case of Block 1. Furthermore, there was evidence for a stronger tendency to choose pits on the assigned side in the together trials than in the separate trials during Block 1. These differences, along with the identity of the means that differ from chance provide some, albeit limited, indication of a social influence on the first choice made by the subject rats.

Discussion

By the second trial block, both the model and subject rats made more than three times as many choices of pits on the assigned side of the arena as on the unassigned side. This is not surprising in the case of the model rats because, for them, the assigned side of the arena was consistently baited over trials, and they presumably learned which locations or which side of the arena were/was baited. However, the baited side of the arena varied unpredictably for the subject rats. Thus, explanation of their ability to accurately choose pits on the assigned side of the arena requires something other than place learning.

Our expectation was that the subject rats would use information obtained from the behavior of the model rats to locate the baited pits. However, when all the choices made by the subject rats are considered (the data in Figure 2), there is no indication that they were likely to choose pits on the assigned side in the together trials to a greater extent than they did in the separate trials. This indicates that social information plays little, if any, role in the choices made

Table 2
Comparisons of Proportions of First Choices to Assigned Side (Figure 3) to Chance (0.50) and Comparisons of Separate Trial Proportions to Together Trial Proportions

	Model rat			Subject rat		
	Block 1	Block 2	Block 3	Block 1	Block 2	Block 3
Separate trials versus chance (0.5)						
<i>t</i> test	$t(9) = 2.70, p < .05$	$t(9) = 5.05, p < .001$	$t(9) = 2.24, p = .05$	$t(9) < 1$	$t(9) = 1.99, p = .08$	$t(9) = 2.42, p < .05$
Cohen's <i>d</i> (95% CI)	0.85 (.10, 1.57)	1.60 (.62, 2.53)	0.71 (.00, 1.39)	−0.05 (−.57, .67)	0.63 (.07, 1.30)	0.77 (.04, 1.46)
Bayes factor	2.94 in favor of alternative	55.44 in favor of alternative	1.72 in favor of alternative	3.21 in favor of null	1.26 in favor of alternative	2.15 in favor of alternative
Together trials versus chance (0.5)						
<i>t</i> test	$t(9) = 2.56, p < .05$	$t(9) = 4.50, p < .001$	$t(9) = 8.04, p < .001$	$t(9) = 3.23, p < .01$	$t(9) = 4.49, p < .01$	$t(9) = 3.90, p < .01$
Cohen's <i>d</i> (95% CI)	0.81 (.07, 1.51)	1.40 (.51, 2.30)	2.55 (1.22, 3.84)	1.02 (.23, 1.78)	1.42 (.51, 2.30)	1.23 (.38, 2.05)
Bayes factor	2.56 in favor of alternative	29.34 in favor of alternative	1077.96 in favor of alternative	6.03 in favor of alternative	29.14 in favor of alternative	3.90 in favor of alternative
Separate trials versus together trials						
<i>t</i> test	$t(9) = 1.05, p > .05$	$t(9) < 1$	$t(9) = 1.27, p > .05$	$t(9) = 2.62, p < .05$	$t(9) = 1.245, p > .05$	$t(9) < 1$
Cohen's <i>d</i> (95% CI)	0.47 (−.44, 1.36)	0.03 (−.84, .91)	0.57 (−.36, 1.47)	1.17 (.12, 2.18)	0.56 (−.37, 1.46)	0.22 (−.67, 1.10)
Bayes factor	2.07 in favor of null	3.23 in favor of null	1.70 in favor of null	2.78 in favor of alternative	1.75 in favor of null	2.92 in favor of null

Note. CI = confidence interval. Bayes factors are calculated using the Jeffreys-Zellner-Siow priors and technique described by Rouder et al. (2009).

by the subject rats, leaving two alternative explanations for the tendency of the subject rats to selectively choose pits on the baited side.

First, it is possible that perceptual information (odor, visual cues) is available to the rats and allows them to discriminate baited from unbaited pits. Although we used sham pellets (located under the false floor in every pit) to control any odor cues from the pellets and the pellets were visually occluded by the pit covers, perceptual cues distinguishing baited and unbaited pits remains a logically possible explanation for the pattern of choice shown in Figure 2. In addition, it is possible that choices were guided by odor cues from rats tested earlier in the testing session (i.e., during other trials). Our procedure of ordering the trials of different rats such that all the rats with the same side of the arena baited were tested sequentially was intended to allow comparison of performance in separate and together trials to better isolate social effects due to the presence of the other rat. But this also allows the possibility that odor cues from rats tested in earlier trials could control choices in a way that contributes to discrimination of the assigned and unassigned sides of the arena.

Another source of information available to the subject rats is feedback from the choices they make within a trial. Either the pits on the east side or on the west side are baited in any particular trial. Given this, the subject rats have an opportunity to learn a conditional discrimination such that finding a baited pit serves as a cue that other pits on the same side of the arena are baited (and/or that finding an unbaited pit signals that pits on the other side of the arena are baited). To contrast this with information that could be obtained from the behavior of the other rat, it may be useful to refer to information the rat obtains from the outcome of its own choices as “personal information,” following Templeton and Giraldeau (1996).

Our examination of the first choice made during each trial (see Figure 3) was intended to provide additional evidence relevant to all three of these explanations for the tendency of the subject rats to choose pits on the baited side of the arena. The first choice made during a trial cannot be controlled by the outcome of earlier choices made during that trial. Thus, if neither social information nor the outcome of earlier choices is available, any tendency to choose pits on the baited side of the arena during the first choice of each trial in the separate trials can be explained only by perceptual cues to the presence of the pellets or odor cues left in the maze from rats tested in other, earlier trials. In fact, there was a significant tendency by the subject rats to choose pits on the baited side during the first choice of the separate trial, albeit only during the third trial block. Therefore, it appears that perceptual cues were available and came to be used by the rats to some extent. These cues might be from the pellets or odor trails left by other rats during previous trials. However, the tendency to choose pits on the baited side of the arena during the first choice of each trial was small in comparison to the tendency following the first choice of each trial. We conclude, therefore, that perceptual cues played, at most, a minor role in the tendency to choose pits on the baited side of the arena following the first choice of each trial.

There were also some indications that the behavior of the model rat affected the first choice made by the subject rat. The subject rats chose pits on the assigned side of the arena more than pits on the unassigned side to an extent that was marginally significant. In addition, during the second trial block, the subject rats chose pits

on the assigned side more than expected by chance in the together trials, but not in the separate trials. However, this effect was also minor in comparison to the strong tendency to choose pits on the baited side of the arena in both separate and together trials following the first choice of each trial. The key result is that the choices made by the subject rats were primarily controlled by the outcome of their own previous choices and not by the behavior of the model rats. The lack of social influence on choices is noteworthy, given that the choices of the model rats provided highly valid information about the location of food.

Experiment 2

Experiment 2 was intended to test the subject rats in a situation that rules out the use of feedback from the outcome of their own choices as well as any from perceptual cues produced by the presence of the available pellets. This was accomplished by testing the rats in trials with no pits baited. Behavior in these pellet-absent trials was compared to behavior in trials with the pits baited just as they were in Experiment 1. The rats were always tested in pairs (as in the together condition of Experiment 1).

We assumed that the model rats would continue to search for pellets on the side that had been baited during Experiment 1 (and continued to be baited during half of the trials in the present experiment). The primary question was whether the model rats' search and choice behavior would influence the subject rats in the absence of pellets. In the absence of pellets, the subject rats did not have the feedback from their own previous visits. In the absence of such personal information (Templeton & Giraldeau, 1996), social influences might play a larger role.

We also examined the amount of time spent in the baited and unbaited sides of the arena. This was to expand the scope of social influence that might be detected. In our earlier experiments using the radial-arm maze, the presence of another rat was shown to elicit approach, even when it did not increase choice of the maze arm chosen by the model rat (Brown, 2011). A similar dissociation between social influences on approach and choice might be revealed here.

Method

Subjects and apparatus. The subjects were the same 20 rats that participated in Experiment 1. The apparatus was the same as that used for Experiment 1.

Procedure. There was a 10-week interval between Experiments 1 and 2 due to scheduling issues unrelated to the experimental design. Because of this, the rats first experienced "reminder" trials that were just like those in Experiment 1. Sixteen of these trials were conducted, one together trial and one separate trial per day just as in Experiment 1. Data from these trials are not presented below.

The procedure of Experiment 2 following the reminder training trials was the same as that used for Experiment 1, with the following exceptions. First, all trials involved one model rat and one subject rat making choices in the arena together (as in the together trials of Experiment 1). For half of the trials in each trial block, 15 of the 25 pits were baited in accordance with the procedure used in Experiment 1. However, for the remaining half of the trials, none of the pits were baited. During each of two trial

blocks, each rat experienced five trials in which the pellets were present and five trials in which the pellets were not present. The model rat with which each subject rat was paired was randomly determined for each trial.

Results

One of the subject rats became ill during the first block of trials and died before the second block began. The data from that rat and its cage mate model rat are not included in the analyses below. Its cage mate model rat was dropped from the experiment following the first trial block.

Figure 4 shows the number of pits chosen per trial by the model rats (top panels) and subject rats (bottom panels) during the pellet-present trials and pellet-absent trials during the two trial blocks. The results indicate that the absence of pellets reduced the number of pit choices for both groups of rats. However, whereas the model rats appear to make more choices to pits on the assigned side of the arena even when pits are not baited, the subject rats appear to favor pits on the assigned side of the arena only when the pellets are present there. They do not selectively choose pits on the assigned

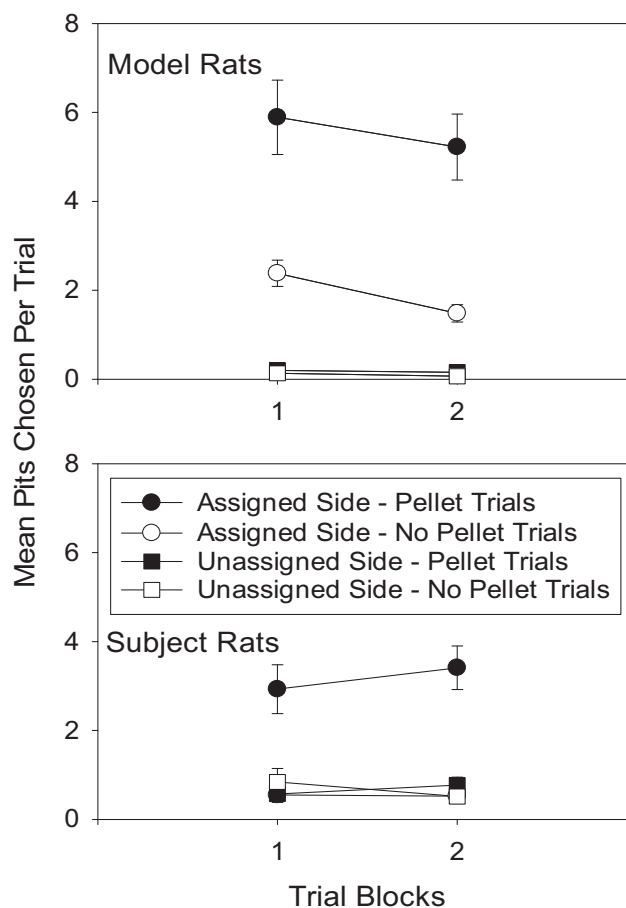


Figure 4. Experiment 2. Mean number of pits chosen per trial from among the 10 pits on the baited side of the arena (Side+) and the 10 pits on the unbaited side (Side-). Data are shown separately for the model rats (top panel) and subject rats (bottom panel) as a function of trial block and trial type. Error bars indicate 1 standard error of the mean.

side in the absence of pellets, despite the selective choice of pits on the assigned side by the model rats.

The above description of the results was supported by ANOVAs. As for Experiment 1, we conducted ANOVAs on the data of the model and subject rats separately, one pair of ANOVAs involving all of the choices made to either side of the arena and a second pair of ANOVAs involving only the first choice of each trial. All of the choices made by the model rats were analyzed with a 2 (Arena Side) $\times$ 2 (Trial Type: Pellet Present vs. Pellet Absent) $\times$ 2 (Trial Block) ANOVA. As for Experiment 1, the ANOVAs were intended to directly contrast choices to the assigned and unassigned sides of the arena, so choices to the middle column of the pits were not included. Also as for Experiment 1, only those factors that include an effect of arena side are reported. It should be emphasized that the “assigned” side refers to the side of the arena that was baited during pellet-present trials for a particular model rat; however, the pits on that side are actually baited with pellets only in the pellet-present trials. There was a significant effect of arena side, $F(1, 8) = 191.77, p < .001, \eta_p^2 = .960, 95\% \text{ CI} = [.80, .98]$; an Arena Side $\times$ Trial Type interaction, $F(1, 8) = 91.03, p < .001, \eta_p^2 = .919, 95\% \text{ CI} = [.64, .95]$; and an Arena Side $\times$ Trial Block interaction, $F(1, 8) = 10.19, p < .05, \eta_p^2 = .560, 95\% \text{ CI} = [.04, .76]$. The Arena Side $\times$ Trial Type interaction indicates a larger tendency to choose pits on the assigned side when the pellets were present. However, an Arena Side $\times$ Block ANOVA restricted to data from the pellet-absent trials confirmed that the model rats selectively chose pits on the assigned side even when the pellets were absent, $F(1, 8) = 82.26, p < .001, \eta_p^2 = .91, 95\% \text{ CI} = [.61, .95]$.

In the case of the subject rats, significant factors involving the arena side were a main effect of arena side, $F(1, 8) = 56.84, p < .001, \eta_p^2 = .877, 95\% \text{ CI} = [.49, .93]$, and an Arena Side $\times$ Trial Type interaction, $F(1, 8) = 32.13, p < .001, \eta_p^2 = .801, 95\% \text{ CI} = [.31, .89]$. In this case, however, the interaction indicates that the subject rats selectively chose pits on the assigned side only when the pellets were present.

As for Experiment 1, the initial (first) choice of each trial made by each rat was analyzed separately in terms of the proportion of choices made to an arena side that were to pits in the assigned side. The mean proportions are shown in Figure 5 as a function of trial type and trial block. In the case of the model rats, a 2 (Trial Type) $\times$ 2 (Trial Block) ANOVA did not reveal a significant effect of either variable or an interaction between their effects. All four mean proportions shown in Figure 5 (top panel) were significantly greater than the chance expectation of 0.5; for the pellet-present trial, the Block 1 mean value was 1.0 for all rats; for the other three means, $t_s(8) > 3.9, p_s < .01$, Cohen's $d = 1.33$ (95% CI = [.40, 2.23]), 1.85 (95% CI = [.73, 2.93]), and 2.66 (95% CI = [1.21, 4.09]) for the pellet-absent trials' Block 1, pellet-present trials' Block 2, and pellet-absent trials' Block 2, respectively. In the case of the subject rats, a 2 (Trial Type) $\times$ 2 (Trial Block) ANOVA did not reveal a significant effect of either variable or an interaction between their effects. Unlike the model rats, however, t tests did not provide evidence that any of the four mean proportions shown in Figure 5 (bottom panel) were greater than the chance expectation of 0.5, $t_s(8) < 2.24$, Cohen's $d_s = -0.13$ (95% CI = [-.53, .78]) and 0 (95% CI = [.00, .00]) for the pellet-present trials' Blocks 1 and 2, respectively; and 0.74 (95% CI = [-.02, 1.47]) and 0.42 (95% CI = [-.28, 1.09]) for the

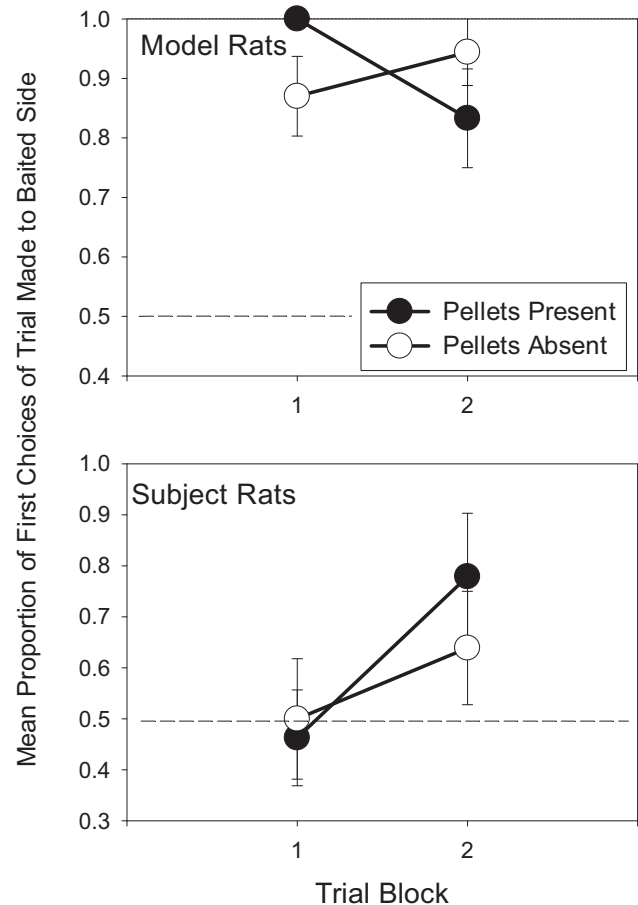


Figure 5. Experiment 2. Mean proportion of pits chosen as the FIRST pit chosen during a trial that were to the baited side of the arena rather than to the unbaited side. Data are shown separately for the model rats (top panel) and subject rats (bottom panel) as a function of trial block and trial type. Error bars indicate 1 standard error of the mean.

pellet-absent trials' Blocks 1 and 2, respectively. The Bayes factors corresponding to these t tests all favored the null model, but substantially only in the case of the pellet-absent trials during Block 1 (2.9, 1.7, 3.2, and 1.7, respectively).

Recall that the technique we used to code the videotaped behavior resulted in recording the location of each rat at 10 Hz. These data were used to specify the location of each rat in terms of the assigned, unassigned, or middle sections of the arena. Figure 6 shows the mean proportions of the 0.1-s bins during which the two rats were both on the assigned side of the arena, the model rat was on the assigned side and the subject rat was on the unassigned side, the model rat was on the unassigned side and the subject rat was on the assigned side, and both rats were on the unassigned side. Bins during which one or both rats were in the middle section of the area are not shown but were included in the denominator used to calculate the proportions.

A striking feature of the data shown in Figure 6 is that, although the model rats spent more time in the assigned side of the arena than the unassigned side, the difference seems rather small given the large tendency of the model rats to choose pits on the assigned

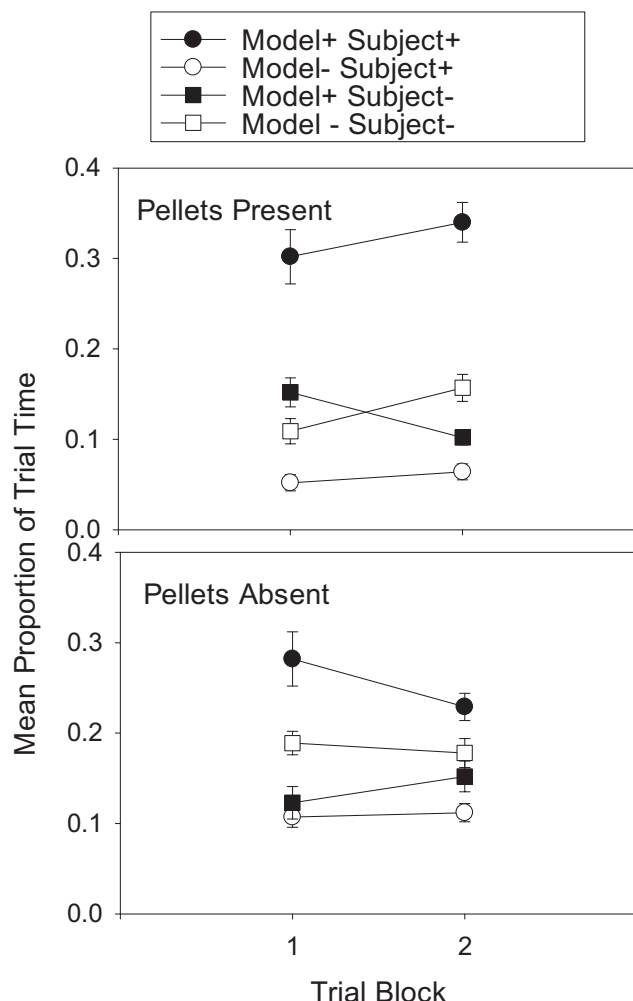


Figure 6. Experiment 2. Mean proportion of trial time during which the model rat and subject rat were on the assigned (+) and unassigned (−) sides of the arena, shown separately for pellet-present trials (top panel) and pellet-absent trials (bottom panel) over the two trial blocks.

side of the arena described above. A second, and more critical, feature of these data is the apparent tendency of the subject rats to spend more time on the arena side in which the model rat was present. This tendency appears to be the case regardless of whether the pellets are present or absent.

This description of the data in Figure 6 is confirmed by a 2 (Trial Block) $\times$ 2 (Trial Type: Pellet Present vs. Pellet Absent) $\times$ 2 (Location of Model Rat: Assigned vs. Unassigned Side) $\times$ 2 (Location of Subject Rat: Assigned vs. Unassigned Side) ANOVA. The values used in the ANOVA were from the perspective of the subject rats—that is, the location of each of the nine subject rats was determined in relation to the location of the model rat with which it was tested during a particular trial. The proportion of time bins during which that subject rat and the model rat with which it was being tested were located on the assigned or unassigned sides of the arena (collapsed over trials) were the values used in the ANOVA.

There was an effect of trial type, $F(1, 8) = 11.52, p < .01, \eta_p^2 = .590$, 95% CI = [.06, .78], indicating that more time was spent on

the sides of the arena (in contrast to the middle of the arena) during pellet-present trials. Model rats spent more time on the assigned side than on the unassigned side, $F(1, 8) = 206.91, p < .001, \eta_p^2 = .963$, 95% CI = [.81, .98]. Subject rats also spent more time on the assigned side than on the unassigned side, $F(1, 8) = 16.84, p < .01, \eta_p^2 = .678$, 95% CI = [.14, .82]. The extent to which model rats spent more time on the assigned side was larger in the pellet-present trials than in the pellet-absent trials, as shown by a Location of Model Rat $\times$ Trial Type interaction, $F(1, 8) = 10.11, p < .05, \eta_p^2 = .558$, 95% CI = [.04, .76]. However, the corresponding Location of Subject Rat $\times$ Trial Type interaction was not significant but did approach significance, $F(1, 8) = 3.60, p = .095, \eta_p^2 = .310$, 95% CI = [.00, .62]. There was a Trial Block $\times$ Trial Type interaction, $F(1, 8) = 9.93, p < .05, \eta_p^2 = .554$, 95% CI = [.03, .76]. Of greatest interest is a significant Location of Model Rat $\times$ Location of Subject Rat interaction, $F(1, 8) = 127.29, p < .001, \eta_p^2 = .994$, 95% CI = [.72, .97], which shows that the tendency of the subject rat to favor the assigned side of the arena was modulated by the side in which the model rat was present. No other factors were significant, although it should be noted that the Location of Model Rat $\times$ Location of Subject Rat $\times$ Trial Type interaction approached significance, $F(1, 8) = 4.51, p = .066, \eta_p^2 = .361$, 95% CI = [.00, .65].

Discussion

The model rats selectively chose pits on the assigned side of the arena even during the pellet-absent trials. Following the first choice of each trial, however, the absence of pellets reduced this tendency among the model rats and reduced the overall number of choices made by both the model and subject rats. Thus, although the vigor and validity of the model rat as a social cue for the subject rats' search and choice behavior was reduced in pellet-absent trials, the model rats continued to make choices selectively to pits on the assigned side of the arena. They thereby served as valid social stimuli in the present experiment.

In the pellet-present trials, the subject rats continued to choose pits on the assigned side of the arena more than pits on the unassigned side of the arena, just as they did in the corresponding trials (together condition) of Experiment 1. However, as in Experiment 1, there was no significant indication that this was the case for the first choice of each trial. This supports our earlier conclusion that the tendency to choose pits on the baited side of the arena is primarily due to feedback from the outcome of the pit choices already made. Critically, the subject rats did not tend to choose pits on the assigned side of the arena during the pellet-absent trials. Thus, these data provide no evidence that the model rats' behavior had an influence on the subject rats' choices.

The data also provide no indication that any odor left on the maze from rats tested in earlier trials controlled behavior (this would result in the choice of the assigned side even in the pellet-absent trials). In the absence of feedback from finding pellets in the pits they chose, subject rats chose pits on the unassigned side of the arena as often as they chose pits on the assigned side.

One complexity should be noted. The model rats also did not find food in the pellet-absent trials. Thus, it is possible to attribute the absence of social influence in this experiment to the absence of cues associated with the model rats finding food (e.g., visual cues corresponding to eating it or odor cues on their breath).

On the other hand, there is clear evidence for a social influence on the location of the subject rats by the location of the model rats in the arena (see Figure 6). Subject rats spent more time in the arena side where the model was present. This social influence on the location of the subject rat occurred in both pellet-present trials and pellet-absent trials. However, the social influence on the subject rat's location did not produce or correspond to a social influence on the spatial choices it made. The implications of this dissociation between social influence on location and choices will be explored in the General Discussion.

Experiment 3

Experiments 1 and 2 provide surprisingly little evidence for social influences on spatial choice, especially given the social influence on the subject rats' location in the arena that was found. Social influences on choice may have been limited because the baited locations could be determined from the outcome of the subject rats' own earlier choices. There was evidence of social influence on the initial choice made by subject rats (which could not be guided by the outcome of earlier choices), but it was limited. There was no indication of a social influence on choices made after the first choice of each trial. Apparently, the subject rats readily learned the contingencies between finding a baited location and the remaining baited locations, and this was the primary determinant of spatial choices, despite the validity of the social information.

From several perspectives, one might predict stronger social influences when the personal information resulting from the outcome of the rat's own earlier choices is not available. Laland (2004) outlined the trade-offs between using information obtained asocially and socially and reviewed both theoretical arguments and empirical evidence that use of social information tends to dominate over personal information unless the former is costly or invalid. The ubiquitous phenomenon of cue competition in laboratory studies of learning also suggests that personal information obtained from the outcome of a rat's own choices and social information obtained from the behavior of another rat would compete for control of spatial choices.

Experiment 3 was designed to explore the possibility that social information would control behavior in a task similar to that used in the earlier experiments but in which personal information was unavailable. In the absence of valid information from the outcome of a subject rat's own choices, would the social influence be a stronger determinant of spatial choice?

The baited locations in Experiment 3 were five pits in the same maze used in Experiments 1 and 2. As in the earlier experiments, model rats experienced the same baited locations on every trial. Unlike in Experiments 1 and 2, these baited locations had no predictable spatial relationship to each other. For each model rat, they were randomly selected from among the locations in the maze (with one restriction described below). Thus, social information from the model rats may have controlled the subject rats' choice in this experiment more than it did in the earlier experiments.

In addition, the baited locations contained a large number of pellets, so that visits to locations previously visited by the other rat would be reinforced. In the radial-arm maze, rats consume only a small number of pellets during each choice and then make additional choices rather than continuing to consume pellets from the

large supply available on each arm (Brown et al., 2009). This may be related to the strong "win-shift" strategy (or exploratory tendency) that is well documented in rats in spatial choice tasks like the radial maze (Olton & Schlosberg, 1978; Timberlake & White, 1990). Unpublished observations in the pit maze had suggested the same phenomenon and, in fact, in the present experiment, rats ate only a few pellets from each pit and then made additional choices despite many pellets being available in each pit. We took advantage of this tendency, in that it results in reinforcement of visits to pits that had earlier been visited by the other rat.

Thus, social information is more informative in the present experiment than it was in Experiments 1 and 2. The locations of baited locations cannot be predicted on the basis of other baited locations. In addition, the choices made by the model rats indicate the specific location of baited pits rather than indicating the general area (arena side) of baited locations.

Method

Subjects and apparatus. The subjects were 28 experimentally naive male Sprague-Dawley rats obtained from the same vendor and housed and food deprived in the same manner as the subjects in Experiments 1 and 2. The experiment began when the rats were approximately 18 weeks old. The apparatus was the same one used in the earlier experiments.

General procedure. Most features of the experimental trials were very similar to those of the earlier experiments. The rats were housed in pairs, and one member of each pair was randomly assigned to be a model rat. The other member of each pair was a subject rat. Prior to each trial, sucrose pellets were placed in a subset of the 25 pits (inside the stem of the cover funnel). The pair of rats was placed in the start box. The door between the start box and the arena was then raised. A timer was started when the rats entered the arena, and the door was then closed. Trials were recorded via a camera mounted directly above the arena. Choices were coded from the resulting videos 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 after 2 min, at which time the rat(s) were removed from the arena. Daily feeding occurred after the experimental procedures.

The procedure differed from the earlier experiments in several ways. Five pits were baited on each trial. Each model rat was assigned a set of five pits, and these same five pits were baited on every trial. The five pits in the assigned set were determined randomly for each of the 14 model rats, with the constraint that the three pits directly adjacent to the start box of the maze were not included in any assigned sets. The five baited pits were baited with a large number of pellets (approximately 20) such that the pits were not depleted when chosen by a rat.

Model rat training. Model rats were trained in several phases to find food in five assigned locations. The performance criterion for the final phase of training was that the rat gathered pellets from all five baited pits. After all model rats reached this criterion, training trials began for the subject rats. During the time that subject rats were being trained, daily training trials for the model rats continued.

Subject rat training. Two weeks of daily training trials were used to habituate the subject rats to the testing arena. Prior to each daily training trial, pellets were scattered on the arena floor. Each

subject rat was allowed to enter the maze after the guillotine door was opened. A trial was terminated 2 min after the rat entered the maze by removing it.

Test trials. On every test trial, a model rat and a subject rat were tested together. The baited pits were those in the assigned set of the model rat. A trial consisted of placing the two rats together in the start box and then opening the guillotine door. The trial was terminated 2 min after the second rat entered the arena.

Each rat experienced one or two trials per day (typically 5 days per week). If two trials were conducted on the same day, the trials were separated by at least 1 hr. Within each trial block, each model rat was tested together with each subject rat during one trial (other than its cage mate; cage mates were not tested together in this experiment, unlike in Experiments 1 and 2, in which cage mates were tested together on approximately 10% of the together trials). The order of the model rat–subject rat pairings was randomized. Trials were structured in blocks of 14 trials each. Three blocks of test trials were conducted.

No-pellet probe trials. Following each of the three blocks of test trials, one no-pellet probe trial was conducted. These trials were identical to the standard test trials except that none of the pit locations were baited with pellets (the sham pellets under the floor of every pit location remained present as always). These probe trials allowed any effects of physical presence of the pellets (e.g., odor or visual cues from the pellets) to be determined.

Results

During the test phase of the experiment, the model rats demonstrated a strong tendency to choose the pits located in the assigned set. As shown in the top panel of Figure 7, the model rats had a much stronger tendency to choose locations in the assigned set than those in the unassigned set. The subject rats had a similar strong tendency to choose pits located in the model rats' assigned set (bottom panel).

The previous description of the results was supported by two ANOVAs. The first of these examined the probability of the model rats choosing baited versus unbaited pits over the three trial blocks (a 2 [Pit Type] $\times$ 3 [Trial Block] ANOVA using the probability of choosing pits in each category for each rat). It revealed an effect of pit type, $F(1, 13) = 2,223.58, p < .001, \eta_p^2 = .995, 95\% \text{ CI} = [.98, 1.00]$, and a Pit Type $\times$ Trial Block interaction, $F(2, 26) = 6.56, p < .01, \eta_p^2 = .335, 95\% \text{ CI} = [.04, .53]$. A second ANOVA conducted on the data of the subject rats also revealed effects of pit type, $F(1, 13) = 2,831.74, p < .001, \eta_p^2 = .994, 95\% \text{ CI} = [.99, 1.00]$, and a Pit Type $\times$ Trial Block interaction, $F(2, 26) = 8.18, p < .01, \eta_p^2 = .386, 95\% \text{ CI} = [.08, .57]$.

Probe trials. Data from the three probe trials (no baited pits) are shown in Figure 8. As in the standard test trials, both the model rats and subject rats were more likely to choose pits in the assigned (but now unbaited) set than pits in the unassigned set, $t(13) = 12.99, p < .001$, Cohen's d (corrected for dependence of means in within-subject comparisons) = 3.72, 95% CI = [2.19, 5.47] and $t(13) = 10.18, p < .001$, Cohen's d (corrected) = 3.14, 95% CI = [2.19, 5.47], respectively.

Effect of earlier choices made by model rat. Data from the probe trials support the idea that social influence is responsible for the tendency of the subject rats to choose baited (or assigned set) locations, because any perceptual cues to the presence of pellets

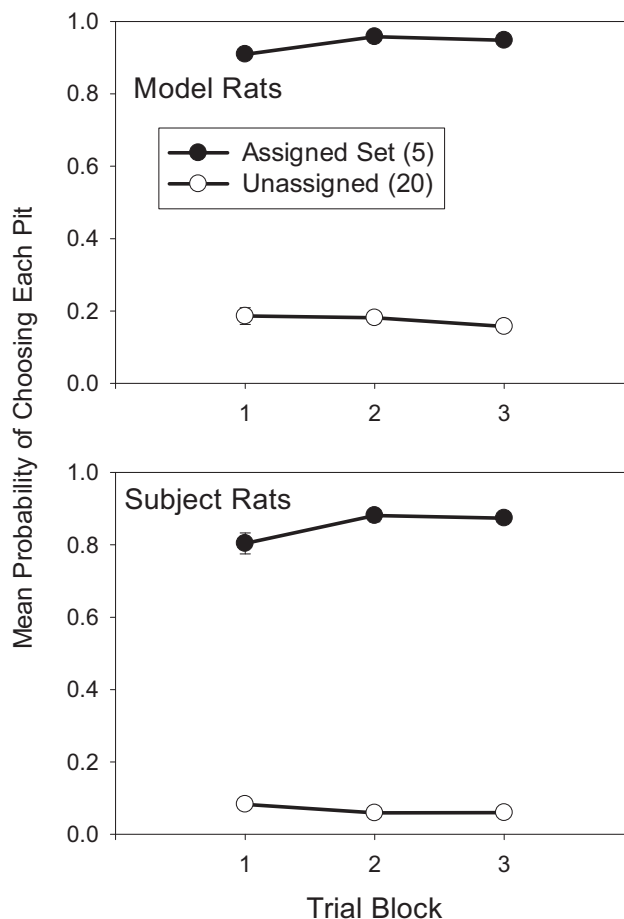


Figure 7. Experiment 3. Mean probability of choosing each of the five pits in the assigned set and each of the 20 pits not in the assigned set over the three trial blocks for the model rats (top panel) and subject rats (bottom panel). Error bars indicate 1 standard error of the mean.

are absent in the probe trials. A second approach to examining the explanation for the subject rats' tendency to choose baited pits is to determine the extent to which the baited pits chosen by the subject rats are those previously chosen by the model rat. Our casual observation suggested that the subject rats had a very strong tendency to "follow" the model rats, choosing pits that were just chosen by them. What follows formalizes this observation.

Each choice made by a subject rat during the test trials was classified in terms of whether it was to a pit location in the model rat's assigned set. The pit locations in the assigned set were further classified as being a location the model rat had not visited earlier in the trial or, if the location had been visited earlier, in terms of how many other visits to locations in the assigned set had been made since the choice being classified.

To provide a measure of how the distribution of visits to these categories of pit locations compared to what would be expected on the basis of chance, all 25 pit locations were classified in the same way for each choice made. This was done because the opportunities to make choices to locations in these categories depend on how many pit locations in the assigned set have been visited by the model rat at the time the subject rat makes a choice. The distri-

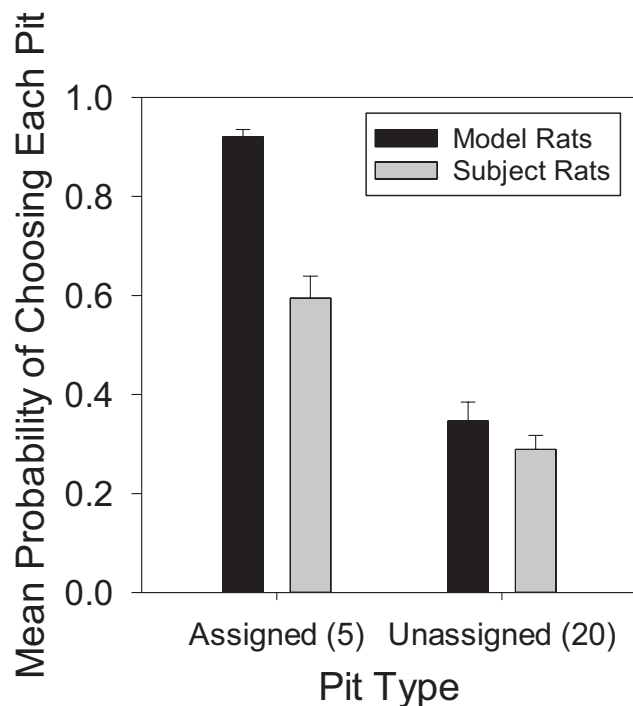


Figure 8. Experiment 3. Mean probability of choosing each of the five pits in the assigned set and each of the 20 pits in the unassigned set during the three probe trials for the model rats and subject rats. Error bars indicate 1 standard error of the mean.

butions of pit locations chosen and locations available to choose were determined for each subject rat, collapsed over trials in all three trial blocks. The mean distributions are shown in Figure 9. There were large differences in the proportions of locations chosen and locations available to be chosen for at least two straightforward, but trivial, reasons. First, there are only five locations (out of 25 in the maze) in the assigned set. Second, there are necessarily fewer opportunities to make choices to locations chosen later in the trial by the model rat than to make choices to locations chosen earlier by the model rat.

The mean proportion of choices made by subject rats to the pit location most recently chosen by the model rat (.457, labeled "Set+ -1" in Figure 9) was much larger than the proportion of locations that had been visited most recently by the model rat, .036, $t(13) = 23.1$, Cohen's $d = 8.7$, 95% CI = [5.3, 12.1]. There was no evidence that any of the other categories of pit locations were chosen more often than would be expected on the basis of the distribution of locations available; in fact, all of the other categories except Set+ -5 were chosen significantly less often than expected on the basis of the distribution of locations available, $t(13) > 5.8$; for Set+ -5, $t(13) = 1.02$.

Discussion

In this experiment, there was a large social influence of the choices made by the model rats on the choices made by the subject rats. This influence was restricted to locations that had just been visited by the model rat. In effect, the subject rat followed the model rat, tending to choose the pit that was just chosen by the

model rat. Although the most recent choice of the model rat had a strong influence on the choices of the subject rat, there was no evidence that pit locations chosen earlier by the model rat had any influence on the choices of the subject rat, nor was there any indication that subject rats selectively chose pits in the model rat's assigned set unless they had been visited by the model rat (as would be expected if the subject rats could discriminate baited pits on the basis of some perceptual cue other than the model rat's behavior).

The experimental design eliminated the personal information that controlled choices in Experiments 1 and 2. The outcome of each choice made by the subject rat did not provide any information about the location of other baited pits, as it did in the earlier experiments. Thus, the results of this experiment show that social influence on spatial choices can be very strong under at least some conditions; these results are consistent with the idea that the relative validity of personal information and social information is important.

General Discussion

The results of these experiments support several conclusions about the role of social information on spatial choices in rats. First, the influence of valid social information about the location of food, provided by the choices of a foraging partner, ranges from having no influence to being a very dominant influence. Specifically, the

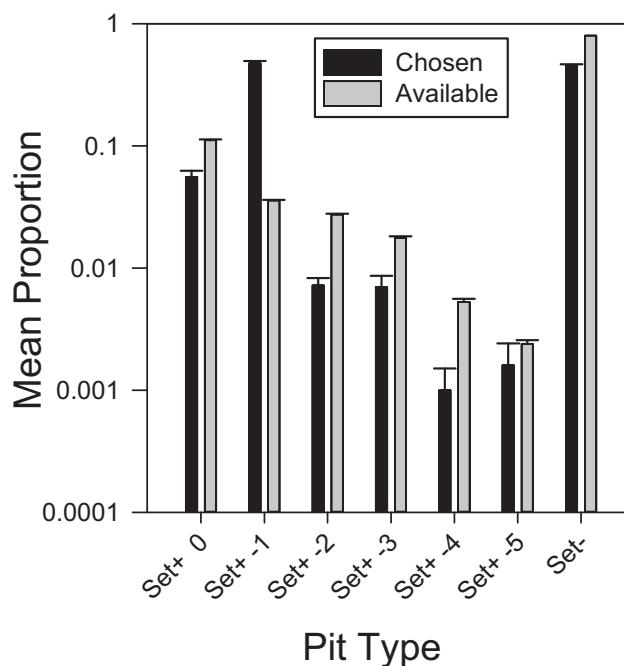


Figure 9. Experiment 3. Mean distributions of locations chosen by the subject rats and locations available to choose. Locations are classified as being in the model rat's assigned set (Set+) or unassigned set (Set-). Locations in the assigned set are classified as not having been previously visited by the model rat (0), being the last location chosen by the model rat (-1) or being chosen previously by the model rat (-2 through -5). Proportions are shown on a log scale. Error bars indicate 1 standard error of the mean. See text for further explanation.

choices of an informed model rat—almost exclusively to locations on the baited side of the arena in Experiments 1 and 2—had a small effect on the first choice made by subject rats but no effect on subsequent choices. On the other hand, choices made by the model rats in Experiment 3 strongly determined the choices made by subject rats.

There are several differences between the first two experiments and Experiment 3 that might account for the differences in social influence. Experiments 1 and 2 encouraged choosing pits on the same side of the arena that the model rat was making its choices, but not to the specific locations chosen by the model rat. Experiment 3, on the other hand, required that subject rats choose the specific pits chosen by the model rat in order to find food. In addition, the baited pits in Experiment 3 contained large caches of food, thereby providing reinforcement when subject rats chose specific locations that had been visited by the model rat. Perhaps social cues are more effective for discrimination of particular locations than for discriminating among general (or larger) areas that contain food (i.e., the side of the arena) or for discriminating locations with large amounts of available food.

Another set of possible explanations for the difference in the influence of social cues points to its redundancy with other information. In Experiments 1 and 2, the outcome of the subject rat's own first choice of a location on either side of the arena could specify the side of the arena that was baited. Thus, following its first choice of a pit on either side of the arena, the social cues provided by the model rat were redundant with the information provided by the outcome of the subject rat's own first (and subsequent) choices. Although the model rats' choices were valid cues to the location of food, they may have been overshadowed by the outcome of the subject rats' own choices. At least under the conditions of these experiments, personal information (Giraldeau & Caraco, 2000; Templeton & Giraldeau, 1996) modulated choices, but social information did not, when both were available as valid indicators of food location.

This information redundancy interpretation of the lack of social influence in Experiments 1 and 2 is consistent with two additional findings. First, in Experiment 1, there was some indication that social cues provided by the model rats' choices affected the subject rats' first choice of each trial. The first choice cannot be influenced by the outcome of the subject rats' own choices. Second, in Experiment 3, the information provided by the other rat's choices was not redundant. The other rat's choices were the only cues available to specify the baited locations in Experiment 3, and there was clear evidence for a substantial social influence on choices.

It has been argued in other contexts that competition for behavioral control among cues serves as an indicator that those cues are processed by common psychological mechanisms. For example, the apparent lack of competition between spatial and nonspatial cues has been interpreted as indicating a modular spatial memory process (e.g., Cheng & Newcombe, 2005; but see Cheng, 2008; Miller & Shettleworth, 2007). Interactions between explicit knowledge and exposure to contingencies among events (or the lack thereof) have been used to discern the independence of associative processes and rational inference in human causal learning (e.g., Beckers, De Houwer, Pineño, & Miller, 2005). Application of this logic to social cues in the present context suggests that social cues are likely processed in the same manner and by the same psychological processes as other cues involved in spatial choice. Thus, the

present results are inconsistent with the modularity of social and spatial cognition. Rather, spatial information obtained from conspecifics and that obtained from other elements of the physical environment jointly control spatial cues and compete for control of spatial choices. This conclusion is also supported by earlier work in the radial-arm maze showing that information obtained by a rat's own visits to maze arms is combined with information obtained from social cues to determine choices (Brown et al., 2008, 2009).

A second conclusion to be drawn from these results is that social influences on behavior occur that are somewhat independent of those modulating choices. The analysis of the rats' location in relation to the other rat (performed for the data of Experiment 2) shows that the subject rat's location in the arena was influenced by the location of the model rats. Specifically, the subject rats tended to be in the same side of the arena as the model rats, whether the model rats were in the assigned side or the unassigned side. The fact that this spatial affiliation revealed by the data of Experiment 2 did not correspond to an increase in choices made to the baited side of the arena indicates that social influences on spatial choice are not simply a matter of modulating the subject rat's location (sometimes referred to as "local enhancement"; e.g., Krebs, MacRoberts, & Cullen, 1972). Rather, the decision process modulated by social cues must occur after the rat has approached a location. This is similar to the decision processes that have been argued to occur in spatial choices involving representations of the spatial locations among familiar locations (i.e., a "cognitive map"). The cognitive map determines approach to locations, but that process can be experimentally dissociated from the decision process that determines whether the location is chosen (Brown, 1992).

A third conclusion, perhaps closely related to the one described above, is that some social influences on spatial choices are labile. At least under some conditions, they do not survive intervening choices made by the rat and/or time. In Experiment 3, we showed that although there was a strong effect of the model rat's most recent choice on choices made by the subject rat, there was no evidence that choices made earlier in the model rat's choice sequence had any effect. This suggests that the physical presence of the model rat is a critical part of the effective social cue. In the radial-arm maze, we have consistently found evidence that the most recent choice made by a foraging partner increases the likelihood of choice of that location but that choices made earlier during the trial by the foraging partner decrease choices of those locations (Brown, 2011). In those experiments, the contingencies supported avoidance of locations visited by the other rat (because those locations were depleted of food) rather than visits to those locations. Similarly, in the earlier experiment using the pit maze (Keller & Brown, 2011), locations that were depleted of food by the other rat tended not to be chosen, even when the other rat was no longer physically present in those locations. In the present experiments, unlike those earlier experiments, the contingencies encouraged visiting either the same side of the arena visited by the other rat (Experiments 1 and 2) or the particular pit locations visited by the other rat (Experiment 3). If the physical presence of the other rat facilitates choices, then—as a consequence of that—the social influence found in the present experiments may have been restricted to the most recent choice made by the model rat. An alternative explanation for the present results is that memories of the choices made by the other rat do not persist long enough for

earlier choices of the model rat to influence choices. However, that explanation is inconsistent with the results of the previous experiments using both the radial-arm maze and the pit maze. Considered together, the results suggest that the physical presence of the model rat encourages approach by the subject rat but that approach itself is not sufficient to elicit choice of the location proximal to the model rat. Rather, facilitation of a choice by the subject rat requires that a choice be made by the model rat.

Learning through direct experience with the environment (personal information) is often argued to be less efficient than social learning, because social learning essentially allows an animal to take advantage of the environmental contingencies experienced by another animal (Boyd & Richerson, 1988; Galef & Laland, 2005; Zentall, 2004). On the other hand, use of social information has potential disadvantages. Systematic misinformation is provided by conspecifics under some circumstances (e.g., Mitchell & Anderson, 1997). Information provided by conspecifics can be outdated or irrelevant to current environmental conditions (Boyd & Richerson, 1988). The present results suggest that social cues control behavior in a flexible manner, according to their validity in relation to those other available cues. This, in turn, encourages the view that social information is used and processed according to the same psychological principles that apply to other kinds of information.

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