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Jerome Cohen
University of Windsor

Marium Arain
University of Windsor

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Hierarchical Use of Cues in the Missing Object Recognition Task by Rats (*Rattus norvegicus*)

Marium Arain and Jerome Cohen

University of Windsor

Corresponding author

Jerome Cohen (jcohen@uwindsor.ca)

University of Windsor, Department of Psychology, Windsor, Ontario, Canada N9B 3P4

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Abstract

This study investigated rats' preferences for using non-spatial and spatial cues by rats in a missing-object recognition task. Rats were trained to find a sunflower seed under any one of four previously missing adjacent objects, the test array of a trial, after having found seeds under three of them in the 'study' array of that trial. On some trials the study and test arrays consisted of a different object at each baited food site and on other trials, of identical objects. A previously missing object's position and orientation within its array and its global position within the large foraging chamber varied over trials but not within trials. Following training, rats received interspersed non- or partially rewarded probe trials with transformed test arrays of dissociated non-spatial (object-specific) and spatial cues on test array feeders. Results from these probe trials revealed that rats preferred to search for a missing object based first on its specific non-spatial features before searching for it based on its local spatial features; that is, its local position followed by its orientation, and finally based on its global position. This hierarchical sequence for using spatial cues was preserved under the identical-objects cueing condition. Rats reversed their preferences between object-specific and local position cues, however, when novel objects replaced the same four different objects in a supplementary experiment. We discussed the implications of these findings in terms of the influence of ecological- and context-dependent factors on information use or retrieval from animals' visuo-spatial working memory.

Key Words: Visuo-spatial working memory. Missing object recognition. Cue use preferences. Rats (*Rattus norvegicus*)

1 Introduction

During foraging expeditions animals often find hidden food at or near specific objects that consist of different redundant non-spatial

visual, olfactory, tactile features and spatial local and global positions. How accurately and flexibly an animal processes and retains these multiple sources of information within its visuo-

spatial working or reference memory affects its foraging efficiency and consequently its survival (Gibbs et al., 2007; Healy and Hurly, 2004). In terms of its working memory, an animal has to remember which cued sites it has already visited (retrospection) and which it has yet to visit (prospection) to reduce search energy and time in potentially dangerous open areas. In terms of its reference memory, it must learn and remember where food is more likely to be found and how often it is replenished. The question of theoretical interest in this study is how animals integrate and use these various spatial and non-spatial cues to find remaining food in a previously inspected patch (array) of cued food sites, a prospective working memory problem.

Several studies reveal that different species of rodents rely more on spatial than non-spatial information within their reference or working memory to find food or a safe location from an open area. In tasks requiring only reference memory, rats, *Rattus norvegicus*, rely more on distal room cues than olfactory or proprioceptive movement information to find a peripheral open escape hole on the Barnes terrestrial platform but can use the less preferred information when necessary (Maaswinkel and Wishart, 1999). In a more natural meadow setting, Columbia ground squirrels, *Spermophilus columbianus*, (Vlasak, 2006), can also use less preferred local proximal landmark objects or easier routes but prefer to use the distal landmarks of the forest outline to find which one of nine raised platforms is always baited. Rats will use widely separated objects as proximal landmarks for finding hidden food at consistent distances and directions from them in large arena (Biegler and Morris, 1993; 1996). Under the latter condition, rats initially treat the object nearest the hidden food as a beacon from which to conduct their search but can eventually learn to use it as a proximal landmark. Rats also treat stimuli

within the radial arm maze only as beacons when the food goal locations randomly vary over trials (Hogarth et al., 2000). Flying squirrels, *Glaucomys volans*, also prefer to use the spatial global and local position of a consistently baited cup rather than its specific distinctive non-spatial visual features (Gibbs et al., 2007).

Several studies with rats, *Rattus norvegicus*, in the interrupted radial maze task, a working memory task, reveal that these animals have difficulty using distally or proximally cued arms independently of their fixed spatial configuration to accurately find a trial's remaining arms (Cohen and Bussey, 2003; Kraemer et al., 1983; Suzuki et al., 1980; Tremblay and Cohen, 2005; Vollmer-Conna and Lemon, 1998). In the two most recent studies, rats were unable to find above chance which one of four proximally cued arms in an enclosed radial maze had been blocked when the spatial configuration of the arms were varied over or between trials. Rats in the more recent study (Tremblay and Cohen, 2005, Experiment 3) eventually learned to find a target arm when the spatial configurations always varied for one set of cued arms but remained severely disrupted by occasional exposures to changed configurations of another set of cued arms otherwise presented in a fixed configuration. Results from these studies suggest that rodents can learn to use both types of cues but prefer spatial over non-spatial information.

A particularly salient feature of the radial arm maze research from our laboratory is that the relative positions of cued arms were fixed during training. The disruption caused by later varying these arms' spatial configuration suggests that rats had fully integrated each arm's relative position with its non-spatial features and simultaneously processed both sources of information. Thus, when later faced

with changed spatial configurations, rats would have had considerable difficulty in matching any newly positioned arm with a retrieved integrated representation of it to find the remaining target arm. This notion logically led us to ask the following question. If rats had always been trained with the spatial configuration of the cued arms always varied over but not within trials; that is, a maze arms' spatial configuration would be fixed only between a trial's three-arm 'study' and four-arm 'test' segment, might they process each of the arms' spatial and non-spatial cues separately? If so, then we might be able to determine whether rats prefer to use one type of information before using another to find the remaining baited arm; that is, would rats display a hierarchical or a random pattern of using these cues? To answer these questions, we had originally planned to train rats with spatial configurations that constantly varied over but not within trials and then to occasionally vary the maze's spatial configuration within a trial. Rats would be expected to continue to find the target arm above chance on such probe trials if they separately processed and retrieved arms' non-spatial and spatial cues. Any pattern of their arm choices in such trials should reflect any cue use preferences. Unfortunately, logistical difficulties in manipulating the cued arms in such a large maze dissuaded us from proceeding with such research with this apparatus. Rather we decided to test these ideas with an object recognition version of this task (Arain et al., 2012) because a previous new-object recognition study from our laboratory demonstrated the ease of carrying out complex within-trial object manipulations (Cohen et al., 2010).

In our latest study (Arain et al., 2012), rats had to find which junk object within a square test array of four adjacent objects in a

large foraging area had been absent in a previously inspected three-object study array. A rat had to displace each of the three objects to obtain sunflower seeds beneath them in the study array before it could receive the four-object test array containing the previously missing, now baited target object in the trial's test array. During training, the location of the study and test arrays within a trial remained unchanged as did the local position of the missing object within a trial; that is, between its study and test segments. However, the location of these array pairs was widely moved between trials as was the position of the missing object to prevent any formation of long-term, consistent redundant combinations of each object's local and global spatial cues. We note that on half the segmented trials both arrays consisted of identical objects and on the other half they consisted of four distinctly different objects. The within-array positions of the different objects also varied over but not within trials to prevent long-term fixed redundant combinations between each different object's non-spatial cues with its spatial cues. As in the interrupted radial-arm maze studies, rats easily learned to accurately find the previously missing, target item (object). More importantly, rats' accuracy for finding the remaining baited object was not disrupted but rather enhanced on post-acquisition probe test trials when the relative positions of different objects and a trial's test array's location under either object-cueing condition were changed from those of its trial's study array. These findings not only provided evidence that rats separately processed objects' local and global positions spatial cues but also that they had a limited-capacity for retrieving information from their visuo-spatial working memory. That is, changing a test array's location or a target object's within-array position from that of its study array allowed rats to reduce their load for

retrieving missing object's relevant non-spatial cues or global spatial cues encoded from the study array. We could not determine whether rats retrieved a target object's spatial and non-spatial cues in a more or less fixed sequential manner because we had only assessed rats' initial choice accuracy in these rewarded probe test arrays. Therefore, we modified this missing-object recognition task to examine rats' cue-use preferences in the present study.

To accomplish this goal, we adapted a non-rewarded cue dissociation probe test procedure from earlier avian research that compared cue-use preferences between food caching and non-caching species (Brodbeck, 1994; Clayton and Krebs, 1994). In those studies, birds were first trained to find one of four feeders that contained inaccessible or partially accessible food during an inspection (study) segment before being allowed to relocate that feeder and remove its food in the test segment after a short retention interval. In post-acquisition non-rewarded probe tests, the arrays of feeders were transformed to dissociate the correct feeder's non-spatial color pattern cues from its correct local (within array) or global (within the larger wall area) position cues over various feeders. These studies found that caching species, black-capped chickadees (*Parus atricapillus*), marsh tits (*Parus palustris*), and jays (*Garulus gandarius*), and non-caching species, dark-eyed juncos (*Junco hyemalis*), blue tits (*Parus caeruleus*), and jackdaws (*Carvus monedula*), were equally accurate in finding the target feeder during regular baseline trials. During non-rewarded probe trials, however, caching birds looked into feeders at correct spatial global and local positions before looking into a feeder with the correct non-spatial cues while the non-storing species showed no specific sequential feeder selection patterns.

The present study is a logical progression from and extension of our recent missing-object recognition study (Arain et al., 2012). Along with presenting rats occasional non- or partially rewarded cue-dissociated probe trials following their acquisition of the basic task, we included another local spatial cue, objects' orientations along with their local positions within a trial's arrays. To accomplish this we mounted objects on rectangular feeders that could be oriented differently from each other as shown by examples in Figure 1. This additional spatial feature made our laboratory foraging arena more similar to rodents' natural foraging environments where food is often widely dispersed or cached around different beacon objects rather than always to the same side of them (Steele et al., 2008; Vander Wall, 1995; Vander Wall et al., 2001). Such differential orientation cues could further allow rats to distinguish a target object from other objects especially in the absence of different non-spatial cues under the identical-objects cueing condition. In the real world where beacons may become less distinctly different over time, feeding site orientations might offer an alternative source of information to that from distal landmarks as suggested by other researchers (Healy and Hurly, 2004; Hurly et al., 2010; Vlasak, 2006).

We expected rats to prefer using (retrieving) a missing object's non-spatial cues over its spatial cues when tested with dissociated cues trials on their first choice. We base this prediction on findings from our most recent study (Arain et al., 2012, Experiment 1) revealing that rats reduced their accuracy for finding the missing object among identical but not among different objects when retention intervals between a study and test arrays were increased from 2- to 10-min. Moreover, rats are very adept at detecting an added or a changed object from an array of previously inspected

objects regardless of whether it replaces an old object or occurs in a new location (Anderson et al., 2003; Berlyne, 1950; Cohen et al., 2010; Ennaceur and Delacour, 1988; Ennaceur et al., 1997). The question then is whether rats will show any fixed (hierarchical) preferences for using a missing object's spatial cues under either object-cueing condition? Given that rats, *Rattus norvegicus*, are opportunistic feeders or, to some extent, larder- rather than scatter-hoarders (Phelps and Roberts, 1989), they would not be expected to show any hierarchical spatial cue preferences. While this prediction follows from comparisons of cue preferences between caching and non-caching avian species (Brodbeck, 1994; Brodbeck and Shettleworth, 1995; Clayton and Krebs, 1994), findings from more recent studies with other rodent species also promote this prediction. They find superior retention of spatial information in working memory in scatter hoarding than in larder hoarding rodents (e.g., grey squirrels, *Sciurus carolinensis*, vs. red squirrels, *Sciurus vulgaris*, Macdonald, 1997; Merriam's kangaroo rats, *Dipodomys merriami*, vs. sympatric pocket mice, *Chaetodipus intermedius*, Rebar, 1995; or vs. Great Basin kangaroo rats, *Dipodomys microps*, Barkley and Jacobs, 2007).

The present study consisted of a major experiment (Experiment 1) and a supplementary one (Experiment 1b). In Experiment 1, we exposed rats to the same four different objects on some trials (different objects cueing condition) and to four identical objects of a fifth type on other trials (identical objects cueing condition). In the supplemental experiment, however, these rats received only arrays consisting of four different objects selected from a larger pool of novel objects over trials to approximate the trial-unique condition used in earlier avian research (Brodbeck, 1994).

2 Experiment

2.1 Basic Design

This experiment consisted of a missing-object recognition training phase similar to that used in Arain et al. (2012), followed by four successive test phases each containing a different series of cue-dissociated probe trials similar to those used by Brodbeck (1994). Unlike Arain et al. (2012), we exposed rats to three different geometrical configurations of adjacent rectangular feeders rather than a square array of objects. This modification allowed us to dissociate a missing object's feeder orientation from its local within-array position on probe trials' test arrays. The panels A, B, and C in Figure 1 show the three different basic geometrical feeder configurations used throughout this study. The mounted objects on the feeders shown in Panels A and B are the five different types of objects used in Experiment 1. The four mounted objects in Panel C are from the 20 novel objects used in Experiment 1b. As is evident in these panels, the feeders in each configuration were arranged to allow a rat unimpeded access to the front of each feeder that could contain an object mounted on the feeder's food well cover. During the course of this study, rats were exposed to four different rotated versions of each configuration over trials during training to create twelve different array configurations. As in Arain et al. (2012), all possible combinations of the non-spatial and spatial sources of information about the missing object were randomly varied over but not within trials.

[See Figure 1]

Following acquisition of the basic missing-object recognition task, rats received a series of four probe cue preference phases containing dissociated-cues probe trials interspersed among regular (baseline) trials.

Figures 2a and 2b show examples of each type of probe test trial derived from one of the many possible baseline trials under each object-cueing condition. This figure is only for illustrative purposes in that a probe trial under either object-cueing condition containing a dissociated-cued test array never occurred with the same three-object study segment as the baseline trial in a session. As seen in this figure, slight transformations in the position of a previously missing, target object, the missing object's feeder orientation, and displacement of location of a test array allowed for dissociation of any combination of the missing object's spatial and non-spatial cues. The number of different types of cues separately dissociated from each other was increased over phases from 2 (Phases 1 and 2) to three (Phase 3) and then to all four (Phase 4) under the different-objects cueing condition. The number of three different types of spatial cues under the identical-objects cueing condition was increased from two (Phases 2 and 3) to all three cues (Phase 4). In the interests of space, we confine a more complete description of the type of dissociated-cues test and the missing object's cues that could be controlling a rat's choice in each phase's probe test arrays to captions in Figures 2a and 2b.

[See Figures 2a and 2b]

2.2 Method

2.2.1 Subjects

Seven male Long-Evans hooded rats purchased from Charles River Breeding Farms, St. Constant, Quebec, served in this study. They were three months old and weighed over 300 g at the beginning of Experiment 1. They were allowed to consume 20-25 g of food (Purina Rodent Chow) within 2 h in their individual holding cages following each experimental session and before being returned to their large

group cages (three rats per cage) in our colony room. Water was freely available in holding and group cages. This regimen maintained rats at approximately 90% of their free-feeding weights. The colony room was maintained on a 12:12 h dark/light cycle and experimental sessions began within three hours of the beginning of the dark cycle.

2.2.2 Apparatus and Materials

2.2.2.1 Foraging Arena: We used the foraging arena from our previous two studies (Cohen et al., 2010; Arain et al., 2012). It consisted of a 1.2 m square aluminum platform that stood 56 cm above the floor of the experimental room. It was enclosed by 46 cm high grey wood walls and surrounded by a black curtain suspended from the ceiling. A black plastic guillotine door was located mid-way along each wall but only the guillotine door on the west wall's side was operated by the observer to allow rats to enter and exit the foraging area into an external start/exit holding chamber. A webcam (Logitech) above the west wall, connected to a nearby pc laptop computer, allowed the experimenter to monitor and record rat's search behavior out of the animal's sight. The floor of the arena contained twenty-five 2-cm diameter holes arranged in a 5 by 5 matrix. As seen in Figure 1, holes not covered by feeding stations were capped with aluminum disks.

2.2.2.2 Feeding stations, bait, objects: As shown in Figure 1, each feeding station (feeders) was a rectangular (16.5 cm by 7.6 cm by 2.5 cm) aluminum block with a 2-cm dia. 0.5 cm recessed food well covered by a moveable 200 g stainless steel metal plate. A rat could uncover the food well by pushing the plate back with its nose only when it was unlocked by a set screw. When locked, the rat could only push this plate up to the food well preventing it from accessing its unsalted roasted sunflower seeds. A vertical

tube extending from the bottom of the feeder (not shown) allowed it to be positioned in any orientation at any uncapped floor holes. We note rats could not move these feeders from their locations or orientations. The five different types of junk objects used in this experiment are also shown in Figure 1 with four different (Panel A) and four identical objects (Panel B) as examples of test arrays. Their preceding study arrays would have consisted of any three of the four feeders with mounted objects and a fourth feeder without an object. These are only illustrative examples as we gave each rat a different set of four different objects and a set of identical objects because each of the five objects consisted of four replicates. Each object had a flat-head metal screw embedded into its base to allow it to be easily attached to and removed from a magnet embedded into each feeder's food well cover plate (not shown).

2.2.3 Procedure

Prior to training rats on the missing-object recognition task and testing them on cue-use preferences phases, we used shaping procedures similar to those from our earlier research (Cohen et al., 2010; Arain et al., 2012). Rats learned to enter the foraging arena from the west wall's side chamber, to push feeder covers off only object-cued (unlocked) food wells for sunflower seeds, and then to exit the arena back into the side chamber.

2.2.3.1 Missing-object recognition training phase. During this phase, rats were introduced to the two different object-cueing conditions with the five different types of junk objects in the segmented trials. Each rat had one set of four different objects for one object-cueing condition and another set of four identical objects for the other object-cueing condition. We randomly selected objects to be placed into a set of different objects and a set of

identical objects for each animal so that all but two animals received a different set of four different and of four identical objects. A training session consisted of two distributed segmented trials separated by at least one hour, each under a different object-cueing condition. The order of these two types of object-cueing conditions randomly varied over sessions with the restriction that the same order not occur on more than two sessions in a row. A trial consisted of a study array with an object on each of three feeders with unlocked food covers and the fourth feeder without an object and with its food well cover locked. Every feeder was baited with one sunflower seed. After a rat had obtained a seed from each object-cued feeder in the study array it was allowed to exit the foraging arena into the side start/exit from where it was removed and placed into a separate holding chamber beneath the foraging apparatus to wait while the experimenter prepared the foraging arena for its test array with the procedures as described in our recent study (Arain et al., 2012). The experimenter baited all feeders in the test array with three seeds but only unlocked the feeder with the previously missing (target) object. These inter-segment preparations took between 2 and 4 minutes before the rat could be replaced in the west wall's start/exit side chamber to begin its test segment. If a rat failed to obtain all available seeds within three minutes in the study array the experimenter removed it from the arena and terminated its trial. The rat was also allowed up to three minutes to find the target object in the test segment. As already stated, we varied the array location within the foraging arena, its geometrical pattern of different oriented feeders, and the position of different objects within the array over trials but not between a trial's study and test segment.

After completing a session's first trial, a rat was placed into a different individual holding cage in

a rack outside the running room where it waited until all other rats had completed that trial before starting its second segmented trial. Rats waited about one hour before their second trial in a session. A rat was run in this phase until it found the test array's 'target' object on its first choice on nine out of its last twelve trials (75% criterion) under each object-cueing condition. Upon reaching this acquisition criterion it was run on the following four cue preference probe test phases.

2.2.3.2 Cue preference probe test phases. Each probe test phase consisted of 20 sessions, each containing three distributed segmented trials: one being a regular (baseline) trial with arrays of different objects; another being a regular (baseline) training trial with arrays of identical objects, and the third being a probe (test) trial that either consisted of different or identical objects in its study and cue-dissociated test arrays. Figures 2a and 2b illustrate each of these types of trials under each object-cueing condition. The nature and rationale of each of the four cue preference phases is further explained in the caption under each figure. The within-session order of the three types of trials and the object-cueing condition of a session's probe trial were randomly determined over sessions with the same restrictions as in the training phase. Thus within each cue preference phase, rats received ten probe trials under each object-cueing condition that occurred as the 1st, 2nd or 3rd trial on an equally probable basis. Aside from the various opposed-cues transformations in the probe trials' test arrays, they differed from those of baseline trials in that all their feeders were unlocked and not baited in the first three cue preferences phases. In phase 4, we randomly baited two of the four unlocked feeders with a seed on three of the ten test arrays within each object-baiting condition. These baited test arrays were evenly distributed over the probe

test trials to encourage rats to completely search all feeders in this phase. We incorporated this partial reinforcement procedure because we had observed that each rat occasionally ceased searching a probe test array after their second or third non-rewarded feeder choice. While such spontaneous search terminations would not seriously affect an assessment of hierarchical cue use preferences in the first three phases, it could in the last phase where each of the four feeders in the different objects cueing condition and three feeders in the identical objects cueing condition contained a single correct dissociated cue. We note that under this partial reinforcement schedule only two animals failed to open all probe test array feeders. Both rats opened three test array feeders on an identical objects cued probe trial, and one rat opened only two feeders on a different objects cued probe trial before exiting the foraging arena.

2.2.3.3 Data analysis. The data analyzed in each cue preference phase were the distributions of the number of choices rats needed to find (open) the baited target object-cued feeder and each correct cue-dissociated feeder during baseline and probe test trials respectively. Rats would be expected to find each type of feeder an equal number of times (trials) by their first, second, third, or fourth choice if they were randomly searching within the baseline or probe trials' test arrays, a chance performance distribution. Following earlier studies on avian cue preferences (Brodbeck, 1994; Clayton and Krebs, 1994), we separately summed the individual rats' baseline and probe trial distributions and analyzed their marginal distributions by the G statistic (Sokol and Rohlf, 1981) with an open source statistical program (<http://udel.edu/~mcdonald/statgtestgof.html>) to determine whether each significantly ($p < .05$) departed from the chance distribution. To determine whether individual rats'

distributions did not significantly depart from their observed, summed distribution, we calculated a Fisher's Exact Probability test from an open source statistical program in R (<http://darwin.eeb.uconn.edu/eeb348/supplements-2006/chi-squared/chi-squared.html>). Only in the absence of any significant inter-subject variation from the overall distribution might one confidently conclude that any significant departure of the overall distribution from chance reliably represents rats' individual distributions. We departed from earlier research that used G-tests to determine inter-subject variations (e.g., Brodbeck, 1994) because the Fisher test does not require correction for non-continuity that could not be conducted on the chi-squared distributed G statistic. We further determined whether the actual proportion of trials a rat selected any of the cue-dissociated feeders at each choice during probe trials significantly departed from chance of .25 by conducting single sample t-tests. We also directly compared rats' initial choice accuracy for finding a correct feeder between baseline and probe trials under each object-cueing condition in each phase by conducting a within-Ss analysis of variance (ANOVA). To conduct these comparisons we used only data from those 10 of the 20 baseline trials in each phase that accompanied probe trials with the same object-cueing condition in their three-trial sessions. All statistical effects were considered significant at $p < .05$.

2.3 Results

2.3.1 Missing Object-Recognition Training and Baseline Trials

All seven animals found an identically-cued target-object and six found a differently-cued target object on its first choice on nine of more trials within its first twelve training sessions. The one animal that failed to reach

this 75% criterion within these 12 sessions did so after receiving two more training sessions. We further note that no rat required more than two choices to find the baited target object under either cueing condition after its fourth training session or during any baseline trial on subsequent phases in this study. As seen on the baseline trials graphs in Figures 3-6, animals overwhelmingly found the target object on their first than second choices under each object-cueing condition to yield summed distributions significantly different from chance within these choices, $G1s > 27.48$, $ps < .001$, without any accompanying significant inter-subject variations, $ps > 0.39$. Object-cueing had no apparent or significant effect on rats' baseline performance.

2.3.2 Cue Preferences Test Phases.

Figures 3-6 summarize the distributions from baseline and probe trials under each object-cueing condition in each cue preference phase.

[See Figures 3-6]

2.3.2.1 Different-Objects Cueing Condition.

As seen on the bottom left hand probe trial graph in each figure, rats opened the feeder with the correct object more often on their first choice than on any other choice whether its non-spatial cues were partially (phase 2, Figure 4) or completely dissociated from its spatial cues (phase 1, Figure 3; phase 3, Figure 5; phase 4, Figure 6). These distributions significantly departed from chance, $G3s > 71.26$, $ps < .001$, and were not accompanied by any significant inter-subject variations, $ps = .12; .07, .99; .92$. The proportion of trials rats opened a correct object-cued feeder on their 1st choice was significantly well above chance in every phase, $t6s > 4.66$, $ps < .01$, and significantly below chance on any other choice in phase 1, $t6s > 4.07$, $ps < .01$, or on their 3rd or 4th

choices in the other three phases, $t_6s > 9.56$, $ps < .01$. Although rats also selected the correct object-cued feeder significantly above chance on their 2nd choice in phase 4, $t_6 = 3.13$, $p < .01$, each selected this feeder less often than on their 1st choice.

Rats' distributions for selecting a partially or completely dissociated spatially correct feeder significantly departed from chance in each phase, $G_3s > 15.61$, $ps < .001$, without being accompanied by significant inter-subject variations except when they selected a feeder at a correct global position in phase 2, $p < .001$. As seen in Figures 3, 5, and 6, rats selected a feeder in the correct local position more on its 2nd choice than on any other choice whether that feeder was both correctly oriented and globally located (phase 1), only correctly oriented (phase 3), or was dissociated from each of the other correct spatially cued feeders (phase 4). The proportion of trials rats selected such a feeder was significantly well above chance on their 2nd choice in each phase, $t_6s > 4.15$, $ps < .01$, significantly below chance on any other choice in phases 3 and 4 or on their 1st or 4th choice in phase 1, $t_6s > 2.16$, $ps < .05$. As seen in Figure 6 (phase 4), rats selected a correctly oriented feeder more on their 3rd choice than on any other choice to select it significantly well above chance, $t_6 > 7.05$, $p < .01$, at that choice and significantly below chance on their 1st or 4th choices, $t_6s > 6.98$, $ps < .01$. When confronted with one of the cue-dissociated feeders only at a correct global position (phases 2, 3, and 4), rats selected this feeder far more often on their 3rd or 4th choices than on any other choices in phases 3 and 4 respectively but only selected it slightly more on their 2nd than on either their 1st or 3rd choices in phase 2. Although rats' distribution for selecting this feeder in phase 2 significantly departed from chance, $G_3s = 15.61$, $p < .001$, it was accompanied by a significant

inter-subject variation, $p < .001$, and the proportion of trials they selected this feeder on each of their first three choices did not significantly differ from chance but just missed being significantly below chance that for selecting it on their 4th choice, $t_6 = 1.92$, $p(\text{one-tail}) = .052$. In phases 3 and 4, rats selected this feeder significantly well above chance on their 3rd and 4th choices, respectively, $t_6s = 4.28$; 23.78 , $ps(\text{one-tail}) < .01$ and significantly below chance on their 1st and 2nd choices in each phase, $t_6s > 6.31$, $ps(\text{one-tail}) < .01$, and on their 3rd choice in phase 4, $t_6 = 16.53$, $p(\text{one-tail}) < .001$.

2.3.2.2 Identical-Objects Cueing Condition. As seen on the bottom right hand graphs of probe trials in Figures 3-6, rats selected a feeder at its correct local position more often than on any other choice whether it was also correctly oriented (phase 2), at its correct global position (phase 3), or dissociated from the other two spatially cued feeders (phase 4). These observed distributions significantly departed from chance performance, $G_3s > 78.91$, $ps < .001$, without being accompanied by any significant inter-subject variation, $ps > .15$. In these phases, rats selected this feeder significantly well above chance on their 1st choice, $t_6s > 5.18$, $ps < .01$, and significantly below chance on their 3rd and 4th choices, $t_6s > 6.50$, $ps < .01$. Figures 4 and 6 show that rats selected the correctly oriented feeder more often on their 2nd choice than on any other choice. These distributions significantly departed from chance, $G_3s = 50.20$; 83.40 , $ps < .001$, without being accompanied by any significant inter-subject variations, $ps = .21$; $.78$. In both phases, rats selected this feeder significantly well above chance on their 2nd choice, $t_6s = 3.59$; 17.83 , $ps < .01$, and significantly below chance on their 3rd and 4th choices, $t_6s > 3.99$, $ps < .01$. Figures 4 and 6 show that rats selected a feeder at its correct

global position in phases 2 and 4 more often on their 2nd or 3rd choices respectively than on any other choice. Both distributions departed significantly from chance, $G3s = 40.50; 170.40$, $ps < .001$, but only that in phase 4 was unaccompanied by any significant inter-subject variation, $p = .13$ while that from phase 2 was accompanied by inter-subject variations that bordered on significance, $p = .054$. However, in phase 2, rats selected this feeder on their 2nd choice significantly well above chance, $t6 = 4.73$, $p < .01$, and significantly below chance on either their 3rd and 4th choices, $t6s = 2.03; 4.51$, $ps < .05$. In phase 4, they also selected that feeder on their 3rd choice significantly well above chance, $t6 = 16.12$, $p < .01$, and significantly below chance on any other choice, $t6s > 3.44$, $ps < .01$.

2.3.3 Comparisons between Baseline Target Cue and Initially Preferred Cue.

We compared the proportion of trials rats selected their initially preferred feeder during probe trials with the proportion of trials they selected the baited baseline feeder on their first choice with a two-way (Object-cueing x Trial type) within Ss ANOVA for each phase. Results from these analyses revealed that rats found their initially preferred probe trial feeder under either object-cueing condition significantly less often than their baseline baited feeder on their first choice in each phase, $F1, 6s > 13.34$, $ps < .01$.

3.1 Discussion

Findings from this experiment clearly indicate that under different-objects cueing condition, rats were more likely to select a cue-dissociated feeder with a correct object before selecting any other feeders with correct dissociated spatial cues. Of the latter, they were more likely to select a feeder at a correct local position before selecting correctly

oriented feeder and then finally one at the correct global location. Rats maintained this selection pattern for spatially correct feeders under the identical-objects cueing condition where they could not encode or retrieve a missing object's specific non-spatial cues. Consequently, their final selection of a feeder at a correct global position under different-objects cueing condition could not be solely attributed a default choice of the last unopened feeder. We note that when faced with a feeder at a globally correct position and another containing all other correct cues (phase 2), rats distributed their selection of the former more evenly over their first three choices under the different objects cueing condition but were more reliably likely to select it more on their 2nd choice than any other choice under the identical-objects cueing condition. One possibility for this difference is that rats were less able to accurately retrieve a missing object's correct global position under the different objects cueing condition because they had not retrieved all of previously selected feeder's three cues. Further examination of selection patterns of these two types of feeders however does not support this limited retrieval capacity hypothesis (Kendrick and Rilling, 1986; Arain et al., 2012). That is, we found that rats were as likely to immediately select the feeder at a correct global location after selecting one with the correct object combined with the other two local spatial cues as after selecting one with only both local spatial cues.

It is also noteworthy that our rats never responded as accurately to the feeder containing their most preferred cue on probe trials as to the remaining baited feeder on baseline trials under either object-cueing condition. One seemingly obvious explanation is that the feeder containing the most preferred 'correct' cue also contained other 'incorrect' cues that might inhibit cover pushing responses.

The problem with this account is that rats also showed reliably lower accuracy for finding the completely correct non-baited feeder in phase 1 probe trials under the identical- objects cueing condition. Perhaps given their keen olfactory sense, rats may have detected the absence of any odor of seeds in unlocked probe trial feeders that reduced their incentive for a more accurate search.

4 Experiment 1b.

Unlike earlier avian research that used similar cue-dissociated probe tests (Brodbeck, 1994; Clayton and Krebs, 1994) and found that caching and non-caching birds preferred spatial to non-spatial cues or showed no preferences respectively, our first experiment showed that rats preferred non-spatial to spatial cues. Among the methodological differences between these studies that could account for these different findings is the fact that birds in the earlier studies (e.g, Brodbeck, 1994) received different color-patterned feeders on every trial randomly drawn from a large pool while our rats received their same four different junk objects in each different objects cueing trial. Perhaps if rats had also received trial-unique objects, they also might have preferred to look for a feeder's correct spatial cues before looking for its correct non-spatial cues as did chickadees or show no preferences as did juncos. To test this idea we replicated the different objects condition of phase 4 of Experiment 1 on the same rats with a larger pool of novel junk objects.

4.1 Basic design and procedures

Rats from Experiment 1 received 10 sessions of two distributed trials per session with feeders cued by different objects selected from a pool of twenty novel objects, four of which are shown in Figure 1c. One trial in each session was a baseline trial while the other trial

was a probe test trial with all four cues completely dissociated from each other as in phase 4 of Experiment 1. We randomly selected junk objects for each segmented trial without returning them to the pool until all had been used in each of four 'blocks' of five trials. The only restriction to this repeated selection procedure was that none of the four objects from the last trial from the preceding 'block' could be used over the next two trials. These object selection procedures insured that rats always received a different set of four different junk objects on each trial within each session.

4.2 Results

As seen in the baseline distribution graph in Figure 7, rats continued to show highly accurate performance on their 1st choice comparable to that of baseline trials in Experiment 1, $G1 = 56.09$, $p < .001$, without any significant inter-subject variation, $p = .95$. As seen in the lower probe trials graph of Figure 7, rats selected the feeder at a correct local position more often on their 1st than on any other choice, the feeder with the correct object more often on their 2nd than on any other choice, the correctly oriented feeder more often on their 3rd than on any other choice, and feeder at the correct global position more often on their 4th than on any other choice. Each of these distributions significantly departed from chance, $G3s > 34.40$, $ps < .001$. Significant inter-subject variations only occurred with distributions for correct local or global positions, $ps = .03$; $.006$, but rats selected each of these cue-dissociated feeders significantly well above chance only on their 1st or 4th choices respectively, $t6s = 4.93$; 10.26 , $ps < .01$, and selected the feeder at a correct local position feeder significantly below chance on their fourth choice, $t6 = 4.51$, $p < .05$, and the feeder at a correct global position on each of their first three choices significantly below

chance, $t_6s > 4.25$, $ps < .05$. Rats also selected a correct object-cued feeder or a correctly oriented feeder significantly well above chance, $t_6s = 5.74; 6.23$, $ps < .05$, on their 2nd or 4th choices respectively, and each of these feeders significantly below chance on their 3rd and 4th choices, $t_6s > 3.77$, $ps < .05$. This figure also shows that rats found their initially preferred probe trial feeder significantly less often than their baseline baited target feeder on their first choice, $F_{1, 6} = 29.96$, $p = .002$.

[see Figure 7]

4.3 Discussion

When rats were exposed to objects randomly drawn from a large pool of novel objects, they switched their cue-use preferences over their first two choices from those they displayed in the last phase of Experiment 1. That is, they selected a correct locally positioned feeder before correct object-cued feeder. As in the previous experiment, however, they continued to select a correctly oriented feeder before a correct globally located one. Thus the previous hierarchy seen in phase 4 was only partially rather than completely eliminated or reversed. A Bayesian analysis of the integration of spatial information (Cheng et al., 2007) might account for this switch in cue-use preferences. That is, increasing the pool of available objects also increased the variability of objects' non-spatial information to reduce its relative salience below that of the now less varied local position information. However, rats did not also select the less varied oriented feeder before the more varied correct object-cued feeder. Perhaps rats encoded or represented a missing object's feeder orientation as part of the array's geometrical configuration rather than as a separate orientation. Rats have been shown to represent the geometry of an array of objects within a

larger area and to be similarly affected by geometrical transformations of their arrays (Gibson et al., 2007) as they are when in the middle of an enclosed space and its transformations (Cheng and Gallistel, 2005).

5 General Discussion

Results in this study extend the notion from our recent research (Arain et al., 2012) that rats separately retrieve different spatial and non-spatial sources of information from their working memory in a missing-object recognition task. Rats' patterns of sequential feeder selection in cue-dissociated probe trials suggest that they retrieve a missing object's global spatial information after initially retrieving its local non-spatial (object) and then local spatial (within-array position or feeder orientation) information. This hierarchical cue use pattern among the four types of cues, however, is not fixed as seen in a supplementary experiment where rats received novel objects instead of the same four different objects. Under these conditions, they retrieve a correct local position before a correct object but still retrieve a correct orientation before a correct global position.

As already noted, rats' final selection of the correct globally positioned feeder in an array of different object-cued feeders was not because it was only the remaining unopened one. Their preference for using local cues before global spatial cues seems to accord with an ecological-dependent explanation (Healy and Hurly, 2004; Shettleworth, 2010). According to this perspective, scatter hoarders rely more on relocating their cached food sites from fixed global distal cues than from local cues because the latter change over the typical long intervals between caching and retrieval. Opportunistic feeders or larder hoarders, however, revisit an array of food sites (a patch) to deplete its

resources between shorter intervals when local cues are less likely to have changed. Therefore, these types of active foragers may be able to base their cue-use preferences on the current context-dependent value of information of each type of cue than on any acquired or evolved predisposition to prefer one type over or before another. Perhaps non-caching juncos showed no specific pattern for preferring global and local spatial or non-spatial cues (Brodbeck, 1994) while our rats preferred local over global cues because the former animals had a more enriched environment of distal cues in their laboratory. The walls of our foraging arena did not provide any distinctly different distal cues and rats had no direct perceptual access to the different distal room cues while searching within an array of feeders. Thus it is not surprising that our rats, as opportunistic feeders, would have preferred to use feeders' local cues that would have provided better informational value before using any of their possible global spatial cues.

That rats in our study did finally use the missing object-cued feeder's global position is in accordance with parallel spatial map theory (Jacobs and Schenk, 2003). According to this model, rats would be able to develop a bearing map in their reference memory from the consistent distal room they might notice as they were being transported to and from the foraging chamber. They could have integrated this representation with any temporary sketch map of available cues from the feeder arrays. Perhaps had our rats been able to perceive distal room cues while on the foraging area as had rodents in other studies (Beigler and Morris, 1993; 1996; Gibb et al., 2009; Maaswinkel and Whishaw, 1999; Vlasak, 2006), they would have retrieved this information earlier in their choice sequence. Research with pigeons, also a non-caching species, (Sturz and Katz, 2009) show that when precautions are

taken to make global location irrelevant, they do use it when it becomes relevant. In that study, pigeons learned to find hidden food midway between two spaced proximal landmarks in the absence of any distal cues within the enclosed circular foraging arena. When pigeons were later exposed to a single orienting stimulus, a black vertical stripe on the surrounding white curtain, they used it to search at the correct location from one of the proximal landmarks when the other had been removed.

As others have pointed out cue-use preferences are subject to context-dependent as well as to ecological-dependent factors (Barkley and Jacobs, 2007; Healy and Hurly, 2004). For example, food-caching mountain chickadees, *Poecile gambeli*, prefer visual over spatial cues (Ladage et al., 2009) where the target feeder visually differed from all other non-baited identically cued feeders. Non-caching great tits, a species previously reported to show no preferences between a target feeder's location and its visual cues (Krebs and Clayton, 1994), do prefer the former over the latter when exposed to the target feeder several times before being tested in a trial (Hodgson and Healy, 2005). Non-caching European green finches, *Carduelis chloris*, will prefer visual to spatial cues after a single inspection exposure to the target feeder but reverse their preferences after ten inspection exposures (Herborn et al., 2011).

Finally, we must consider another context-specific factor, the spatial separation among feeders. Feeders in our preparation were closely adjacent to each other while those in the early avian research (Brodbeck, 1994; Clayton and Krebs, 1994) were widely separated. Field experiments on the non-caching rufous humming bird, *Selasphorus rufus*, (Healy and Hurly, 1998; Hurly and Healy, 1996) demonstrate that these birds switch from

relying more on the local to the global positions of previously sampled 'flowers' within their arrays when they become separated from each other by more than 40 cm.. Rats also reduce their use of the geometry of a rectangular enclosure and increase their use of their corner positions of cues to find hidden food as a rectangular enclosure is enlarged (Maes et al., 2009). Perhaps rats in our study would have

also preferred to use or retrieve the correct feeder's global position earlier during their choice sequence in arrays of more widely separated feeders. As already noted, if feeders had been more widely separated from each other, rats might have attended more to their individual orientations than to the overall geometrical pattern of the array from these oriented feeders.

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Figures

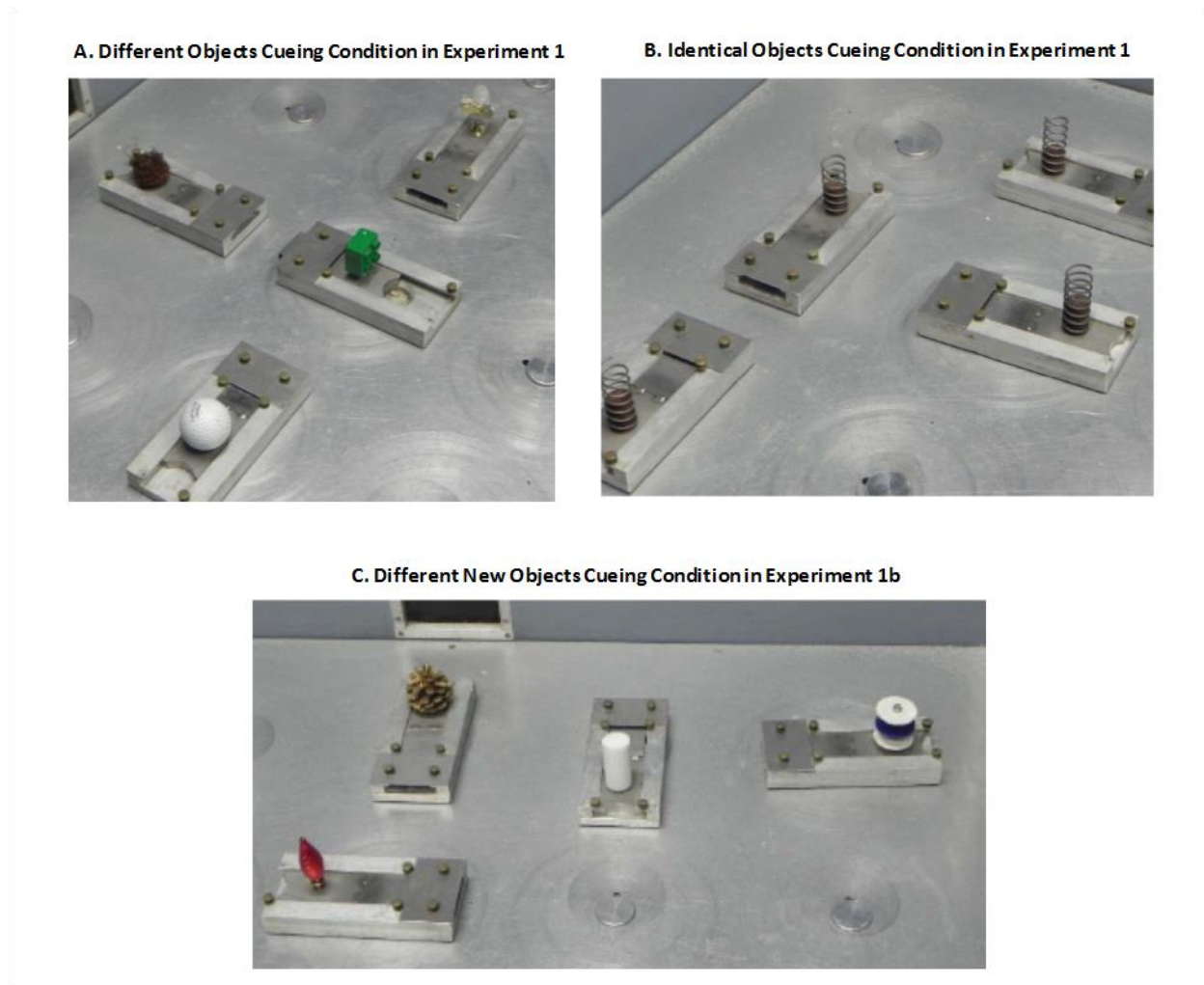


Figure 1: The five types of objects used in Experiment 1 are shown in panels a and b and four objects from the pool of twenty objects used in Experiment 1b are shown in panel c as they might appear on feeders in the foraging chamber. Panel b shows only an example from an identical objects cueing condition as any one of these five different types of objects could serve in that condition as explained in the test. The three basic geometrical arrays of the feeders used in each experiment are shown over the three panels. An example of how far a cover could be pushed on an unlocked feeder (e.g., golf ball cued feeder) and on a locked feeder (e.g., green Lego object-cued feeder) is shown in panel a. The position of objects seen in each of the three test arrays is only one of the possible configurations used in this study. See text for further details.

Different-Objects Cueing Condition

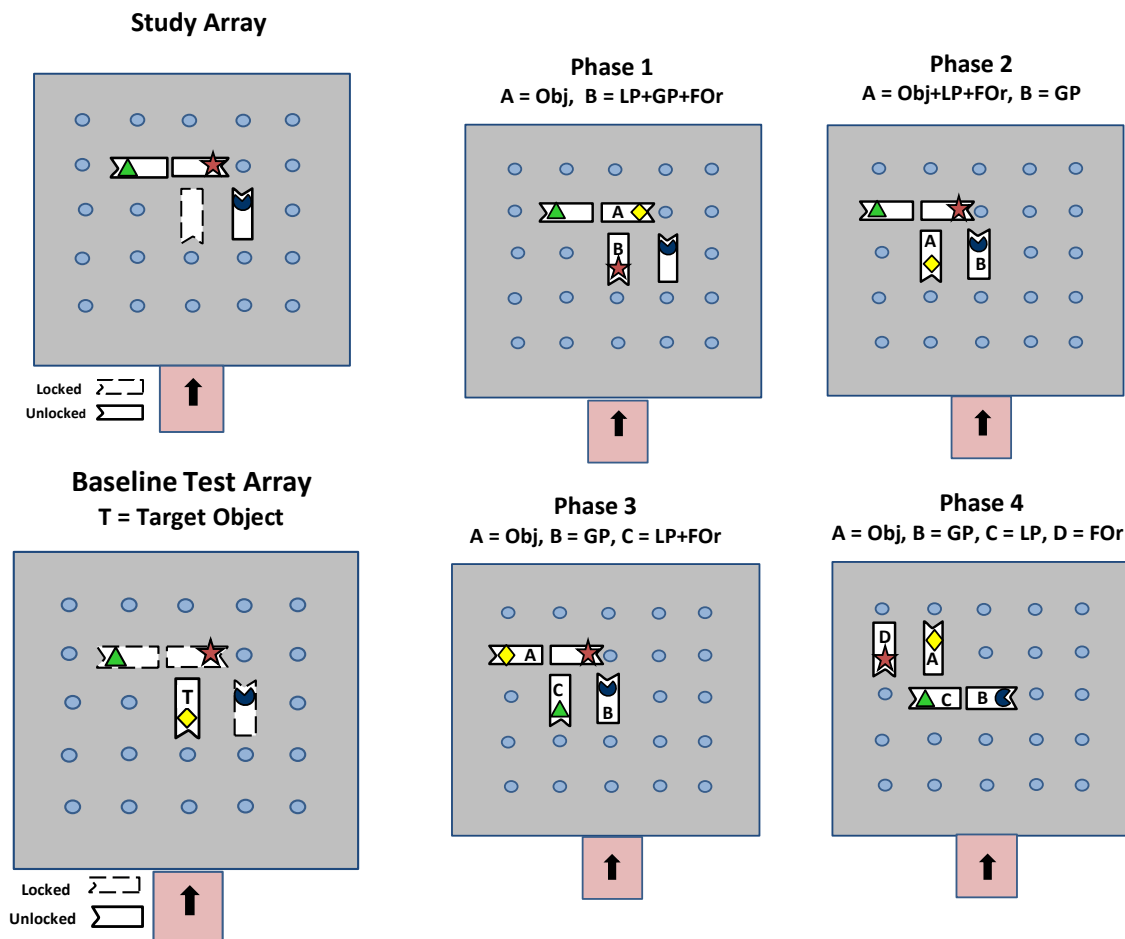


Figure 2a: An example in the different-objects cueing condition of a study array and its baseline test array with a missing target (T) object icon on the remaining baited unlocked feeder and the four cue-dissociated probe test arrays on unlocked and non-baited or partially baited (in Phase 4) feeders. The indented portion of the rectangular feeder represents the front of the food well cover from where the rat had to push to uncover the food well as shown in Figure 1. The cue dissociated feeder labels noted under each phase's probe test configuration title are: Obj = correct object, LP = correct local position, GP = correct global position, FO = correct feeder orientation. In Phase 1's probe test array, if a rat opened feeder A or B on its first choice it would have selected a feeder with the correct object or that with all correct combined spatial cues respectively. In Phase 2's probe test array, if a rat opened feeder B or A on its first choice, it would have selected a feeder at a correct global position or one with the correct object combined with its other two spatial cues respectively. In Phase 3's probe test array, if a rat opened feeder A or B, or C on its first choice it would have selected a feeder with a correct object or one at a correct global position, or one at a correct combined local position and orientation respectively. In Phase 4's probe test array, if a rat had opened feeder A or B or C or D, it would have selected a feeder with the correct missing object or at a correct global position or at a correct local position or, correctly oriented respectively.

Identical-Objects Cueing Condition

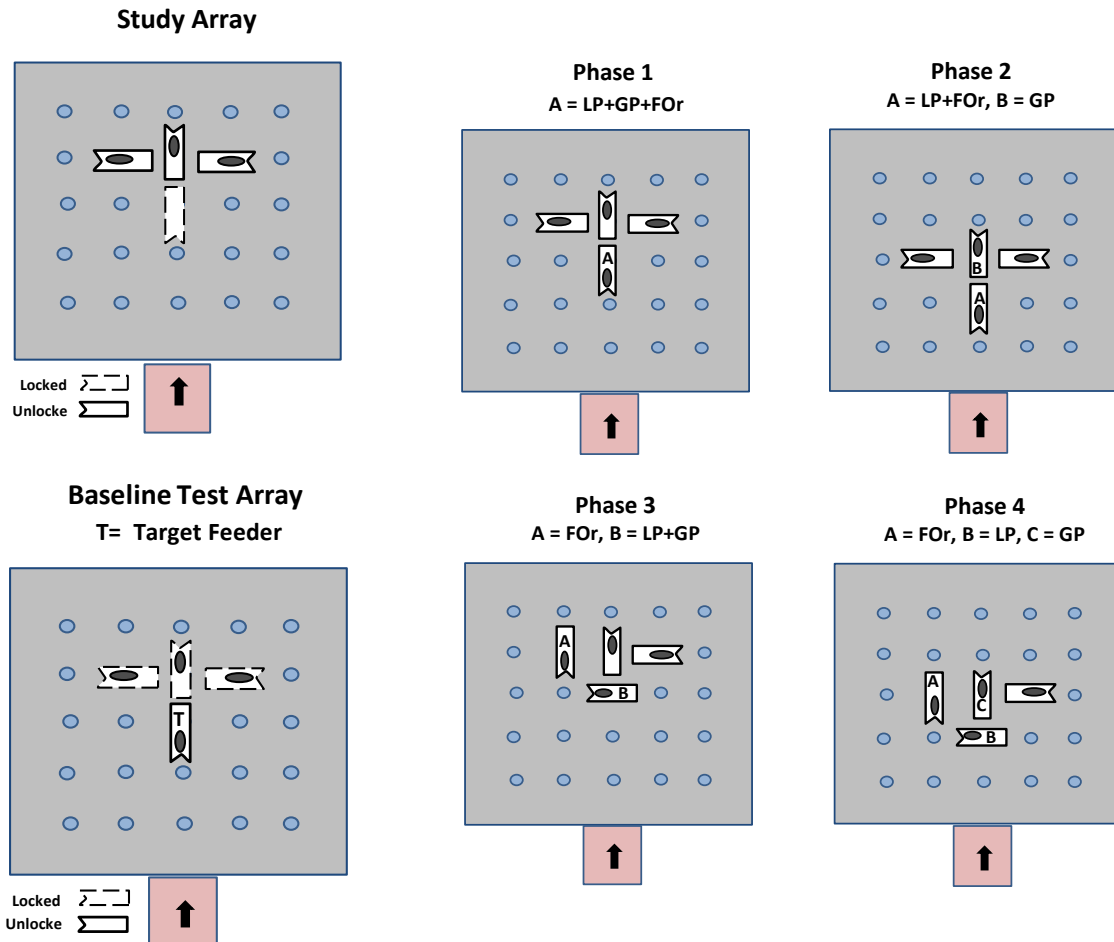


Figure 2b : An example in the identical-objects cueing conditions of a study array and its baseline test array with a missing target (T) object icon on the remaining baited unlocked feeder, the missing target object on the non-baited unlocked feeder in Phase 1 probe test and the remaining three partially or completely cue-dissociated probe test arrays on unlocked and non-baited or partially baited feeders in the remaining three phases. The dissociated spatial feeder cues noted under each phase's probe test configuration title are: LP = correct local position, GP = correct global position, FOr = correct feeder orientation. In Phase 2's probe test array, if a rat opened feeder B or A on its first choice, it would have selected a feeder at a correct global position or one at a correct local position and feeder orientation respectively. In Phase 3's probe test array, if a rat opened feeder A or B on its first choice, it would have selected a correctly feeder or one at a correct combined local and global position respectively. In Phase 4's probe test array, if a rat had opened feeder A or B or C on its first choice it would have selected a correctly oriented feeder or one at a correct local position or one at a correct global position respectively. We note that except in Phase 3, we made each dissociated cues test under the identical-objects cueing condition correspond to that of that phase's different-objects cueing condition based on dissociated spatial cues. Consequently in Phase 1 the non-rewarded probe test arrays under the identical-objects cueing

condition had to be the same as its rewarded baseline test arrays to meet this requirement and are thus are not actually cue-dissociated trials..

The side chamber from which the rat always entered into and exited from the foraging arena is designated by an arrow. The other three side chamber entrances are not shown.

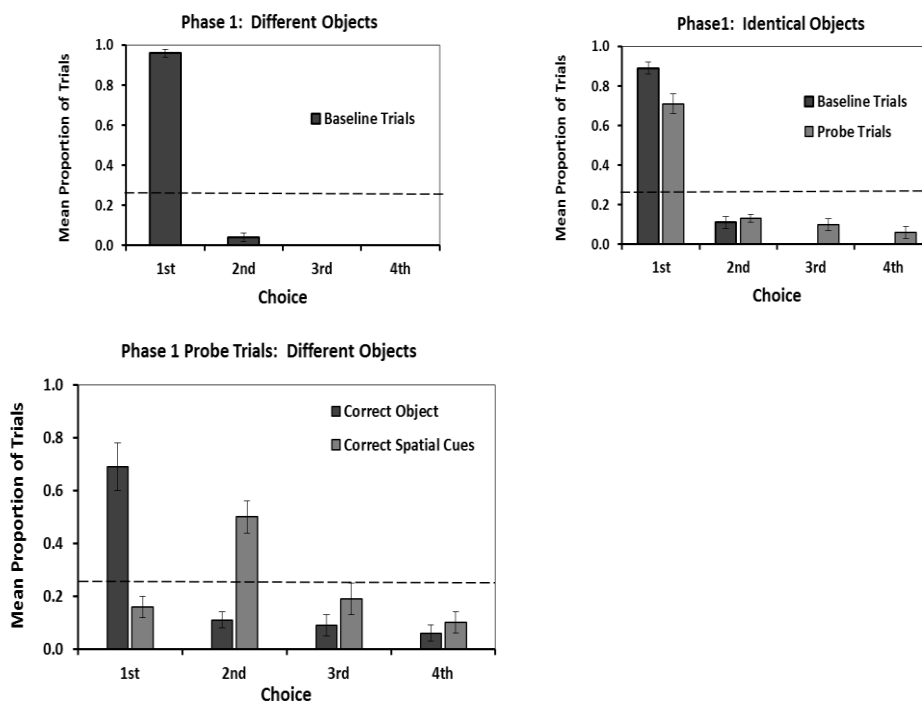


Figure 3: Distributions of mean proportions of trials that the baited target object-cued feeder in baseline arrays and each of the two denoted non-baited correct cue-dissociated feeders in probe trial arrays were opened by rats on each of their choices in Phase 1 of Experiment 1 under the different-objects cueing condition. As already noted in Figure 2b, under the identical-objects cueing condition, probe test trials did not contain any cue-dissociated feeders but only a correct target-object cued non-baited feeder and therefore a summary of data from baseline and probe tests are presented within the same graph. The vertical lines on each bar represent + SEM and the horizontal dashed line in each graph represents chance performance.

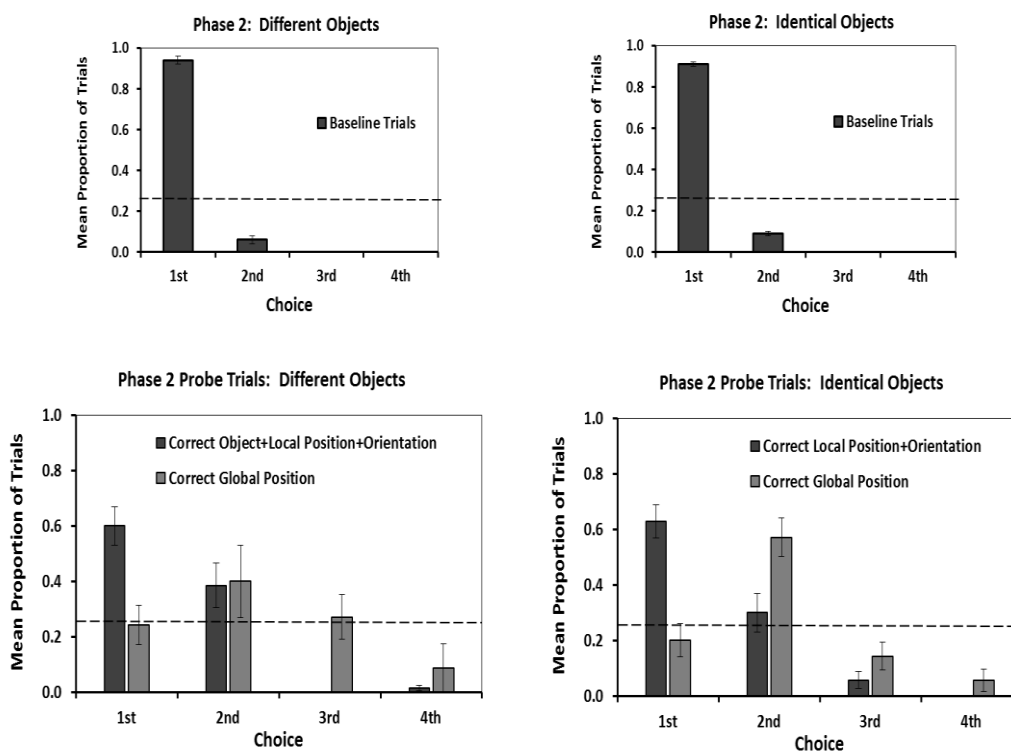


Figure 4 : Distributions of mean proportions of trials that the baited target object-cued object in baseline arrays and each of the two denoted non-baited correct cue-dissociated feeders were opened by rats on each of their choices under each object-cueing condition in Phase 2 of Experiment 1. The vertical lines on each bar represent + SEM and the horizontal dashed line in each graph represents chance performance.

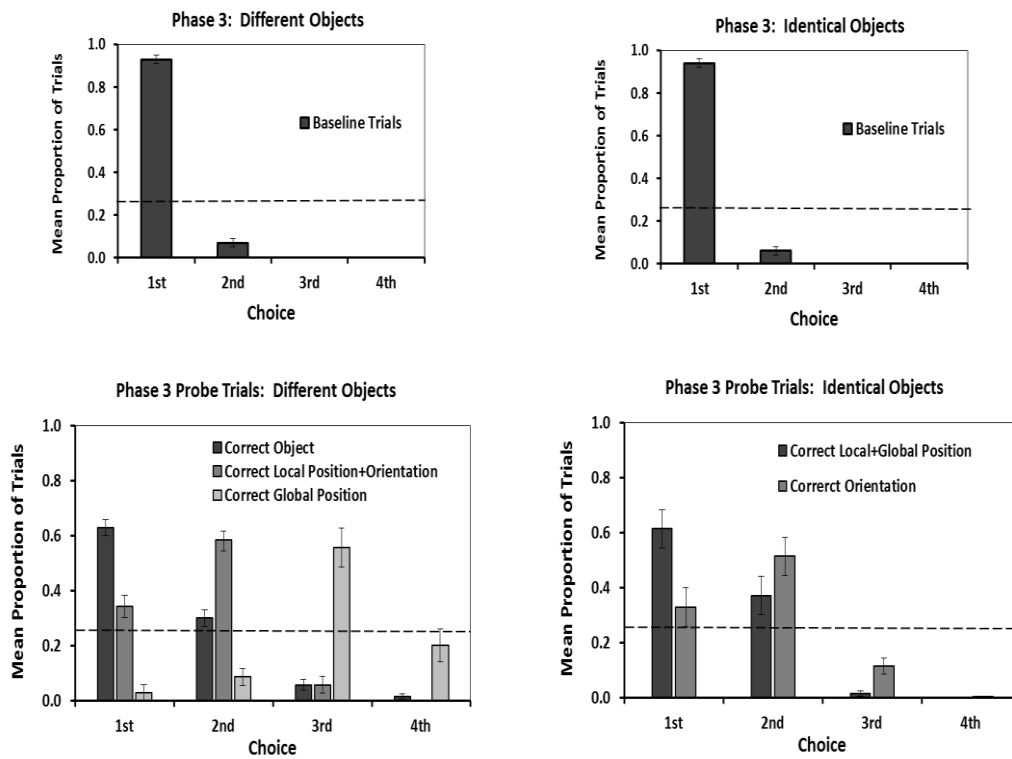


Figure 5

Distributions of mean proportions of trials that the baited target object-cued object in baseline arrays and each of the three of two denoted non-baited correct cue-dissociated feeders were opened by rats on each of their choices under the different- and identical-objects-cueing conditions respectively in Phase 3 of Experiment 1. The vertical lines on each bar represent + SEM and the horizontal dashed line in each graph represents chance performance.

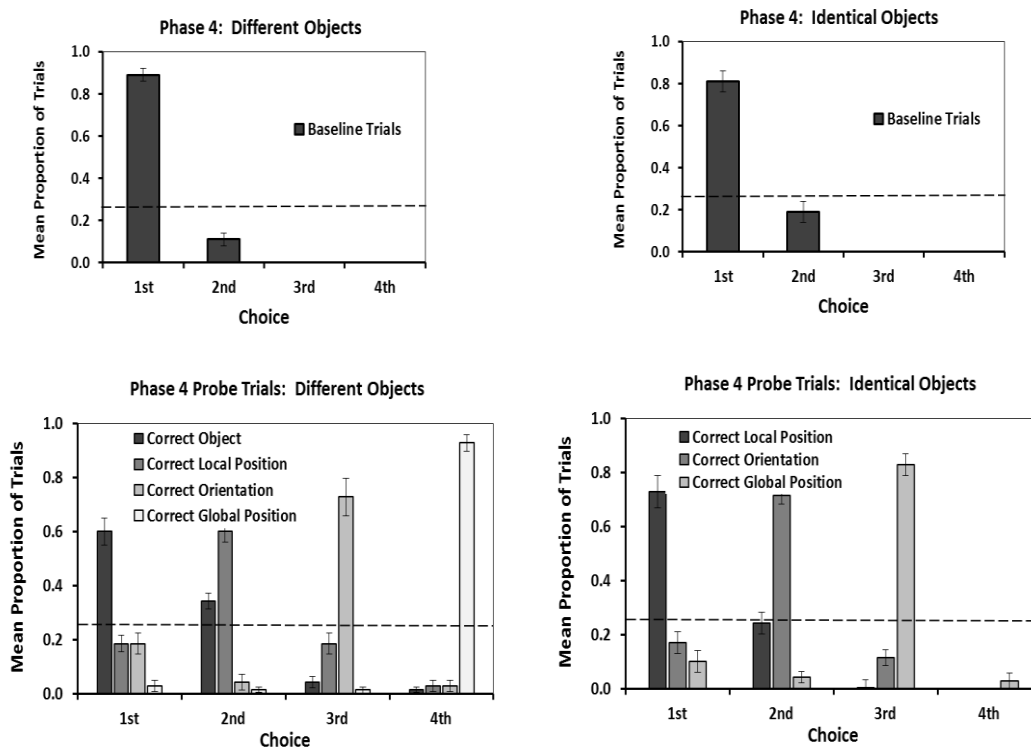


Figure 6: Distributions of mean proportions of trials that the baited target object-cued object in baseline arrays and each of the four of three denoted partially- baited correct cue-dissociated feeders were opened by rats on each of their choices under the different- and identical-objects cueing conditions respectively in Phase 4 of Experiment 1. The vertical lines on each bar represent

+ SEM and the horizontal dashed line in each graph represents chance performance.

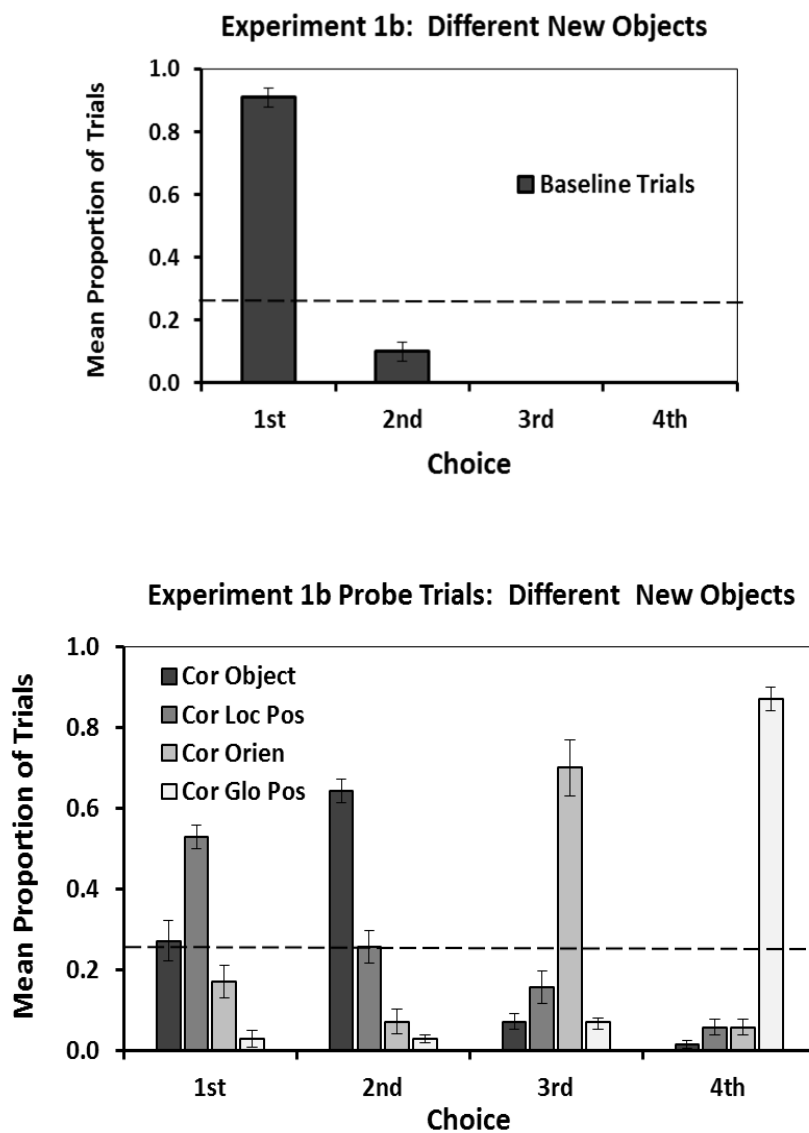


Figure 7: Distributions of mean proportions of trials that the baited target object-cued object in baseline arrays and each of the four denoted partially- baited correct cue-dissociated feeders were opened by rats on each of their choices under the different-objects cueing condition in Experiment 1b. The vertical lines on each bar represent + SEM and the horizontal dashed line in each graph represents chance performance.