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Five on one side: Personal and social information in spatial choice

Michael F. Brown*, Marie E. Saxon, Teagan Bisbing, Jessica Evans, Jennifer Ruff, Andrew Stokesbury

Department of Psychology, Villanova University, 800 E. Lancaster Ave., Villanova, PA 19085, USA

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ABSTRACT

To examine whether the outcome of a rat's own choices ("personal information") and the choice behavior of another rat ("social information") can jointly control spatial choices, rats were tested in an open field task in which they searched for food. For the rats of primary interest (Subject Rats), the baited locations were all on one side of the arena, but the specific locations baited and the side on which they occurred varied over trials. The Subject Rats were sometimes tested together with an informed "Model" rat that had learned to find food in the same five locations (all on the same side of the arena) on every trial. Unintended perceptual cues apparently controlled spatial choices at first, but when perceptual cues to food location were not available, choices were controlled by both personal information (allowing the baited side of the arena to be determined) and social information (allowing baited locations to be determined more precisely). This shows that control by personal and social information are not mutually exclusive and supports the view that these two kinds of information can be used flexibly and adaptively to guide spatial choices.

This article is part of a Special Issue entitled: tribute to Tom Zentall.

1. Introduction

1.1. Theoretical background

Animals acquire information about their world from several kinds of sources. The sources that have received the most attention in psychological studies of learning involve exposure to contingencies among events in the world and contingencies between the animal's own behavior and the outcome of that behavior. The processes corresponding to these two kinds of contingencies are typically understood to be classical and instrumental learning, respectively (e.g., Dickinson, 1980). For present purposes, an important property of these sources of information is that they are based on the individual experience of the animal.

Animals also acquire information from other animals (typically, conspecifics), apparently taking advantage of information acquired directly by others. A wide range of social learning phenomena have been studied during the past few decades, using a variety of species and from a variety of theoretical perspectives (e.g., Box and Gibson, 1999; Byrne and Whiten, 1988; Giraldeau and Caraco, 2000; Heyes and Galef, 1996; Zentall and Galef, 1988). In principle, socially acquired information has the advantage of allowing contingencies to influence behavior adaptively without having to experience them directly, but rather by taking advantage of the experiences of other animals (Danchin et al., 2004; Templeton and Giraldeau, 1996). The focus of the experiment reported here is the distinction between information that an animal acquires directly from its own experience with the environment ("personal information") and social information that an animal acquires from another animal (Templeton and Giraldeau, 1996; Valone and Templeton, 2002).

1.2. Empirical background

Previous work from our laboratory has examined social influence, social learning and social memory in two similar laboratory spatial search tasks. First, when two rats are tested together in the radial-arm maze, they are influenced by two counterveiling social influences (Brown, 2011; Brown et al., 2008, 2007, 2009). On the one hand, they tend to approach a familiar (cage mate) conspecific and (perhaps as a result) choose maze locations in which the other rat is present. On the other hand, they avoid choice of maze locations that were visited by the other rat earlier during the trial (and thereby depleted of food). The latter tendency persists over short delays during which any odor cues left by the other rat are rendered irrelevant (Brown et al., 2007). It is also modulated by both the qual-

* Corresponding author.
E-mail address: michael.brown@villanova.edu (M.F. Brown).

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ity and quantity of food present following a visit by the other rat. Specifically, if locations contain large caches of food not depleted when a rat chooses the maze location, then previous visits by the other rat either increase or decrease the tendency to choose that location, depending on whether the food is a relatively more preferred or less preferred food type (Brown et al., 2008). Furthermore, the quantity of food available in locations also modulates the social effect; previous visits by the other rat either decrease or increase the tendency to choose a maze location, depending on whether the quantity of food there is such that it was or was not depleted by the other rat's visit, respectively. Thus, social information appears to increase choice efficiency by guiding rats to locations more likely to contain food or relatively preferred food.

More recently, work from our laboratory has examined social influences on spatial choices made in an open field task with a matrix of discreet choice locations, known as the Pit Maze (Bisbing, 2015; Keller and Brown, 2011). The apparatus consists of a 5×5 matrix of locations ("pits") in which food can be hidden under covers that must be lifted by the rat to determine whether food is available in the location. Keller and Brown (2011) tested pairs of rats in the Pit Maze in trials that started with all 25 pits baited with a single, small food pellet. Under these conditions, rats tended to avoid visits to locations that had been previously visited (and thereby depleted of food) by the other rat, just as they do in the radial-arm maze.

Bisbing et al. (2015) reported four experiments using the Pit Maze. All of them involved a procedure in which only a subset of the 25 locations was baited on each trial. In addition, some trials involved testing two rats together. One of the two rats (referred to as the "Model Rat") had consistently experienced the same subset of locations being baited over trials. The other rat ("Subject Rat") had experienced different subsets of baited locations over trials. Thus, the Model Rat potentially provided social information to the Subject Rat about the locations of food during a particular trial and the key question was the extent to which this information controlled the choices made by the Subject Rats. When all of the pits on one side of the arena were baited with a single food pellet and the pits on the other side of the arena were not baited (Bisbing et al., 2015, Experiments 1 and 2), Model Rats quickly learned to restrict their choices to the pits on the baited side of the arena. Subject Rats, for which the baited side of the arena varied unpredictably, quickly learned to locate the baited side of the arena after making a single choice. On half of the trials, Model and Subject Rats were tested together, with the matchups of Model and Subject Rats varying over trials. On those trials, the Subject Rats were socially influenced by the Models rats to choose a location on the correct (baited) side of the arena, but that social influence was restricted to the first choice of each trial only. This is important because it is only during the first choice that individual experience cannot guide the Subject Rats' choices to the baited side. During subsequent choices, when the outcome of choices made earlier during the trial reveal the locations of the baited pits, there was no difference in choice accuracy of the Subject Rats when they were tested together with the Model Rats in comparison to the control trials in which they were tested alone.

In another experiment using different rats (Bisbing et al., 2015, Experiment 3) the relevance of the social information was increased, relative to the experiments just described. Specifically, the subset of locations baited on each trial was 5 of the 25 pits, randomly chosen. As in the earlier experiments, the baited subset remained constant for Model Rats, but varied unpredictably over trials for the Subject Rats. In addition, the five baited pits were baited with a large supply of pellets that was not depleted when chosen by a rat. Thus, the Model Rats potentially provided information to the Subject Rats about the location of food that was not otherwise available. In fact, the choices made by the Subject Rats were strongly controlled by the choices of the Model Rats in this experiment. The results of the experiments reported by Bisbing et al. (2015) considered as a whole strongly suggest that social information was used to locate food by the Subject Rats only when personal information (the outcome of the Subject Rats' own choices) did not specify the remaining baited locations. It suggests that social information controls behavior only when it is not redundant with personal information.

1.3. Goals and logic of the present experiment

In the experiments of Bisbing et al. (2015), primary control of spatial choices was either by personal information or by social information. Can both kinds of information jointly or flexibly control spatial choices? The present experiment was designed with a combination of the contingencies in the experiments of Bisbing et al. (2015) to reveal relationships between control by individual experience and social information. Specifically, partial information about the location of food could be acquired via individual experience. However, more complete information about the location of food was available if another rat (the Model Rat) was making choices at the same time.

This experimental design was implemented using sets of baited locations consisting of five pits selected randomly from among the 10 pits on either side of the arena. Half of the Model Rats in the experiment were assigned a set of five baited pits on the east side of the arena and the remaining half were assigned a set of five baited pits on the west side of the arena. As in the earlier experiments, the assigned set remained constant over trials for the Model Rats but Subject Rats were paired with different Model Rats over trials, and therefore had different sets of baited pits over trials (on the east side for half of the trials and on the west side for half of the trials). The Subject Rat and the Model Rat with which it was paired for a particular trial were tested together on half of the trials and separately on the other half of the trials.

From the perspective of the Subject Rats, individual experience can provide partial information about the location of baited pits. Specifically, once the location of one or more baited pits is determined, the baited side of the arena is determined. Also, if pits on one side of the arena are chosen and found not to contain food, it becomes decreasingly likely that baited pits are located on that side of the arena. Although the arena side containing the baited pits can be determined based on the outcome of a Subject Rat's own choices, the specific pits baited within the baited side cannot be so determined. However, the choice behavior of the Model Rat during trials in which rats are tested together provides information about the specific locations of baited pits (assuming the Model Rats learn the assigned locations and selectively choose them).

1.4. Empirical predictions

Control by individual experience (i.e., the outcome of the rat's own choices) would be indicated by the Subject Rats acquiring an ability to choose pits on the baited side of the arena after making a choice or two, even when they are tested alone. However, assuming there are no unintended perceptual cues to the location of the food, they should show no ability to choose baited pits over unbaited pits on the baited side of the arena. If their choices can also be controlled by social information, the Subject Rats are predicted to also acquire a tendency to choose the baited locations that the Model Rat chooses over the unbaited locations on the baited side of the arena.

The earlier findings of strong control by personal information with very limited control by social information (Bisbing et al., 2015, Experiments 1 and 2) or strong control by social information when there is no personal information available (Bisbing et al., 2015, Experiment 3) suggest that spatial choices may be controlled in

the Pit Maze task either by personal information or by social information, but not by both. The possibility that only personal or social information are used to locate the hidden food in this task is also consistent with a number of suggestions that personal information and social information are "strategies" or alternative means of behavioral control that are somewhat mutually exclusive (see Kendal et al., 2004; Lanland, 2004; Rieucau and Giraldeau, 2011 for reviews). One possible mechanism for exclusivity of personal and social information is a cue competition effect of the sort that is ubiquitous in laboratory learning paradigms (e.g., Dickinson, 1980; but see Galef and Durlach, 1993 for an exception in the context of social learning).

Because the present experimental design renders both personal and social information relevant and allows behavioral control by the two types of cues to be measured separately, it provides an opportunity to detect simultaneous control by both personal information and social information.

2. Method

2.1. Subjects

Twenty-four male Sprague-Dawley rats were 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 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 cagemate pairs occurred when the rats were received from the vendor at approximately four weeks of age. The experiment began when the rats were approximately 13 weeks old.

2.2. Apparatus

The rats were tested in a 1.17 m square arena enclosed by 14 cm tall walls and painted flat black (Fig. 1 shows a schematic of the apparatus; see also Keller and 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 lip of the funnel directly on top of the lip of the cup (See Keller and Brown, 2011, Fig. 2 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 of which sucrose pellets 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 the pellets that might be detectable by the rats (these "sham bait" pellets were present in all pits, regardless of whether accessible pellets were present on the bottom of the pit).

The pits had a second ("cover") funnel placed inside that acted as a lid that had to be lifted to gain access to the pellets that might be 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 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 (because of the weight) after it was lifted so that there were no visual cues as to which pits had been visited.

2.3. General and preliminary procedures

Prior to each trial, approximately eight sucrose pellets (BioServe 45-mg sucrose pellets, Product F0042) were placed in the bottom of a subset of pits (the baited pits; see below). The pellets were placed inside the stem of the cover funnel (except during the first few preliminary training trials, during which the cover funnel was not present). A small swab of black cotton was placed in the stem of the funnel to eliminate any visual cues from the pellets. 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) 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 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). Daily maintenance feeding occurred after the experimental procedures.

During five preliminary 10 min exposures to the pit maze, cagemate pairs of rats were allowed to explore the maze with sucrose pellets scattered on the floor of the arena, in pits from which the cover funnel had been removed and in pits with the cover funnel in place. Over the course of these five preliminary training trials (one per day), the number of pellets scattered on the floor and the proportion of pits with the cover funnel removed were reduced over these five trials.

One member of each cage mate pair was randomly assigned to be a Model Rat and its cagemate was thereby assigned to be a Subject Rat. Model and Subject Rats were differently marked on their tails for identification. For Model Rats, five pits were assigned to be the baited pits and the identity of their baited pits was consistent over trials. For each of the 12 Model Rats, the five baited pits were chosen randomly from among either the ten pits on the east side of the arena or the ten pits on the west side of the arena (i.e., the ten pits in the leftmost two columns of pits shown in Fig. 1 or the ten pits in the rightmost two columns). For six Model Rats, the baited pits were chosen from among those on the east side and for the remaining six they were chosen from among those on the west side. Thus, for all the Model Rats, the five baited pits were all on the same side of the arena. Fig. 1 shows six examples of the pits assigned to be baited for particular Model Rats.

2.4. Training procedure

Model and Subject Rats then experienced 12 daily training trials. For Model Rats, the five assigned pits were baited prior to each trial. For Subject Rats, five randomly chosen pits from among the 10 pits on either the east side or the west of the arena were baited prior to each trial. The side with the baited pits varied randomly for the Subject Rats, with the constraint that the baited pits were on the east side for six trials and on the west side for six trials. Each trial started by placing the rat in the start box and then opening the guillotine door to allow the rat to enter the arena. The video recording was initiated just prior to opening the door and the training trials lasted for five minutes. The rat was removed from the arena immediately at the end of a trial. Choice of a pit was defined whenever a rat moved the cover funnel with its head. This was usually (but not always) followed by lifting the cover funnel and probing the inside of the funnel for pellets.

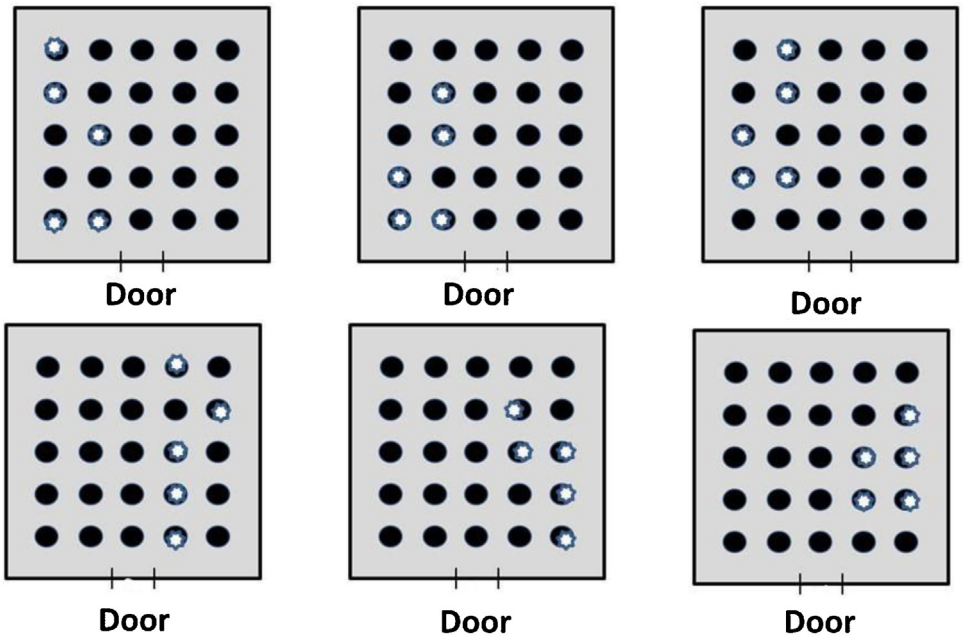

Fig. 1. Six example sets of baited pit locations. Each panel shows a schematic of the matrix of pits in the testing area, with the location of five baited pits indicated. Each Model Rat was assigned a set of five baited pits, randomly chosen with the constraints that all five baited pits were from among the 10 on the east side of the arena for from among the 10 on the west side of the arena. For Subject Rats, the baited pits were always those in a set assigned to one of the Model Rats, but the set varied over trials.

2.5. Test procedure

Test trials began immediately following the training trials. There were two kinds of test trials. In Alone trials, rats were tested individually as during the training trials. In Together trials, one Model Rat and one Subject rat were tested together, by being placed together in the start box and released into the arena. During Together trials, the baited pits were the five pits assigned to the Model Rat. During the Alone trials, the baited pits were also those assigned to the Model Rat being tested or, in the case of the Subject Rat the pits assigned to one of the Model Rats (with which the Subject Rat was paired that trial for purposes of determining the baited pits only). The Model Rat with which a Subject Rat was paired each trial (either tested together or alone) varied over trials, with each of the 12 Model Rats being paired with each of the 12 Subject Rats twice during each of three blocks of trials (once for an alone trial and once for a together trial, thus, there were a total of 72 test trials). The sequence of Model Rat/Subject Rat pairings and together vs. alone trial types varied randomly for each trial block. It should be emphasized that this procedure resulted in the Model experiencing the same baited pits on every trial. The Subject Rats experienced different sets of five baited pits on different trials. Critically, however, for all rats the five pits baited on every trial were always either among the 10 on the east side of the arena or among the 10 on the west side of the arena.

Trial duration varied over the three trial blocks, with the duration being 2 min during the first trial block, 1.5 min during the second trial block, and 1.0 min during the third trial block. Either one or two trials were conducted for each rat each day (generally, five days per week). On days when two trials were conducted, the trials for any particular rat were separated by at least 2 h.

The choice data were coded from the video recordings of the test trials, using the same technique described by Bisbing, et al. (2015). Specifically, coders observed each rat on the video record and coded the sequence of pit choices made by the rat(s). In the case of together trials, each rat was observed and its choices coded in a separate run of the video record and the time of the choices (relative to a signal that marked the beginning of the trial on the video record) was used to collate the sequence of choices made by the two rats.

2.6. Measures and analysis approach

Data of the Subject and Model Rats were analyzed separately, using Analysis of Variance (ANOVA), with a decision criterion of $p < .05$ for rejection of the null hypothesis. For each group of rats, choices were analyzed in term of two metrics. The first was the proportion of choices made to pits on a side of the arena that were to pits on the baited side of the arena (choices to the five pits in the middle section of the arena were not included in the denominator of this proportion). The second was the proportion of choices made on the baited side of the arena that were to the five baited pits (rather than to the five pits not baited but were on the baited side of the arena). Because of the ambiguities associated with choices of pits that had been chosen earlier in the trial by the same rat (see Bisbing et al., 2015), revisits of pits that had been chosen earlier in the trial by the same rat were not included in the analyses.

3. Results

3.1. Model Rats

The primary goal of analysis of the Model Rats' choices was simply to confirm that they tended to choose the baited pits, thereby providing relevant information to the Subject Rats. The left panels of Figs. 2 and 3 show mean proportions of choices to pits on the baited side of the arena by the Model Rats and the mean proportions of choices on the baited side that were to the baited pits, respectively. The means are shown separately for the Alone trials and Together trials and for each of the three trials blocks as a function of choice number. The means for Choices 1 through 5 are calculated separately and choices made following the fifth choice are collapsed in a sixth category. There were only five baited pits and some rats tended to stop making choices after making about five choices. As a result, the formal data analyses and interpretation of the data were restricted to performance during the first five choices.

The Model Rats exhibited a strong tendency to choose pits on the baited side of the arena (left panels of Fig. 2) and to choose baited pits from among the pits on the baited side of the arena (left panels of Fig. 3). A 5 (Choice: choices 1 through 5) × 3 (Trial Block) × 2 (Trial Type: Alone vs. Together) within-subjects ANOVA was performed on the proportions of choices of the Model Rats that were to the baited side of the arena. It revealed a significant effect of Choice, $F(4, 44) = 9.34$ and a Choice × Trial Block interaction, $F(8, 88) = 5.04$. Here and below, any unreported ANOVA factors did not reach the level of significance. The Model Rats were close to the ceiling level of only choosing baited pits under most conditions and the ANOVA results can be interpreted as showing that their tendency to make choices on the baited side was somewhat less during later choices (after they had chosen most of the baited pits), especially during the first trial block.

A 5 (Choice: choices 1 through 5) × 3 (Trial Block) × 2 (Trial Type: Alone vs.Together) within-subjects ANOVA was also performed on the proportions of choices of the Model Rats among those on the baited side of the arena that were to one of the five baited pits (left panels of Fig. 3). It revealed significant effects of Block, $F(2, 22) = 28.06$, Choice, $F(4, 44) = 4.12$, and a Choice × Trial Block interaction, $F(8, 88) = 3.46$. These results show that the tendency to choose baited pits from among the pits on the baited side of the arena increased with experience (i.e., over trial blocks) and decreased over choices (i.e., as more baited pits had been chosen). However, Model Rats generally tended to choose baited pits and therefore provided relevant information to the Subject Rats about the location of food.

3.2. Subject rats over all Trial Blocks

The data of the Subject Rats are shown in the right panels of Figs. 2 and 3 and are structured just like the data of the Model Rats. A 5 (Choice: choices 1 through 5) × 3 (Trial Block) × 2 (Trial Type: Alone vs. Together) within-subjects ANOVA was performed on the proportions of choices of the Subject Rats that were to the baited side of the arena (right panels of Fig. 2). It revealed significant effects of Trial Block, $F(2, 22) = 8.92$, Choice, $F(4, 44) = 30.00$, Trial Type, $F(1, 11) = 127.30$, a Choice × Trial Block interaction, $F(8, 88) = 5.94$, and a Trial Block × Trial Type interaction, $F(2, 22) = 8.81$.

A 5 (Choice: choices 1 through 5) × 3 (Trial Block) × 2 (Trial Type: Alone vs. Together) within-subjects ANOVA was performed on the proportions of choices of the Subject Rats among those on the baited side of the arena that were to one of the five baited pits (right panels of Fig. 3). It revealed significant effects of Trial Block, $F(2, 22) = 73.56$, Choice, $F(4, 44) = 4.28$, Trial Type, $F(1, 11) = 88.10$, and a Trial Block × Trial Type interaction, $F(2, 22) = 8.61$.

3.3. Different patterns of performance over trial blocks in Subject Rats

A striking feature of data from the Subject Rats is the difference between the apparent pattern of results for the first trial block and the subsequent trial blocks. First, in Alone trials, the Subject Rats appear to have a tendency to choose pits on the baited side starting with their first choice during the first trial block, but choose pits on the baited side at a chance level (0.5) during at least the first two choices during subsequent trial blocks. Second, in Alone trials, the Subject Rats appear to choose baited pits from among the pits on the baited side at a chance level (0.5) during Trial Blocks 2 and 3, but more than expected by chance during Trial Block 1. The apparent pattern of results during Trial Blocks 2 and 3 is as expected, assuming that during Alone trials the rats have no information about the baited side during Alone trials until making a choice or two and have no information about the location of baited pits until choosing a particular pit. These behavioral phenomena indicate that the rats had some kind of unintended perceptual information about the location of baited pits during Trial Block 1 that they did not have during subsequent trial blocks.

To confirm that some kind of information about the location of baited pits was available during the first trial block that was not available subsequently, we performed a series of *t*-tests. First, the proportions of choices that were to pits on the baited side of the arena by the Subject Rats during the Alone trials (means shown as blue circles in the right panels of Fig. 2) were compared to chance (0.5). During Block 1, the mean proportions for Choices 1 through 5 were all significantly greater than 0.5, $ts > 5.4$. During Block 2, none of the mean proportions for Choices 1 through 5 were significantly different from 0.5, $ts < 3.1$. During Block 3, Choices 3 ($t = 5.65$), 4 ($t = 3.56$) and 5 ($t = 6.57$) were greater than 0.5 but Choices 1 and 2 were not different from 0.5 ($t < 1$). Second, the proportions of choices among those on the baited side of the arena that were to the baited pits by the Subject Rats during the Alone trials (means shown as blue circles in the right panels of Fig. 3) were compared to 0.5. During Block 1, the mean proportions for Choices 1 through 5 were all significantly greater than 0.5, $ts > 3.6$. During Blocks 2 and 3, none of the mean proportions for Choices 1 through 5 were significantly different from 0.5, $ts < 1.1$. Thus, during Blocks 2 and 3, Subject Rats selectively chose the baited side of the pit only after making two choices (the outcome of those choices providing information about which side of the arean was baited). In addition, during Blocks 2 and 3, there was no indication that Subject Rats could discriminate the baited pits on the baited side of the arena from the unbaited pits on the baited side of the arena prior to choosing those pits. During Block 1, on the other hand, the Subject Rats selectively choose baited pits even during the first choice.

3.4. Subject Rats during Trial Blocks 2 and 3

Given that unintended perceptual cues to the location of baited pits were available to the Subject Rats during Block 1 but not subsequently, additional analysis of the Subject Rats' performance was restricted to the data from Blocks 2 and 3. Specifically, a 5 (Choice: choices 1 through 5) × 2 (Trial Block: blocks 2 and 3) × 2 (Trial Type: Alone vs. Together) within-subjects ANOVA was performed on each of the two dependent measures, in order to isolate the effects of these factors under conditions without perceptual cues to the baited pits.

A 5 (Choice: choices 1 through 5) × 2 (Trial Blocks 2 vs. 3) × 2 (Trial Type: Alone vs. Together) within-subjects ANOVA, performed on the proportions of choices of the Subject Rats that were to the baited side of the arena, revealed significant effects of Trial Block, $F(1, 11) = 5.62$, Choice, $F(4, 44) = 25.50$, Trial Type, $F(1, 11) = 111.26$, a Choice × Trial Block interaction, $F(4, 44) = 3.34$, and a Choice × Trial Type interaction, $F(4, 44) = 3.83$. These results can be explained as follows: the tendency to choose pits on the baited side of the arena was greater in Trial Block 3 than in Trial Block 2, increased over Choices 1–5, and was much greater during the Together trials than during the Alone trials. The increase over choices was enhanced during Block 3 relative to Block 2. Finally, the social effect on choice of pits on the baited side increased over choices. As shown by the *t*-tests reported above, during Alone trials the Subject Rats had no tendency to choose pits on the baited side during the first two choices, but after two choices choose pits on the baited side more than expected by chance even during the Alone trials.

A 5 (Choice: choices 1 through 5) × 3 (Trial Blocks 2 vs. 3) × 2 (Trial Type: Alone vs.Together) within-subjects ANOVA, performed on the proportions of choices of the Subject Rats among those on the baited side of the arena that were to one of the five baited pits, revealed significant effects of Choice, $F(4, 44) = 3.54$ and Trial Type, $F(1, 11) = 137.87$. The effect of choice number appears to be due to a decrease in the tendency to choose baited pits from among the

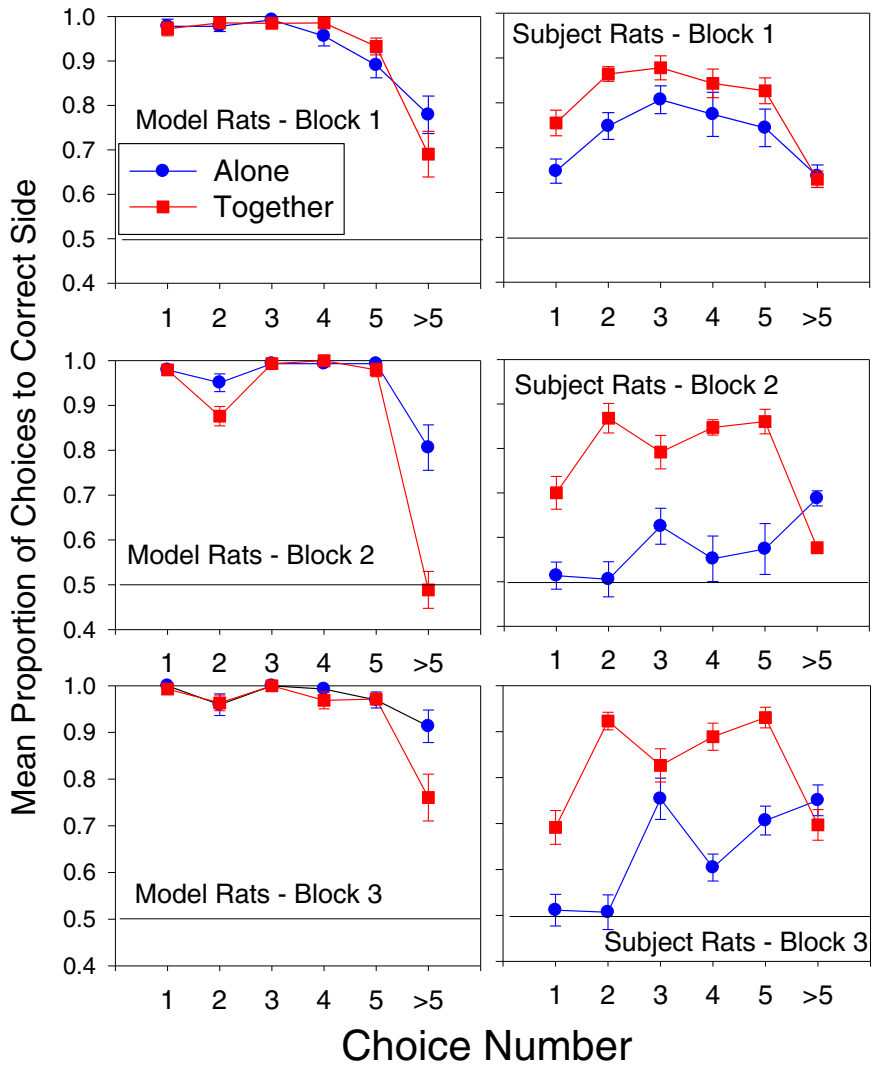

Fig. 2. Mean (over rats) proportion of choices that were to pits on the baited side of the arena for the Model Rats (left panels) and Subject Rats (right panels) during the Alone and Together trials over the three trial blocks. Choice number ">5" includes all choices made following the fifth choice. Error bars show one standard error of the mean.

pits on the baited side of the arena. The effect of trial type shows a large tendency to choose baited pits from among the pits on the baited side of the arena in the Together trials in comparison to the Alone trials (the *t*-tests reported above provide no evidence for any tendency to do so during the Alone trials).

4. Summary of key results

The key results can be summarized as follows. During the first trial block, the Subject Rats tended to choose baited pits during Alone trials as well during Together trials. Thus, some perceptual cue(s) provided information about the location of baited pits during Block 1. During the remaining two trial blocks, however, the Subject Rats in Alone trials did not demonstrate a tendency to choose pits on the baited side of the arena until after they had made two choices. Furthermore, during Alone trials, they did not choose baited pits any more than unbaited pits among the choices made on the baited side of the arena. These two findings clearly indicate that no perceptual cues to the location of baited pits were available during Trial Blocks 2 or 3. During those trial blocks, there was a larger tendency to choose pits on the baited side of the arena in the Together trials than in the Alone trials. There was also a large tendency to choose baited pits from among the pits on the baited side of the arena in Together trials and no such tendency in the Alone trials.

4.1. Perceptual cues during Trial Block 1 but not subsequently

We have not identified the perceptual cues that were present during Block 1 but not during Blocks 2 and 3. There may have been some seemingly minor changes in the details of how the pits were baited that are, in fact, important. It also appears that we started using a new shipment of sucrose pellets at about the same time that Block 2 began and it is possible that, as a result, there was an odor cue present during Block 1 that was not present during Blocks 2 and 3. We have examined all the information available about these kinds of details but none of it provides determination of a likely explanation. However, the data of Blocks 2 and 3 contain no indication of perceptual cuing of the baited pits. Therefore, the choices of rats during those trial blocks can be used to examine the relative contribution of individual experience and social influence in control the choices of the Subject Rats.

4.2. Use of both personal and social information

During Blocks 2 and 3, Subject Rats showed no tendency to make choices on the baited side of the arena during Alone trials until they had made two choices. Additionally, among the choices they made on the baited side of the arena during Alone trials, Subject Rats were equally likely to choose baited and unbaited locations. Individual

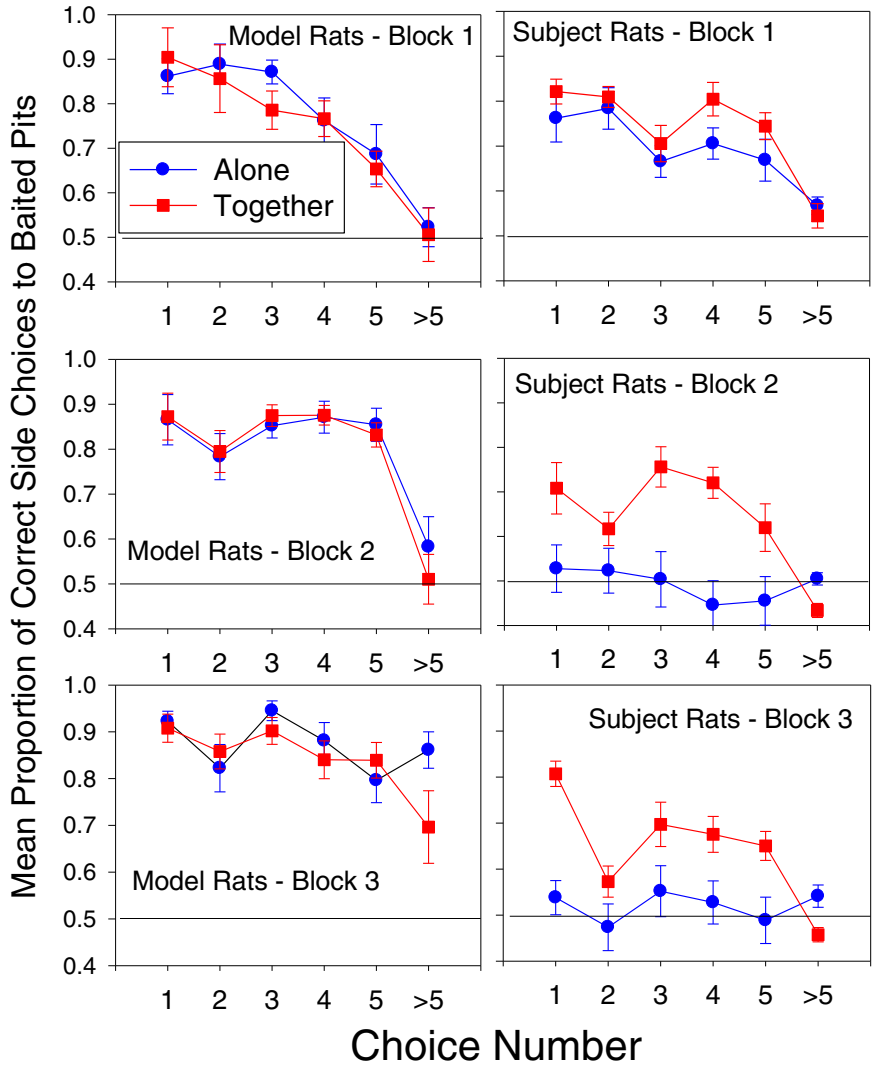

Fig. 3. Mean (over rats) proportion of choices among those made to pits on the baited side of the arena that were to baited pits for the Model Rats (left panels) and Subject Rats (right panels) during the Alone and Together trials over the three trail blocks. Choice number ">5" includes all choices made following the fifth choice. Error bars show one standard error of the mean.

experience (specifically, the outcome of the first few choices they made) allowed them to selectively choose locations on the baited side of the arena rather than the unbaited side. Furthermore, choice of locations on the baited side of the arena was facilitated by the presence of Model Rats. Thus, personal information and social information jointly controlled the side of the arena on which the Subject Rats made choices. Social information also controlled the specific locations chosen on the baited side of the arena.

It should be noted that our measurement of the arena side chosen by the rat (correct (baited) side vs. incorrect (unbaited) side of the arena) and the ability of rats to choose accurately in terms of this measure do not imply that the rats necessarily represent the arena in terms of two sides nor that they are making a binary choice between the two arena sides. It is possible that the rats acquire spatial representations that include the two sides of arena and this possibility is encouraged by the complex representations of spatial configurations in similar apparatus for which there is evidence (Brown, 2006). The five pits between the two "sides" of the arena (the middle column of pits in the examples shown in Fig. 1) were never baited in the present experiment partly to encourage representation of arena sides (but also to reduce complexities of interpretation caused by rats' thigmotaxic avoidance of the pit in the middle of the arena and choices of the pit most proximal to the arena entrance). However, we have no direct evidence in the present experiment that rats were representing the side of arena in which baited pits were located. Among the alternative mechanisms of performance related to the side of the arena is the spatial proximity of the chosen pit to the last pit chosen. Rats may tend to choose a pit closer to the pit most recently chosen when the pit most recently chosen was baited.

Regardless of the mechanism(s) involved in modulating the extent to which rats choose pits on the baited side of the arena, the data from Blocks 2 and 3 show that this tendency was produced by the outcome of the first two choices made by Subject rats in the alone trials. Thus, Subject rats' choices were somehow modulated by personal information such that they choose pits on the baited side of the arena during the later choices in Alone trials. During Together trials, the tendency of Subject rats to choose pits on the baited side of the arena was larger (and occurred during the first two choices they made).

4.3. Theoretical implications of joint control by personal and social information

Bisbing et al. (2015) found that the choices of Subject Rats were controlled by individual experience under some conditions

(Experiments 1 and 2) and by social influence under other conditions (Experiment 3). In the former case, information provided by personal information and social information were redundant (the baited side of the arena could be determined by either kind of information). One possibility, suggested by Bisbing et al. (2015) is that under these circumstances the outcome of a rat's own choices and the information provided by a Model Rat's choices compete for control of behavior, just as perceptual cues compete for behavioral control in the form of overshadowing and blocking. Furthermore, this cue competition between very different kinds of cues indicates that social information is processed by at least some of the same learning and memory processes as the spatial cues specifying the location of pits chosen by the Subject Rat. Converging evidence for this conclusion comes from experiments in the radial-arm maze suggesting that information about maze location obtained during a rat's own visit to the location and information obtained about another rat's visit to the same location are integrated before they influence subsequent choices (Brown, 2011).

The present results are consistent with this view that individual experience and social influence compete for control of spatial choices. In the present experiment, both kinds of information were relevant, but they were not redundant. The outcome of a Subject Rat's own choices allowed it to make additional choices that were more likely to be to baited locations (i.e., locations on the baited side of the arena) but did not specify the baited locations. The addition of social information (in the Together trials) allowed choices to be made more precisely to the baited locations. This pattern of results is analogous to that found when perceptual cues that provide different degrees of information are presented in compound (e.g., Wagner et al., 1968).

The present results indicate that personal information and social information can be used flexibly and within the same task. This is consistent with conclusions drawn on the basis of natural and semi-naturalistic foraging experiments, in which animals show evidence of using both kinds of information in a flexible manner that corresponds to their relative information value and on the relative costs (metabolic costs and risks) associated with acquiring information in these two ways (e.g., Galef et al., 2008; Kendal et al., 2004; Laland, 2004; Rieucau and Giraldeau, 2011).

Although personal information and social information were both used in the present experiment, we cannot distinguish between two possible versions of the manner in which they jointly controlled choices. It may be that, when the rats were tested in the social situation, they used personal information as well as social information to determine the arena side (or, more generally, the approximate location) of the baited pits. Alternatively, it may be that personal information was not controlling choices during the Together trials. Instead, choices of the Subject Rat could have been controlled entirely by the Model rat's choices, with the enhanced tendency to choose locations on the baited arena side during the Together trials being a side effect of social control of the specific locations chosen. The latter possibility is less parsimonious in that it attributes the ability of Subject rats to choose pits on the correct side of the arena to two different mechanisms in the Alone trails and Together trials. It will require additional empirical work to explicitly dissociate these two possibilities. It should be noted, however, that either possibility requires the flexible use of both personal and social information.

It has been argued by those studying both human and non-human social cognition from a variety of perspectives that social cognition is likely to be structured in "modules" that function independently of the processes responsible for learning about non-social cues (e.g., Adolphs, 1999; Cacioppo, 2002). The present data, along with those reported by Bisbing et al. (2015) are more consistent with the view that social cues are processed by the same learning and memory mechanisms as other kinds of cues. Social information competes for control of behavior with non-social cues to spatial location and conforms to the same principle that the degree of behavioral control by a particular cue or type of cue depends on its information value in relation to other available cues. Whether there is anything unique about the psychological mechanisms that detect and process information provided by the behavior of conspecifics remains an open question.

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