Spatial configuration and list learning of proximally cued arms by rats in the enclosed four-arm radial maze

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In an enclosed four-arm radial maze, after sampling three experimenter-selected baited arms (the *study* segment) and following rotation of the maze, rats had to find the fourth baited arm among all four unblocked arms (*test* segment). The rats learned this task with two sets of arm cues, objects at arms' entrances and full arm inserts, each maintained in a fixed configuration. When we changed the configuration of one set of arms to its *mirror image* and that of the other set to a more *mixed* variation by switching opposite and adjacent cued arms, the rats' accuracy was similarly disrupted (Experiment 1). In Experiment 2, the same rats rapidly recovered their high search accuracy on four new configurations recombined from pairs of adjacent arms and pairs of opposite cued arms from the previous final two configurations. Their test segment search accuracy, however, was again disrupted when these configurations were varied either only over trials' study segments or only over trials' test segments. In Experiment 3, however, these rats attained accuracy as high on two sets of cued arms with constantly changing configurations as on two sets with constant configurations. Thus, the rats were able to separately represent four different spatially stable configurations, and then they could learn to represent two of these configurations as lists of spatially irrelevant items. We discuss these findings in terms of association theory and parallel map theory (Jacobs & Schenk, 2003).

Rats seldom reenter previously sampled arm locations on the elevated open radial maze despite maze rotations between choices and without having to use choice algorithms (Olton, 1978; Olton, Becker, & Handelmann, 1979; Olton & Samuelson, 1976). Such accurate performance under these conditions was initially thought to reflect the formation of a list of location cues by the rat in its reference memory (Olton, 1978). The rat simply "checked off" each cued location within working active memory as it entered each arm. This list hypothesis was challenged by other studies demonstrating that rats were severely disrupted when the spatial configuration of distal cues beyond the end of each arm was varied (Suzuki, Augerinos, & Black, 1980) or when their views were restricted only to stimuli at the end of each arm (Mazmanian & Roberts, 1983). These effects seemed to confirm Tolman's (1948) notion that the rat forms a kind of integrated spatial cognitive map of arm locations. According to this spatial map *hypothesis*, the animal simultaneously views in its "mind's eye" all cued locations of the arms in the radial maze and categorizes which it has visited or has yet to visit on the trial. Its decision about

whether to enter an arm is determined by its current upgraded assignment of arms to these categories in its imagined map. Changing or restricting a rat's views of distal cues disrupts its performance by confusing it when it tries to match its learned map-like representation with the current arrangement of distal cues.

According to Brown (1993), however, the distinction between map and list representation models becomes blurred if rats notice distal cues of adjacent arms, as well as those of the arm they have entered. Thus, rats could form a list of overlapping, rather than discrete, separate location cues for each arm. Consequently, varying the configuration or restricting the rats' views of distal cues might simply reduce their performance through decrements in stimulus generalization of these overlapping location cues. Brown (1992) presented direct evidence that rats use a sequential, list-like search process in the radial maze. In that study, rats made partial arm entries (microchoices) independently of, rather than determined by, previous complete entries (macrochoices) at the end of their choice sequences. However, in a subsequent study (Brown, Rish, VonCulin, & Edberg, 1993), rats did direct their observing responses at the remaining baited arms when they had to open an opaque door at the entrance of each arm.

In recent replications of Suzuki et al. (1980), investigators have tried to eliminate overlapping distal cues by exposing rats to configurations of proximally cued arms in a semienclosed eight-arm radial maze (Vollmer-Conna & Lemon, 1998) or in a completely enclosed four-arm

radial maze (Cohen & Bussey, 2003). In the eight-arm maze study, rats entered any four baited arms (*study* segment) and, after a brief removal from the maze, had to find the remaining four baited arms (*test* segment). After learning this task with a fixed configuration, the rats were exposed to variations of these configurations. Vollmer-Conna and Lemon (1998) found that the rats reduced their test accuracy only when exposed to changed configurations, rather than when exposed to rotated configurations or to a fixed configuration with the proximal cues removed from two of the arms. In the four-arm maze study, rats had to enter three experimenter-selected arms in the study segment and then, after a brief interruption during which arm cues were rotated, had to find the remaining baited cued arm among all four cued arms. After learning this task with a fixed configuration, the rats were exposed to configurations that changed over trials but remained unchanged between a trial's study and test segments (Experiment 1). This manipulation also severely reduced the rats' test segment accuracy. In subsequent training, the same rats were able to learn to use two different configurations from the same four proximal cues when each occurred at a specific time of day (Experiment 2). Other rats (Experiment 3) were able to learn two different fixed configurations when each consisted of a different type of proximal cues, full arm inserts in one and objects at the arms' entrances in the other. They subsequently developed high test segment accuracy when exposed to two new configurations recombined from pairs of right-angled arms from the original configurations (same-pairs group). Other rats in that experiment were unable to achieve test choice accuracy above chance on two new configurations when the pairs of right-angled cued arms came from the opposite cued arms of the original configurations (changed-pairs group).

Results from Cohen and Bussey (2003) suggest that rats not only can develop different representations of spatial configurations of cued arms in the X-maze, but also can learn to recombine parts of them into new configurations. These findings raise two interesting questions. One question concerns the degree of rats' flexibility for recombining portions of two originally learned spatial configurations. That is, can they learn to represent all four possible recombined spatial configurations, two based on pairs of right-angled cued arms and the other two on pairs of opposite arms? The second concerns whether rats can learn to represent the maze as a *pure* list of four spatially irrelevant cued arms. To answer these questions, we trained and tested rats in three experiments that were modified versions of Experiment 3 in Cohen and Bussey (2003).

EXPERIMENT 1

In their original report of Experiment 3, Cohen and Bussey (2002) observed that rats were unable to recombine configurations from pairs of opposite cued arms derived from their two originally learned configurations after hav-

ing learned to recombine configurations from pairs of right-angled cued arms. However, the rats were able then to reacquire the originally experienced two configurations. These results suggest either that the rats represented the configurations only on the basis of the positions of cued arms at right angles or that initial training with recombined configurations interfered with their subsequent training with the other two recombined configurations.

We conducted Experiment 1, to determine whether rats are unable to represent fixed configurations in the enclosed four-arm radial maze on the basis of pairs of opposite cued arms, as follows. The rats initially were trained with two different configurations, as in Experiment 3 of Cohen and Bussey (2003). Following acquisition with these two configurations, they were retrained with two new fixed configurations. One configuration had the left and the right positions of the arm cues reversed to preserve the positions of the opposite cued arms from the previous configuration. This new configuration is designated as a *mirror image* configuration. The other configuration had the opposite and the right-angled cued arms from the previous configuration reversed. It is designated as a *mixed change* configuration. An example of the two training phases and their configurations is schematically shown in Figure 1. If rats represent each spatial configuration only from the positions of their right-angled "adjacent" cued arms, they should be equally disrupted when exposed to each new configuration and take as long to reacquire accurate test accuracy. On the other hand, if they represented the two initially acquired configurations by both adjacent and opposite cued arm locations, they should be more disrupted when exposed to the mixed change configuration and take longer to relearn the task than with the mirror image configuration.

Method

Subjects

Eight male hooded Long-Evans rats, 120 days old, from the Charles River Breeding Farms, St. Constant, Quebec, served as subjects. They were housed in large group cages (4 animals per cage) in a colony room maintained on a 12h:12h light:dark cycle. They were run at the beginning of their dark cycle and were kept in individual holding cages during each experimental session. They remained in these holding cages for 2h after each session while they consumed their daily ration of 20 g of Purina Rat Chow. Water was freely available in both the home and the holding cages. These maintenance conditions ensured that the rats remained at approximately 90% of their free-feeding weight. We removed 1 animal from the study when it stopped running in the maze during the course of the experiment. The results of this and the following two experiments are based on data from the remaining 7 rats.

Apparatus

We used the same enclosed four-arm radial maze in the same running room as in Cohen and Bussey (2003). Therefore, we will provide only the following brief description. The maze consisted of a 45-cm-high, 30-cm-wide octagonal central chamber, from which radiated four equally separated 20-cm-high, 40-cm-long, and 15-cm-wide arms. An overhead 15-W incandescent light above each arm illuminated the maze interior. We used the seven removable proximal arm cues described in Cohen and Bussey (2003, Experiment 3).
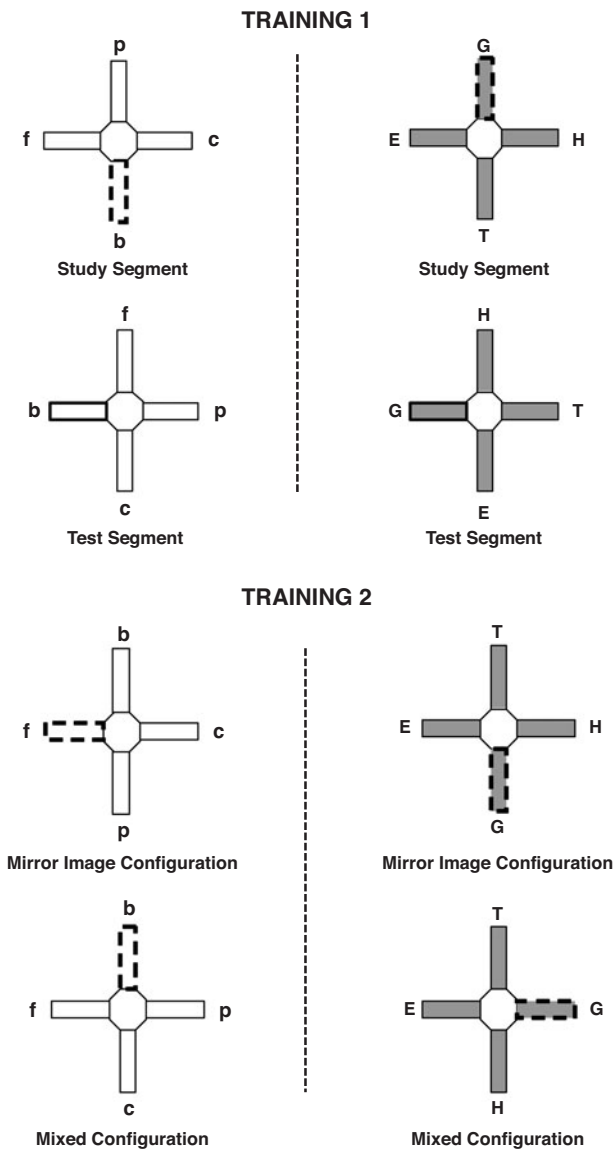
TRAINING 1

TRAINING 2

Figure 1. Configurations during Training 1 and Training 2 phases in Experiment 1. A bold dashed line outlines the blocked arm during the study segment, and a continuous bold line outlines it as the remaining baited arm in the test segment as shown during the Training 1 phase. Only examples of 90° and 270° clockwise rotations are illustrated. See the text for further description of rotation procedures. The locations of the cued arms do not correspond to compass directions. Arm cues: (Objects at arm entrances) p, post; c, chains; b, block; f, funnel; (Full arm inserts) G, grid; H, hurdles; T, tunnel; E, empty.

They are categorized as *arm entrance objects* and as *full arm inserts*. As is labeled in Figure 1, the four objects consisted of an aluminum block (b), a small plastic funnel (f), a vertical plastic post (p), and a set of four hanging chains (c), and the three arm insert cues consisted of an opaque tunnel (T), a wire grid floor, and wall (G), and hurdles (H). An empty arm (E) was labeled as the fourth insert cue.

Procedure

Shaping. Over five daily sessions, the rats were shaped to run down each empty maze arm from the central chamber when its guil-

lotine door was raised. They received two sunflower seeds by displacing a 50-g steel disk over a food cup at the end of each arm.

General training. Over the next 80 sessions, the rats were trained on an interrupted or segmented trial task in which they had to find a remaining baited arm after having sampled some of the arms of the maze. The rats received approximation training with two- and three-arm versions of the final task over the first 8 sessions. Throughout training, the animals received two segmented trials per session with the second trial occurring approximately 1 h after the first trial. The rats experienced arm inserts on one trial and arm entrance objects on the other trial in each session in random sequence over sessions, without experiencing the same sequence on more than two sessions in a row. Figure 1 shows the relative clockwise order (configuration) for each set of cues during this training phase. We exposed each rat to the same two configurations to maintain relatively short intersegment intervals and to run all the rats within a reasonable time for each trial. These logistical considerations became more relevant in the later experiments, in which different rats received different manipulations of configurations, as is shown in Figures 3 and 5.

Each trial segment began when the rat was placed in the central chamber of the maze. The rats remained in their holding cages during short intersegment intervals and the longer intertrial intervals within a session. Over the first eight sessions, the rats received training on a two-arm trial and then on a three-arm trial version of the task in each session. The rats could enter any one of two open arms on the first trial and any two of three open arms on their second trial for their *study* segment. On the second trial, the rats had to wait 10 sec in the center chamber between their first and second choices. The experimenter randomly selected arms on each trial, to ensure that the rats were exposed to all the baited arms over this training phase. After a rat had entered its last baited arm in a study segment of a trial, it was removed from the maze and placed in its holding cage in a rack out of view of the maze area for approximately 1–2 min. During this intersegment interval, the experimenter rotated the arm cues of the maze 90°, 180°, 270°, or 360°, replaced the disk(s) on the unbaited, earlier sampled cued arm(s), and baited the remaining cued arm in its new location. We note that each configuration was randomly rotated both within and between trials over sessions. The rat was then placed again into the central chamber and was presented with the same two or three cued arms for that trial's test segment. The trial ended after the rat entered the remaining baited arm. An entry into a previously sampled, now unbaited arm resulted in a 30-sec delay in the arm before the rat was allowed back into the center chamber.

Training 1. The rats were trained on the final version of the segmented trial task over the remaining 72 sessions. In this version, the study segment consisted of three experimenter-selected open arms that the rat had to sample before proceeding to the test segment with four open, rotated arms, one of which was the previously blocked, baited arm. The only other change in this phase was an increase in each trial's intersegment interval to 6–10 min. While one rat waited in its holding cage during its intersegment interval, another rat ran its respective study segment. The first rat then ran its test segment with all four arms unblocked and with only its previously blocked cued arm baited. To further mask any study segment odor trails, every rat received a different set of three arms from that given the previously run rat. The delay in an incorrectly entered arm was increased to 60 sec after the 30th training session.

Training 2: Changed configurations. Over the next 48 sessions, the rats were trained with a different configuration for each set of cued arms. As has already been described, we changed the configuration of one set to a mirror image by reversing the relative positions of the cued arms, thereby leaving the same pairs of opposite cued arms as in their original configuration. We changed the configuration of the other set by switching the opposite cued arms to become adjacent and adjacent arms to become opposite, creating the mixed change configuration. As can be seen in Figure 1 (lower

panel), these changes were counterbalanced between animals across each set of proximal cues.

Dependent measure. For each block of 12 sessions, we noted the number of trials on which each rat selected the remaining, fourth baited arm on its first choice in the four-arm test segment. These data were analyzed for each type of arm cue (arm entrance objects and arm inserts) during Training 1 and for each type of configuration change (mirror image and mixed) during Training 2 by separate within-subjects two-way (configuration change × blocks of 12 sessions) analyses of variance (ANOVAs). These data are summarized graphically as percentage correct. Unless otherwise noted, simple effects analyses were carried out with Scheffé post hoc comparisons. Significance for any effect was considered at $p < .05$. We did not analyze the rats' study segment search accuracy, because they made no reentries.

Results and Discussion

Training 1

Logistical considerations required us to expose each rat to the same arm object and arm insert configurations. Consequently, we did not control for any inadvertent differences in similarities among proximal cues that might be confounded with subsequent changes in each configuration. Therefore, we calculated each rat's accuracy in finding each cued arm within each cue set during the first training phase, to check for any effect of this possible confound. Since the rats received each cued arm, within each set of proximal cues, as the fourth baited arm only three times within each block of 12 sessions, we calculated their accuracy scores for each cued arm over successive blocks of 24 sessions. Thus, the percentage of accurate choices for each cue was determined from six trials within each block of trials. Our observations of these data and a two-way (three 24-trial blocks × 4 arm cues) ANOVA within each set of cues failed to detect any differences among object or insert cues over the three blocks of 24 sessions [$Fs(6,36) = 0.50$ and $1.13, ps > .30$].

Figure 2A (upper graph) shows the rats' test segment accuracy for each configuration of proximal cues over the six 12-session blocks during training with the final version of the task. As can be seen in this figure, the rats maintained consistently low but above-chance levels of choice accuracy until the final block of sessions, where they greatly increased their level of accuracy to close to 80% for each type of arm cue. These observations were confirmed by a significant blocks effect [$F(5,30) = 35.49$] and by significant pairwise comparisons establishing that accuracy on the final block was greater than that on any of the preceding blocks. No consistent or significant differences for cue type were found in this or the next training phase.

Training 2: Changed Configurations

Figure 2B (lower graph) shows the rats' test segment accuracy over the four 12-session blocks for each type of changed configuration. As can be seen in this graph, the rats reduced their accuracy to close to chance on the first block of sessions for each changed configuration, and similarly, they increased their accuracy to levels obtained on the last block in the previous phase. A significant
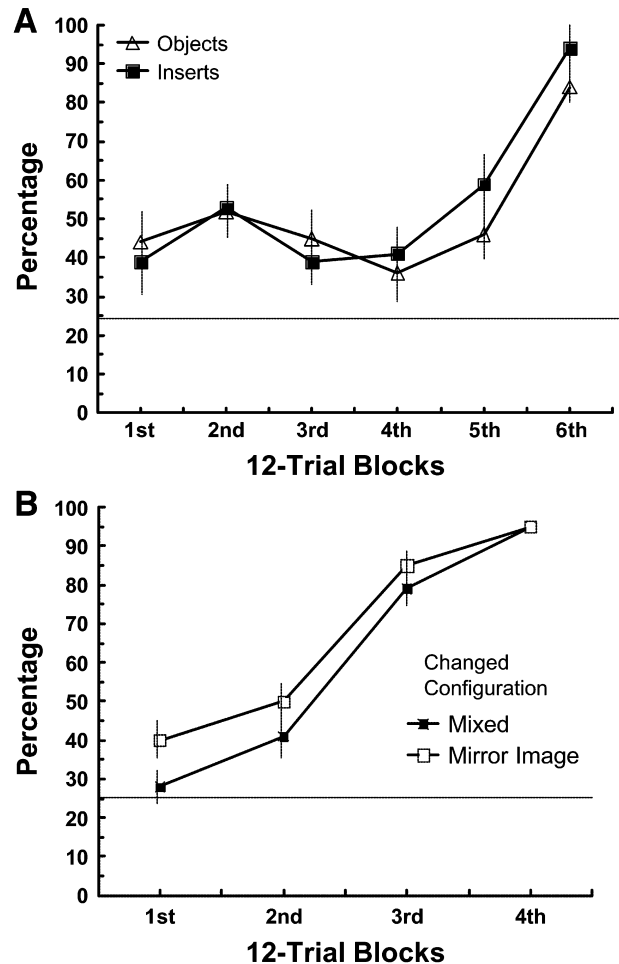

Figure 2. (A) Training 1: mean percentage of trials on which the rats selected the final baited arm on their first test segment choice for arm entrance object and arm insert configurations in Experiment 1. (B) Training 2: Mean percentage of trials on which the rats selected the final baited arm on their first test segment choice for the mirror image and mixed configuration changes in Experiment 1. Arm cue sets are pooled in this graph. Vertical lines represent *SEM*s.

blocks effect [$F(3,18) = 295.85$] and significant pairwise comparisons confirmed these observations. It should be noted that although the rats displayed slightly greater accuracy on the mirror image than on the switched configuration over the first three blocks of sessions, these differences failed to generate a significant main effect for configuration change over blocks [$F(1,6) = 1.14, p = .33$] or within any block. Thus, preserving the positions of opposite cued arms did not reliably help the animals learn the new configuration. It should be noted, however, that one pair of right-angled cued arms in the mixed changed configuration was invariably carried over from the original configuration. Consequently, differences between the two changed configurations might not have been great enough to produce differences in performance. This possibility prompted us to examine this question by

exposing the rats to different types of recombined configurations in the next experiment.

EXPERIMENT 2

As has already been mentioned, rats in an earlier study from our laboratory (Cohen & Bussey, 2002) may have been unable to use recombined configurations derived from pairs of opposite cues because they had already been trained with recombined configurations derived from pairs of right-angled arms. To eliminate the possibility of such proactive interference, in Experiment 2, we concurrently trained the rats from Experiment 1 on both types of recombined configurations derived from their two last acquired configurations. Two of these configurations were derived from two pairs of adjacent cued arms, and the other two from pairs of opposite cued arms, from these two final configurations in Experiment 1. On any one training session, the rats received each of the two recombined configurations of one type. If the rats had initially learned to represent these configurations only from positions of cued arms at right angles, they should recover their test segment accuracy more quickly with the recombined configurations derived from pairs of right-angled arms than from those derived from pairs of opposite cued arms.

The rats received extensive training with these four recombined configurations to determine whether they could eventually acquire each. Given that they could, we asked how they might generally process information from these configurations. We considered three possibilities. They might form a separate representation for each configuration, which they store in reference memory. On the other hand, they might learn to temporarily retain any spatial arrangement from a study segment, which they retrieve from working memory. Finally, the rats might process cued arms as a nonspatial list of items. That is, they might simply retain any three cued arms presented during a study segment without regard to their spatial configuration and then simply choose the cued arm that they remember not having previously seen. We tested these three possibilities by giving the rats postacquisition probe test trials on sessions that alternated with sessions containing regular training trials. As Figure 3 (lower panel) shows, the rats received two types of probe test trials: one in which configurations randomly changed over, but not within, trials and another in which a trial's test configuration randomly varied from one of the acquired configurations presented during the study segment. Neither type of configuration change would be expected to affect the rats' test segment accuracy if they were representing cued arms as a spatially irrelevant list of items. On the other hand, if they were retrieving a temporary spatial configuration of cued arms from working memory, varying the configuration only during test segments should disrupt their test segment performance. Finally, if they had formed a separate representation of each spatial configuration, either way of changing these configurations should disrupt their test segment performance.

Method

Subjects and Apparatus

We used the same subjects and apparatus as those in Experiment 1.

Procedure

Training. As is illustrated in Figure 3 (upper panel), the rats were exposed to four different configurations, two recombined from pairs of adjacent arms and the other two recombined from pairs of opposite arms from the final configurations in Experiment 1. Every session contained two widely separated trials of the same type of recombination (from pairs of adjacent arms or from pairs of opposite arms), so that no cued arm on the first trial ever occurred on the second trial in a session. This procedure prevented within-session proactive interference. Each pair of recombined configurations occurred equally over sessions in a randomly determined sequence, without occurring on more than two sessions in a row. Each configuration within each type of recombination also occurred equally on each trial over sessions. We originally had planned to train rats for at least 36 sessions, as had Cohen and Bussey (2003, Experiment 3). However, we terminated this phase after only 16 sessions, because the rats quickly attained highly accurate performance within each of the four recombined configurations.

Probe test trials phase. As is illustrated in Figure 3, sessions containing original training trials alternated with sessions containing probe test trials over the next 24 sessions. Half of the probe test trial sessions contained trials in which the configuration of arms randomly varied over study segments, but not between segments within trials. On the remaining trials, the configurations varied randomly only on the test segment of each trial. Each type of test session occurred equally often in a random sequence over the even-numbered sessions, without the same type of configuration change occurring on more than two even-numbered sessions in a row.

Results and Discussion

Training Phase

Since the rats quickly mastered the task with the four recombined configurations, we analyzed their test segment accuracy over blocks of 4, rather than 12, sessions. As Figure 4A shows, we pooled each rat's accuracy scores over each of the two recombined configurations from the pairs of adjacent cued arms and from the pairs of opposite cued arms to obtain a minimum number of trials (four) per block of sessions. Thus, chance performance was one out of four trials, or 25%, correct. To justify this pooling procedure, however, we first compared the rats' performances between the four configurations pooled over the 16 sessions. The rats averaged the same level of accuracy of 77% (*SEM*s, ±3.8% and ±4.2%) for each configuration made from pairs of adjacent arms and averaged only slightly different levels of 75% (±1.0%) versus 80% (±2.5%) between the configurations made from pairs of opposite arms. These slight differences were not statistically significant [$F(1,6) = 0.49, p = .51$].

As can be seen in Figure 4A (upper panel) and as confirmed by a significant effect for blocks [$F(3,18) = 29.33$], the rats significantly increased their accuracy over the first two blocks to near-perfect accuracy over the last two blocks of sessions. The slight differences observed between the two types of recombined configurations over the first two blocks produced neither a significant interaction [$F(3,18) = 2.21, p = .12$] nor any significant differences between type of configuration ($ps > .10$,
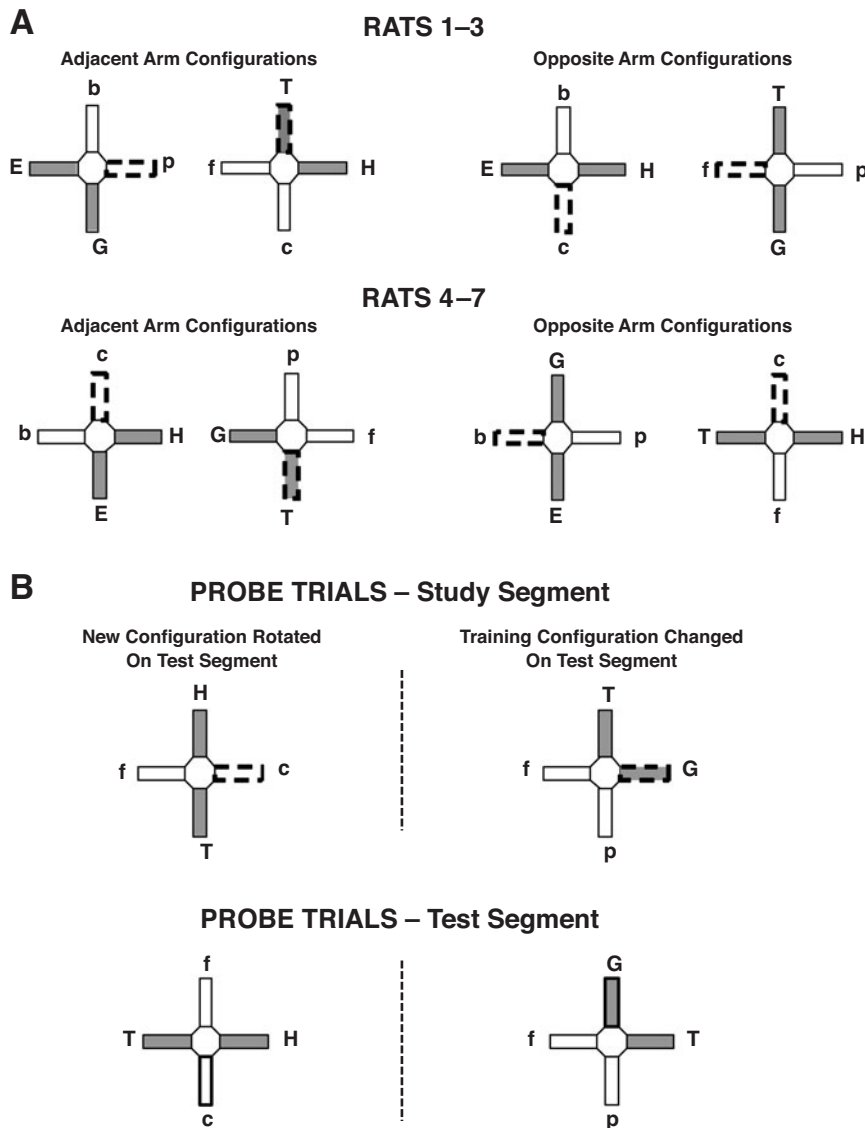
Figure 3. (A) The four recombined configurations used in the training phase in Experiment 2. (B) Examples of two of the training configurations as probe trial configurations in Experiment 2. See the text for further description of procedures. Arm cues and blocked and baited test segment arm designations are the same as in Figure 1. The locations of the cued arms do not correspond to compass direction. Arm cues: (Objects at arm entrances) p, post; c, chains; b, block; f, funnel; (Full arm inserts) G, grid, H, hurdles; T, tunnel; E, empty.

Newman–Keuls pairwise comparisons). Only on the first block of trials did the rats fail to perform significantly above chance within either type of configuration.

Probe Test Phase

Each type of probe test trial occurred 12 times. We compared each rat's accuracy on a test probe trial on an even-numbered session with that of the corresponding original training trial on the previous odd-numbered session. As can be seen in Figure 4B (lower panel), the rats maintained perfect accuracy on the originally recombined configurations but reduced their accuracy signifi-

cantly to slightly below chance on each type of probe trial [$F(1,6) = 761.76, p < .01$].

Acquisition data in the present experiment failed to show that the rats learned to represent a fixed configuration of four cued arms primarily on the basis of their adjacent (right-angled) locations rather than on the basis of opposite locations. As has already been pointed out, our rats required far fewer sessions to recover test accuracy with recombined configurations than did Cohen and Bussey's (2003) rats in the same-pairs group (Experiment 3, Figure 5, p. 181). Unlike their rats, however, our animals had received successive training concurrently, with each con-
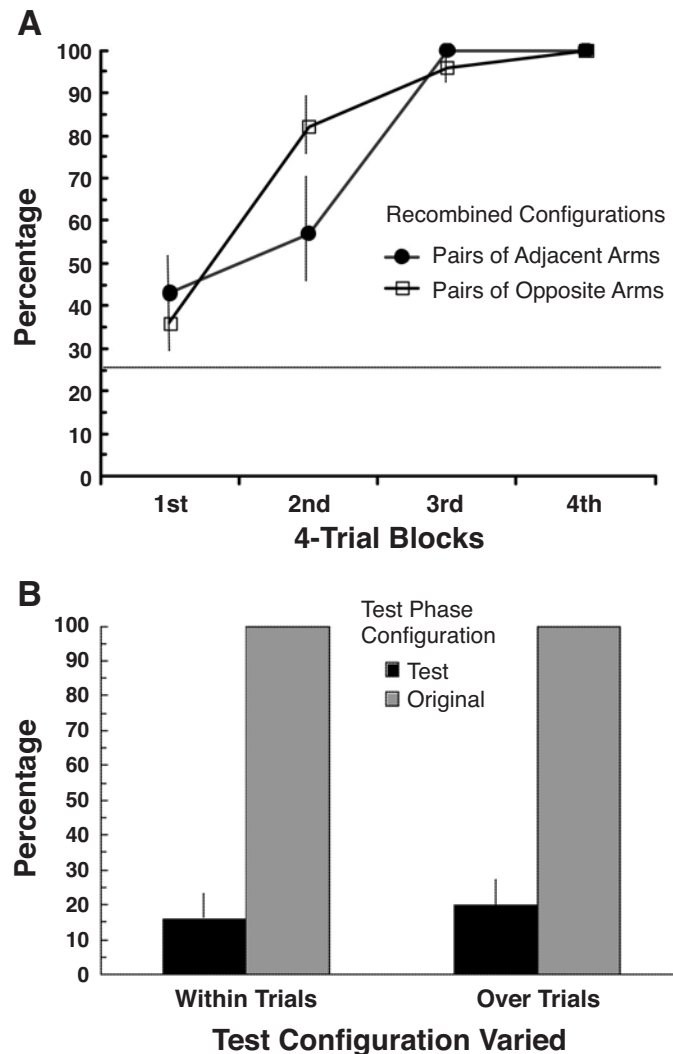
A

B

Figure 4. (A) Training phase: mean percentage of trials on which the rats selected the remaining baited arm on the first test segment choice on the recombined configurations from Experiment 1 in Experiment 2. (B) Probe test phase: mean percentage of trials in Experiment 2 on which the rats selected the remaining baited arm on the first test segment choice on regular training and on test probe trials in which the configuration was varied during test segments (changed within trials) and in which it was varied only during the study segment (changed over trials). Vertical lines represent *SEM*s.

figuration, changed in a different way in Experiment 1, before being trained on recombined configurations. Perhaps exposure to these successive changes in each configuration in Experiment 1 allowed the rats to adapt or habituate more quickly to subsequent changes in Experiment 2. The results from the test phase indicated that such rapid acquisition with these recombined configurations did not reflect a basic change in how the rats retained and retrieved information from these fixed spatial configurations. That is, rats did not develop spatially irrelevant lists of cued arms, nor did they temporarily retain spatial configurations from the study segments in their working memory. Rather, they

formed separate spatial representations of these configurations to be retrieved from their reference memory. That they had not developed spatially irrelevant lists of cued arms, however, does not eliminate the possibility that, with continued training under test conditions, they could have developed spatially irrelevant lists. In Experiment 3, we explored this possibility.

EXPERIMENT 3

We designed Experiment 3 to determine whether the rats from Experiment 2 could learn to process some cued

arms as spatially irrelevant lists of proximally cued arms. We continued to train these rats with the two configurations derived from pairs of adjacent cued arms and the two configurations derived from pairs of opposite cued arms from Experiment 2. We varied the positions of arm cues randomly over and within trials for one configuration within each pair (the random configurations) but maintained the relative positions of arm cues in each of the other two configurations (the constant configurations). If rats can learn to represent cued arms as spatially irrelevant list items, they should increase their test segment choice accuracy on the random configurations to levels comparable to those they maintain on the constant configurations. Given this possibility, we asked whether the rats might develop a general list-like search strategy or represent the random configurations separately from those of the constant configurations. To answer this question, we devised two types of postacquisition test probe trials with one of the random and one of the constant configurations. For one of these test probes, we randomly varied the positions of the arm cues from the constant configuration while maintaining them from the random configuration. For the other type of test probes, we exposed the rats to two new recombined configurations. Each of these configurations was composed of a pair of cued arms from the random configuration and a pair of cued arms from the constant configuration. If the rats had developed a general list-like search strategy, neither of these test probe variations should disrupt their acquired choice accuracy. If they had developed separate representations for the random lists, however, each type of test probe should disrupt their accuracy.

Method

Subjects and Apparatus

We used the same subjects and apparatus as those in the previous experiments.

Procedure

Training phase. The rats received 36 two-trial sessions. As in Experiment 2, half of the sessions contained both sets of arms derived from recombined configurations of pairs of adjacent arms, and the other half contained sets of arms derived from recombined configurations of pairs of opposite arms. The only modification we imposed in this training phase was to continuously vary the positions of cued arms over and within trials for one of the configurations in each session (a random configuration). That is, a rat received any one of six possible configurations during a study segment, followed by any one of the remaining five configurations during the test segment. The relative positions of the cued arms in the other configuration were not varied (the constant configuration). Which configuration always remained constant and which always varied within each pair of the previously acquired configurations was randomly determined for each rat. The sequence of the random and the constant configurations within a session also randomly varied over sessions so that the same sequence never occurred on more than 2 sessions in a row.

Test probe configurations phase. Over the next 24 sessions, the rats were exposed to test probe configurations. We modified only their random and constant configurations that had been derived from pairs of opposite cued arms from Experiment 2. We did not modify the random and constant configurations derived from

pairs of adjacent cued arms, because of the complexity of our design for testing and the same logistical considerations for running experimental sessions already discussed. Furthermore, we note that the rats' performance during training was virtually identical for configurations derived from pairs of adjacent and pairs of opposite cued arms.

The upper panel of Figure 5 shows the four test probe trials consisting of the original sets of cued arms. Of the 12 sessions containing these probes, six consisted of the random configuration and the fixed configuration as presented during training. For this phase, we designated these probes as *random/varied* and *constant/unchanged* configurations, with the first term referring to the set of cued arms from the training phase configuration and the second term referring to the manipulation of the test segment configuration. On the remaining 6 sessions, we varied the configuration of those cued arms originally presented in the constant configuration, but we maintained it for those presented in the random configuration. Therefore, we designated these two probe test trials as *constant/varied* and *random/unchanged* configurations, respectively. The lower panel of Figure 5 shows another four test probe trials consisting of the combined sets of cued arms in which each configuration contained a pair of arms from the random configuration and a pair from the fixed configuration. We labeled these four types of probe trials *random 1/unchanged*, *random 1/varied*, *random 2/unchanged*, and *random 2/varied*, with the first term referring the number of cued arms from the random configuration that were open during the study segment and the second term referring to the manipulation of cued arm positions between trial segments. Each of the eight different test probe trials occurred six times during this phase. The two types of test probe sessions randomly varied over this phase, without the same one occurring on more than two consecutive sessions.

Results and Discussion

Training Phase

Figure 6A shows the rats' performance with the fixed and random configurations over blocks of six trials. As can be seen in this figure, the rats maintained perfect accuracy on each block of trials on each constant configuration and increased their accuracy from chance to near-perfect levels on each random configuration. A three-way ANOVA of configuration (from pairs of adjacent cued arms and from pairs of opposite cued arms) $\times$ manipulation of arm positions (constant or random) $\times$ blocks of sessions revealed a statistically significant double interaction between manipulation and blocks [$F(2,12) = 61.96$], but not a statistically significant triple interaction [$F(2,12) = 0.60, p = .57$], which confirmed the observations above. Thus, the rats acquired a list-like search strategy with each random configuration without being disrupted on each constant configuration.

Test Phase

Figure 6B shows the accuracy of the rats' performance for each type of probe test trial. Two separate two-way ANOVAs were conducted on probe test series. The first ANOVA compared the rats' search accuracy among the four types of probes illustrated in the upper panel of Figure 5, and the second ANOVA compared the rats' search accuracy among the four types of probes illustrated in the lower panel of Figure 5.

As can be seen in the left half of Figure 6B, the rats maintained almost perfect accuracy on probe trials containing

ORIGINAL TRAINING SETS – PROBE TRIALS
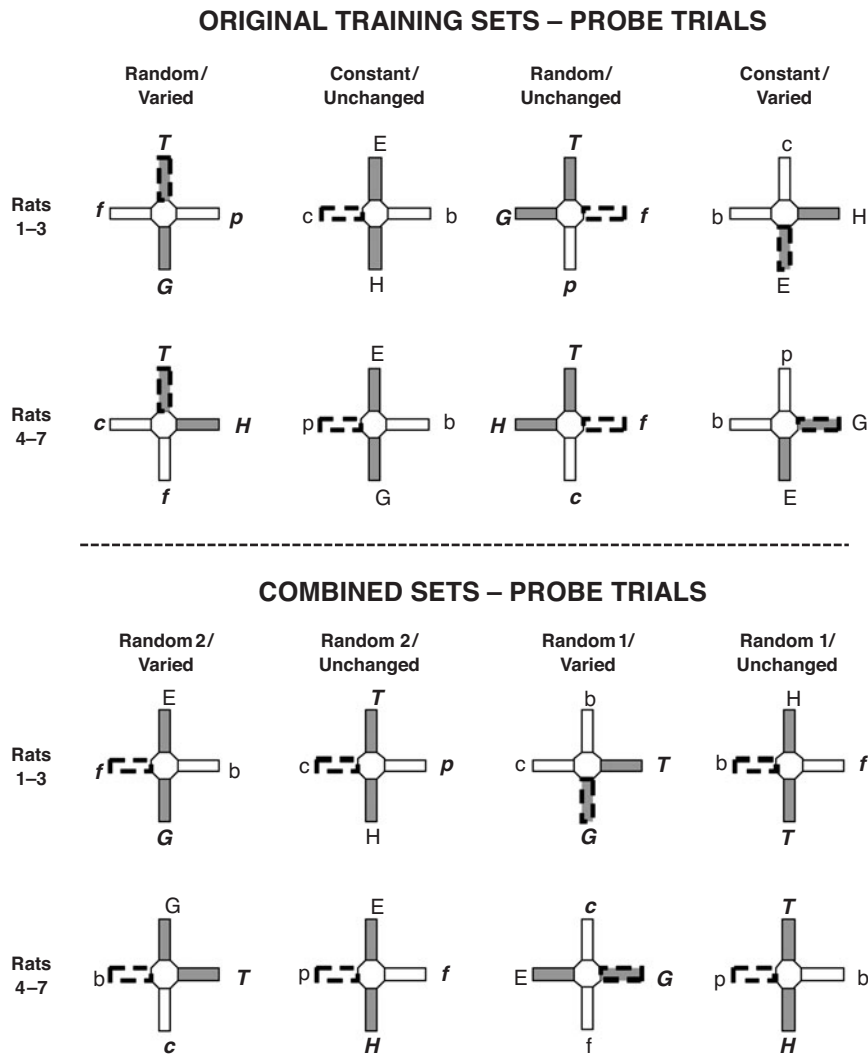

COMBINED SETS – PROBE TRIALS

Figure 5. Configurations for study segments for each type of postacquisition probe trial in Experiment 3. The blocked arm during the study segment is indicated by a bold dashed outline. Examples of test segments are not depicted. Arm cues indicated by bold italic letters designate those cues within the random set. Arm cues indicated by plain letters designate those cues within the constant set. Arm cues: (Objects at arm entrances) p, post; c, chains; b, block; f, funnel; (Full arm inserts) G, grid; H, hurdles; T, tunnel; E, empty.

a random configuration regardless of its test segment manipulation (random/varied and random/unchanged). They reduced their accuracy to below chance on constant/varied probes but only slightly reduced it on the constant/unchanged probe trials (75%). A significant interaction between the study and the test segment's configuration [$F(1,6) = 252.30$] and significant individual differences between the constant/varied and either the random/unchanged or the random/varied probes and between the constant/unchanged and the constant/varied probes confirmed these observations. Consequently, the rats did not transfer their list-like search strategy acquired with a random configuration to a constant configuration. Although training on randomly varied configurations did

not disrupt performance on previously acquired constant configurations, testing apparently did. That is, all but 1 rat displayed lower accuracy on their constant/unchanged configuration on probe trials than on the last block of training trials. These declines in accuracy across phases were statistically significant [$F(1,6) = 18.15$].

The right half of Figure 6B shows that the rats displayed below-chance accuracy on each of the combined configurations. Neither the number of arms from the random configuration presented during the study segment nor the manipulation of the test segment's configuration influenced the rats' performance. The second two-way ANOVA conducted on these data did not generate any significant effects. Furthermore, all the rats un-
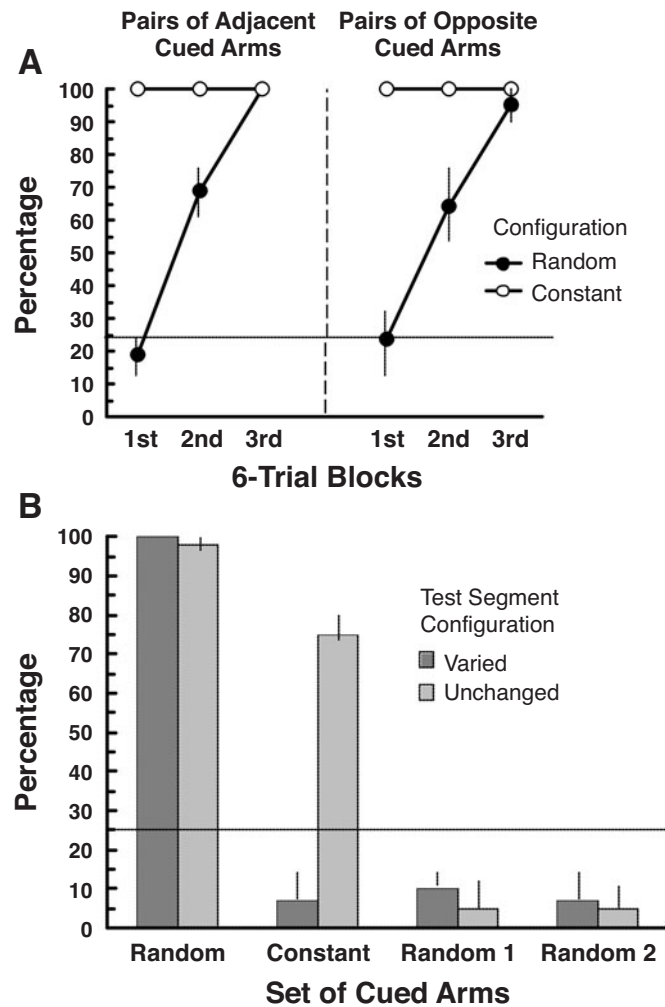
Figure 6. (A) Training phase: mean percentage of trials on which the rats selected the remaining baited arm on their first test segment choice on the random set and constant set of arms in Experiment 3. (B) Probe test trial phase: mean percentage of trials out of six probe trials on which the rats selected the remaining baited arm on their first test segment choice on each type of probe trial. The first four probe trial types contain sets of arms of either the random or the constant configuration from the training phase. The last four probe trial types contain two arms from each set in which either one (random 1) or both (random 2) arms in the random set are open during the study segment. Vertical lines represent *SEM*s.

covered the fourth baited arm on their first choice on fewer than 25% of any of these probe trials. Consequently, presenting some arms from the randomly changing configuration did not prompt the rats to process all cued arms as a spatially irrelevant list. These results suggest that the rats also formed a distinct and separate representation for a spatially irrelevant set of cued arms.

GENERAL DISCUSSION

The findings from this study replicate and extend those in Cohen and Bussey (2003). The rats in the present study not only acquired two spatial configurations from different types of cues (full arm inserts and objects at arm entrances; Experiment 1), but also learned four configurations recombined from pairs of their adjacent and opposite cued arms (Experiment 2). Furthermore, in Experiment 3, they also learned to search within two sets of four cued arms whose spatial relations were made irrelevant, while maintaining their accuracy on two sets of cued arms maintained in fixed spatial configurations from the previous experiment. Subsequent results in Experiment 3 suggest that the rats had developed a list-like representation separate from that for a spatially relevant (constant) configuration.

Although the rats were able to accurately use four different fixed spatial configurations in the enclosed four-arm radial maze, the question remains how they represented these configurations. That is, did the rats represent each configuration as a simultaneously retrieved spatial map or as sequentially activated associations among cued arms? Even though our rats could not observe other cued arms while on any one arm, they still might have learned to associate each cued arm with the locations of the other arms at right angles or opposite to it as they moved around in the center chamber. Such spatial associations may not be equivalent to the proposed local or partial maps rats are considered to initially form and later combine into global maps (Benhamou, 1998; Poucet, 1993; Roberts, 2001). To distinguish between these two notions, we must determine whether principles of association theory might account for various map-like effects as well as or better than cognitive map theory.

This question is particularly relevant in light of the research by Rodrigo, Chamizo, McLaren, and Mackintosh (1997) with rats in the Morris water pool. They observed that rats were unable to use an added fourth landmark after having learned to locate a hidden submerged platform with three distal landmarks. This finding challenges the idea that animals automatically update acquired spatial maps when encountering slight environmental changes (O'Keefe & Nadel, 1978; Poucet, Chapuis, Durup, & Thinus-Blanc, 1986). As has already been noted, our rats reduced their search accuracy to chance when first presented with the four recombined combinations in Experiment 2, but recovered their performance more rapidly than the rats in the same-pairs group in the previous study did (Cohen & Bussey, 2003, Experiment 3). It might be argued that our rats would not be expected to automatically update their spatial maps when half the arms in their original configurations are switched. Their relatively rapid recovery in performance, however, approximates this process and more closely reflects a flexible ability to integrate portions of previously acquired maps, as was suggested by Cohen and Bussey (2003).

Although the rats never received repetitions of cued arms within each session, they repeatedly experienced the same eight cued arms in the same configurations over sessions in Experiment 1 and between some successive sessions in the last two experiments. Association theory, but not cognitive map theory, predicts that repetition of the same items over sessions promotes the buildup of long-term proactive interference over sessions, which slows acquisition and produces postacquisition deterioration in performance. These effects have been reliably demonstrated in monkeys' serial probe recognition performance (Jitsumori, Wright, & Cook, 1988). The fact that the rats in both studies from our laboratory only slowly increased their choice accuracy to acceptable levels in an apparently simple task might support this notion. However, the only postacquisition deterioration in performance we observed occurred on probe test trials with the constant configuration in the final experiment.

A recent version of cognitive map theory, parallel map theory (Jacobs & Schenk, 2003), might also account for the extensive training our rats need to learn the basic task. To fully appreciate this effect, we note that rats trained on eight-arm radial mazes (Suzuki et al., 1980; Vollmer-Conna & Lemon, 1998) and in pilot research with our enclosed four-arm maze, usually required very few sessions (between 10 and 20) to learn their interrupted trial tasks when distal or proximal cues were maintained at fixed room locations. Only those rats trained on eight-arm mazes were not disrupted when later tested with cues rotated on some trials. Parallel map theory might explain these anomalies by suggesting that the rats in those studies learned to use arm location cues as part of a dominant *bearing map*. That is, some aspects of their training or of their maze setup allowed the rats to process any of these cues as directional landmarks, regardless of their actual compass direction. The rats in our laboratory may have been exposed to directional room cues in some way that interfered with their ability to process proximal arm cues in the same way. For example, we always brought the rat to the maze from the same location in the room. Consequently, the rats might have developed a bearing map of arm locations from possible internal or external directional cues with reference to the room, separate from the relative positions of the cued arms in the maze. According to parallel map theory, a bearing map of such directional cues is dominant over other more proximal cues. Evidence for the dominance of a room's geometric module over its distal landmarks (Cheng, 1986) and of its distal landmarks over local cues (Biegler & Morris, 1996) has been shown in rats' food-searching behavior in open foraging arenas. Biegler and Morris, for example, demonstrated that rats were unable to use a stable configuration of proximal landmarks whose position varied randomly within an arena containing distal cues. Dudchenko and Davidson (2002) further found that rats' internal sense of direction in the absence of external directional cues overshadows local arm position cues in the enclosed T-maze. In that experiment, rats could not maintain relatively easy-to-learn win–shift discriminations between parallel T-mazes in adjacent rooms devoid of distal directional cues when the mazes were positioned at right angles to each other. Thus, our rats required extensive training to learn to ignore irrelevant directional cues and only attend to the relative locations of the proximal arm cues. Therefore, we have since adopted different procedures for bringing the rats to the maze and have further changed the apparatus to eliminate possible irrelevant directional cues in current ongoing research.

The results from our first two experiments do not provide unambiguous evidence about how our rats represented these spatial configurations. We cannot determine whether their representations consisted of complex networks of spatial associations among cued arms or of more integrated cognitive topological maps. Perhaps a more important finding in the present study is that our rats developed a list-like representation of proximally

cued arms following extensive training with four fixed configurations of the same arms. To accomplish this, they had to learn to ignore not only any irrelevant extramaze or internal directional cues, but also irrelevant positions of local arm cues. That they could do this after extensive training with stable spatial configurations at first seems to contradict a basic principle of association theory. That is, prior training with fixed configurations might be expected to block or prevent rats from learning to ignore such spatial aspects of cued arms. Moreover, the introduction of spatially irrelevant configurations might be expected to cause postacquisition deterioration of performance on previously acquired spatially relevant configurations by reciprocal (retroactive) interference. Current versions of association theory (Pearce & Bouton, 2001), however, predict that prior training with several different configurations of the same cued arms better prepares rats to disregard temporary, irrelevant spatial configurations of these cues. That is, having first learned that each cued arm is as likely to occur adjacent or opposite to any other cued arm in a consistent or conditional manner (Experiment 2), rats are better able to learn when these variations become unpredictable (Experiment 3). According to this notion, blocking and reciprocal interference should decline as a function of the number of successive or concurrent stable configurations of the same cued arms learned prior to training with spatially irrelevant and with spatially relevant configurations. This testable hypothesis should also be considered part of a broader theoretical issue concerning how organisms learn to represent items as lists. That is, must animals first learn how to represent and retrieve items from stable spatial configurations before they can learn how to represent them as spatially irrelevant lists?

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