

ORIGINAL ARTICLE

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Object-goal positioning influences spatial representation in rats

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Abstract Three tests investigated how the geometric relation between object/landmarks and goals influenced spatial choice behavior in rats. Two groups searched for hidden food in an object-filled circular arena containing 24 small poles. For the “Proximal” group, four distinct objects in a square configuration were placed close to four baited poles. For the “Distal” group, the identical configuration of objects was rotated 45° relative to the poles containing the hidden food. The Proximal group learned to locate the baited poles more quickly than the Distal group. Tests with *removed* and *rearranged* landmarks indicated that the two groups learned to use the objects differently. The results suggested that close proximity of objects to goals encouraged their use as beacons, while greater distance of objects from goals resulted in the global encoding of the geometric properties of the arena and the use of the objects as landmarks.

Key words Animal spatial cognition · Spatial representation · Rats · Navigation mechanisms

Introduction

Whether foraging for food, defending territories, or eluding predators, many animals demonstrate a robust working knowledge of their spatial environment. Two broad theoretical approaches have been proposed to explain how environmental features are encoded and used by animals to navigate their surroundings. One approach holds that it is the spatial relations *between* various cues that is the principal component encoded by many animals in their representation of space. While the storage and retrieval of this relational distance and direction information could be

accomplished in various ways, it is usually expressed in terms of an internal cognitive map (O’Keefe and Nadel 1978; Olton and Samuelson 1976; Poucet 1993; Suzuki et al. 1980; Tolman 1948). According to this notion, animals form a map-like representation that is isomorphic with the environment and reference it as needed for the purposes of orientation and navigation.

The second approach comprises a large class of absolute and non-relational mechanisms. According to these theories, animals form and use discrete cue representations to navigate, using little or no direct information about the spatial relations between the various features of the environment (e.g., Brown 1992; Cartwright and Collett 1983; Leonard and McNaughton 1990). Examples of these types of navigational mechanisms include learning a particular sequence of responses to a goal, or learning to directly approach a distinct object cue or “beacon” in the environment. This latter kind of mechanism often provides all of the information needed to locate a goal, as when we recall where we parked our car by looking for a distinctive signpost or widely visible lamp post located nearby.

Research on animal spatial cognition has usually searched for evidence of the more theoretically intriguing relational spatial mechanisms, while often overlooking or controlling for the role of such non-relational mechanisms. It now seems almost certainly to be the case that animals concurrently and redundantly employ both types of mechanisms (Gallistel 1990; Leonard and McNaughton 1990; O’Keefe and Nadel 1978). At this point, the more critical question now becomes to identify under what conditions animals select or employ these differing navigational strategies.

Cheng (1986) and Gallistel (1990), for instance, have proposed that relational spatial representations have cognitive primacy over non-relational ones. In the experiments of Cheng (1986), rats had to locate hidden food inside a rectangular arena with different stimulus cues located at each of the four corners. He found that the rats relied primarily on the global geometric shape of the apparatus to locate the food despite the availability of disam-

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biguating featural cues in the arena. Cheng argued that the principal mode of rat navigation is geometric in nature and that any encoding of non-geometric information is secondary and subordinate to this processing mode.

Gallistel (1990) similarly proposed that many animals readily construct internal coordinate systems, and use current perceptions only as a secondary verification of the directional information provided by this internal map. He states “the trajectories of animals toward or away from goals are determined by the remembered position of their goal within the macroscopic shape of their environment, not by the current perception of goal characteristics” (Gallistel 1990, p. 172). He further argues that “goals do not function as beacons with respect to which the animal orients, even when the goals make suitable beacons” (Gallistel 1990, p. 172). One implication of this view is that a goal’s spatial proximity to a set of landmarks should have little or no qualitative effect on the encoding of these spatial relations. Thus, a rat should learn the location of goal A when it is *between* landmarks B and C just as quickly as when it is *at* either B or C.

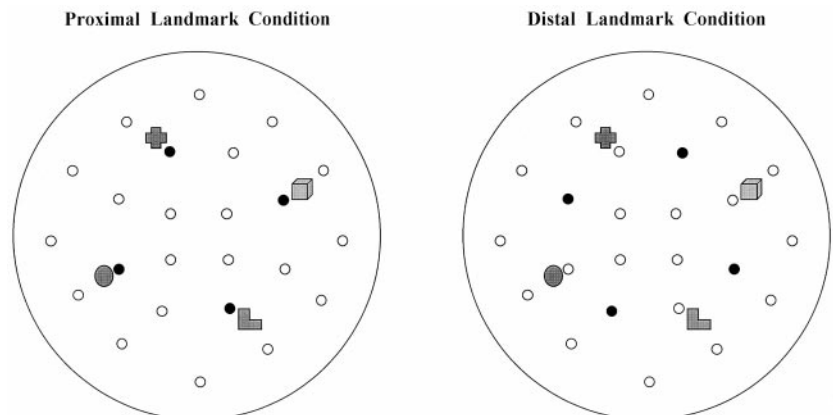
Not all studies of animal spatial behavior in settings highly similar to that used by Cheng (1986) have found the overshadowing of featural cues by global arena cues. For instance, Vallortigara et al. (1990) found that chicks showed stronger reliance on featural cues than on an environment’s overall geometry to guide their spatial behavior. While there are important differences between the studies (such as the species tested) the contrasting nature of the results suggests that unidentified factors do influence the degree to which relational spatial information or absolute featural information are employed or preferred by animals.

One very likely candidate is spatial proximity. Testing pigeons in a touchscreen-based spatial search task, Spetch (1995) found that distant landmarks were overshadowed by landmarks located closer to a hidden goal. Brown (1994) similarly found that rufous hummingbirds (*Selasphorus rufus*) learned a spatial association task more slowly the farther apart the cues and the appropriate response locations were from each other. Studies of associative and discrimination learning have generally demonstrated as well that learning is slowed by the spatial sepa-

ration of cue and response location (Milner et al. 1979; Rescorla and Cunningham 1979; Stollnitz 1965). It would seem likely that the same might be true for spatial behavior and the stimuli potentially controlling it.

The purpose of the present study was to investigate how different types of object/goal proximity and positioning influenced the navigational strategies employed by rats. In this experiment the spatial behaviors of two groups of rats were examined in an open-field pole search task in which the distance between a set of visible objects and the hidden goals was varied. For the “Proximal” group these objects were consistently located directly next to a hidden food goal, while for the “Distal” group these objects were spatially displaced so as to be halfway between the locations of the hidden food (Fig. 1). Although the visual appearance and arrangement of the landmarks were identical for both groups, we expected that these differences in object/goal proximity would result in differences in the way the two groups would learn to solve their respective food searching tasks. Because of the close proximity of the objects and goals in the Proximal group’s task we hypothesized that the rats might learn to treat the objects as “beacons”. By simply approaching each object, this proximal arrangement might result in rapid learning and high accuracy in locating the hidden food. Furthermore, because of the ease and immediate success of this strategy it might also preempt any further learning about the surrounding relational layout of the arena and the landmarks. Because for the Distal group the objects were arranged further away from the hidden food we hypothesized that these animals might be more encouraged to process the overall spatial attributes of the arena and its configuration to solve their task. This would make them more likely to encode the geometric relations between objects and the global geometry of the arena (Greene and Cook 1997). To examine how each group learned to use the objects in the arena after solving their respective tasks, we used transfer tests involving novel arrangements of the objects in the arena to assess the degree to which each group employed different strategies to locate the hidden food. If the groups differed in their behavior on these tests it would indicate that, despite the visually identical *manifest* spatial environment experienced by each group, the *latent* spatial re-

Fig. 1 Overhead view of the testing arena and the arrangement of the four landmarks and baited poles (*darkened poles*) for the Proximal and Distal conditions



relationship between the objects and hidden goals had indeed influenced how they employed these elements and their relations to locate their food.

Materials and methods

Animals

Subjects were 12 adult male Long-Evans rats maintained at 85% free feeding weight (age-adjusted) throughout the experiment. The rats were individually housed in metal cages (18 × 24.5 × 18 cm) with free access to water in a room with 12:12 h light:dark cycle. Any supplemental feeding occurred immediately after a daily session.

Apparatus

The testing arena was a 167-cm-diameter circular platform surrounded by a sheet metal wall 25 cm in height. We surfaced the wooden floor of the testing arena with smoothed plaster to cover the oriented grain of the wood and fill any distinctive holes. The entire apparatus was painted flat black. The arena was elevated 89 cm off the floor and mounted on a rotating base that allowed it to be moved freely to any orientation with respect to the room. Illumination was provided by a square bank of fluorescent lights 157 cm above the center of the testing arena. We completely enclosed the arena within a uniform beige nylon curtain suspended from the ceiling. Four small openings in the curtain at 90° intervals permitted the observation and recording of the sequence and timing of pole choices by rats using a 24-switch event recorder interfaced to an AT-class microcomputer.

Twenty-four wooden poles (15 cm tall; 1.9 cm in diameter) were positioned in three concentric circles within the arena (Fig. 1). The inner ring (38 cm in diameter) consisted of 4 poles, the intermediate ring (85 cm in diameter) consisted of 8 poles, and the outer ring (138 cm in diameter) consisted of 12 poles. We selected this pole configuration to make the distances between adjacent poles both within and between rings as similar as possible (mean inter-pole distance = 30 cm; range 26–33 cm). A small brass food cup (2.5 cm in diameter and 1 cm deep) capped each pole. The same spatial arrangement of four household objects was used for each group. These objects consisted of a pink and white soda can (12 cm in height × 6 cm in diameter), a box-shaped metal feeding cup for pigeons (10 × 8 × 7 cm), a brown digital clock (trapezoidal in shape; 7 × 7 × 6 cm), and an inverted white and blue coffee mug (9 cm in height, 8 cm in diameter).

Procedure

Experimental conditions

A between-groups design compared performance in two experimental conditions. The spatial arrangements of the baited poles and the objects for these two conditions are shown in Fig. 1. For both groups the visual configuration of the objects was the same, with every other pole of the intermediate ring baited with a different number of 45-mg food pellets (8, 3, 5, and 1 pellets in clockwise order). Six rats were tested in the Proximal condition where these four baited poles were immediately adjacent to different objects. The other six rats were tested in the Distal condition where the locations of the four baited poles were rotated 45° with respect to the objects. Each baited pole was now halfway between adjacent pairs of objects, approximately 33 cm away from each one, while each object was still adjacent to a pole.

Initial training

The rats were initially placed in the arena in squads of three or four animals for one pre-training session. The rats were allowed to re-

trieve food from on top of and around the four target poles, which were rebaited as necessary. The food cups were removed from the tops of all poles. The objects were present and positioned according to each squad's assigned test condition. After each rat had begun climbing and retrieving pellets (approximately 5–10 min), the brass food cups were replaced and the animals tested for another 5 min with the food hidden on top of the poles.

Discrimination training

The rats received one trial per day 7 days a week. Rats were tested individually. Each session was started by releasing the animal from one of eight randomized starting locations at the edge of the arena (0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315° relative to a fixed reference point in the arena). A rat was allowed to search the arena until all four baited poles had been visited or 10 min had elapsed, at which point the rat was removed from the arena. A second experimenter used the computerized 24-switch event recorder to document the sequence and timing of each pole choice by the rat. A pole choice was recorded whenever a rat reared up within 3 cm of the food cup. This choice behavior was obvious and easy to record. A hardware failure caused the first day's results for discrimination training to be lost.

In order to eliminate extra-arena cues (e.g., localized noises, curtain features) as sources of spatial information, the entire arena (poles, food, and objects) was randomly rotated each day to one of four orientations (0°, 90°, 180°, and 270° relative to a fixed reference point in the room). To eliminate intra-arena cues as potential sources of information about food location, the food and objects were randomly rotated on a weekly basis in 90° increments relative to a fixed arena reference point. Both of these rotations and the rats' starting locations were randomized independently of each other. Using these same rotation and randomizing manipulations, earlier research using this arena had found that food odors and external arena cues were not factors in the rats' performance of this type of pole searching task (Greene and Cook 1997).

Object removal test

After the two groups had learned to recover the hidden food, a series of transfer tests were conducted. During the 25th, 28th and 30th training sessions, object removal tests were conducted. All objects were removed from the testing arena for both groups, but otherwise these three sessions were conducted in the same manner as described above.

Object rearrangement test

During the 38th, 42nd, and 46th sessions, object rearrangement tests were conducted. The objects were moved to various new locations within the testing arena for each of these sessions (shown in Results). In the first rearrangement test, the objects were pseudo-randomly moved to locations in the inner and outer ring of poles. We attempted to pair the objects so that a pole was located midway between each set. This was to test whether any "between"-pole strategy had been learned by either group. The second test was similar, but this time equal numbers of objects were randomly placed in the inner and outer rings. For the third test the entire object configuration was shifted to mark poles from the inner and outer rings of poles rather than the intermediate ring. These transfer sessions were conducted in the same way as during discrimination training, except that no food was present in the arena and the rats were removed immediately after their sixth pole choice in a session.

Results

The two groups showed a number of differences in the learning and performance of their respective tasks. Over-

all these differences suggested that each group employed different information in navigating the arena and locating the baited poles. The Proximal group learned its task very quickly using the strategy of going directly towards the objects. The Distal group, on the other hand, took longer to learn its task, but apparently did so based on a combination of cues involving the relative positions of the landmarks and their overall location within the arena's geometry. The two groups also exhibited small differences in search behavior with respect to the varied bait sizes. The next sections document these contrasts in more detail.

Discrimination training

The two groups significantly differed in the number of sessions it took to learn how to accurately locate their baited poles. The Proximal group learned the task in considerably fewer sessions than did the Distal group. This is shown in Fig. 2, which depicts each group's mean overall choice efficiency over the first 32 recorded sessions of discrimination training (not including the removal tests). Choice efficiency measures how directly and accurately the rats recover the hidden food in the arena. Choice efficiency is determined by averaging the choice serial position of the four correct choices in a session. For instance, if a rat's first four choices in the arena were all correct, then its choice efficiency score would be 2.5 $(1 + 2 + 3 + 4)/4$ – the best possible score. When any unbaited poles are included among those searched, this causes an increase in the serial position of subsequent correct choices and correspondingly causes the choice efficiency score to increase, e.g., $(1 + 4 + 7 + 8)/4 = 5$. Hence, the better a rat performs, as evidenced by visiting baited poles early in a session, the *lower* its choice efficiency score for

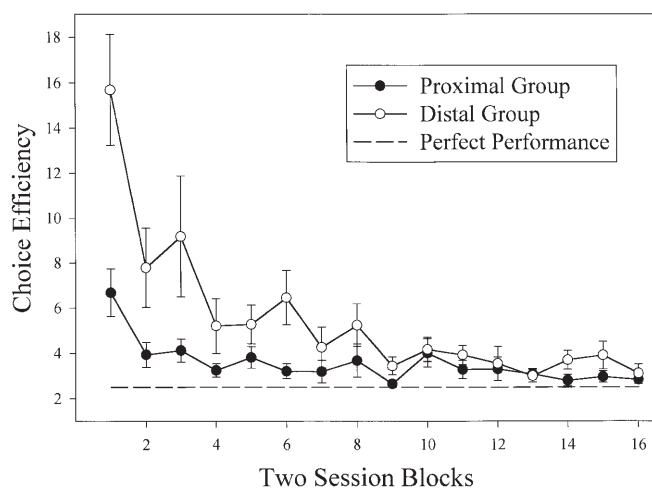


Fig. 2 Average choice efficiency for the Proximal and Distal groups for the 32 sessions of discrimination training. The dotted line represents the best possible search performance (i.e., the lowest possible score) with this measure. Error bars represent the SEM for each two-session block

that session. Greene and Cook (1997) found that this measure was highly correlated with traditional measures of spatial performance (i.e., number of correct choices in the first n choices and total choices in session), but was slightly superior in that it took into account both the sequence and accuracy of all pole choices in a session.

A mixed design ANOVA (Group \times 2-session Blocks) of choice efficiency was used to compare task acquisition in the two groups. This ANOVA and all subsequent statistical tests described in this article were evaluated using an alpha level of $P < 0.05$. As expected from Fig. 2, this ANOVA confirmed that there was a significant interaction between the rate at which the two groups acquired the discrimination, $F(15,150) = 6.8$. Although the Proximal group initially learned the task much faster, by the 20th session of training both groups had reached comparable levels of choice performance in the task. Over the latter stages of training (sessions 20–32), mean choice efficiencies for the Proximal ($\bar{x} = 3.0$) and Distal ($\bar{x} = 3.5$) groups were not significantly different from one another, $F(1,10) = 3.1$. Although the accuracy of the two groups' search behavior was equivalent over these latter 12 sessions, the Distal group did require significantly more time to clear the arena ($\bar{x} = 53.4$ s per session) than the Proximal group ($\bar{x} = 34.6$ s per session), $F(1,10) = 7.2$. Casual observation of the Distal rats suggested they spent a considerably greater proportion of time between choices rearing and looking about the arena, in marked contrast to the more uninterrupted choice sequences of the Proximal group.

We next evaluated each group's sensitivity to the different quantities of pellets associated with specific poles. The Distal group appeared to have learned to retrieve the baits in order of their decreasing quantity going from the largest to smallest rewarded pole, based on mean order of visiting each of the baited poles. The Distal group tended to retrieve the food from the poles in the following order: 8, 5, 3, 1 pellets (mean choice position over the last 12 training sessions = 3.8, 4.0, 4.1, 4.6 respectively). The Proximal group showed the exact opposite behavior, tending to retrieve their food in the following mean order: 1, 3, 5, 8 pellets (mean choice position = 3.0, 3.5, 3.6, 3.7, respectively). Because of the small size of these differences, however, statistical support for these specific orderings was difficult to achieve. A Mann-Whitney test using the difference between in the choice serial position of the two extreme reward sizes (8 vs. 1) did confirm that the Distal group visited the eight-pellet pole significantly earlier in the choice sequence than the Proximal group, $U(6,6) = 30$.

Landmark removal

Removal of the landmarks significantly decreased both groups' capacities to locate the baited poles. This was determined by comparing choice efficiency for the three sessions conducted without landmarks (25, 28, 30) to the three sessions immediately preceding each test where the landmarks were present (24, 27, 29). Mixed design ANOVAs (Group \times Landmark presence/absence) examin-

ing choice efficiency and total session time revealed that choice efficiency was significantly better when the landmarks were present ($\bar{x} = 3.1$) than when absent ($\bar{x} = 5.4$), $F(1,10) = 12.1$. Mean time to complete the sessions when landmarks were absent ($\bar{x} = 60.3$ s) was also found to be significantly longer than the sessions when landmarks were present ($\bar{x} = 44.9$ s), $F(1,10) = 6.5$. In neither of these analyses did the main effect of Group or its interaction with the factor of Landmark presence/absence approach significance.

Landmark rearrangement

Figure 3 shows the results from the three landmark rearrangement test sessions. The total choices for each pole during these test sessions are represented by the number of rings drawn around each pole (except for those poles selected only a single time). The distribution of pole choices among the 24 poles is clearly not a random one for either group. A McNemar test (Sokal and Rohlf 1995)

for frequency data in which there is repeated testing of the same individuals confirmed that the observed frequencies of visits among the 24 poles was significantly different from chance for both the Proximal group (first test session, $Q(23) = 69.1$; second test session, $Q(23) = 55.4$; third test session, $Q(23) = 66.1$) and the Distal group (first test session, $Q(23) = 61.1$; second test session, $Q(23) = 51.9$; third test session, $Q(23) = 66.1$).

An examination of each group's pattern of choices reveals control by different aspects of the objects and the arena. The Proximal group showed a marked tendency to track the objects wherever they were moved in the arena and visit the adjacent poles (51.8% of all choices were of this type, mean number of visits per landmarked pole = 4.7; expected value = 1.5). In addition, this group showed a preference for those poles adjacent to landmarks moved to the inner set of poles in the arena (mean visits = 6.5) in comparison to the outer ring (mean visits = 3.4).

The Distal group clearly did not visit those poles that were adjacent to landmarks (3.7% of their choices were of this type, mean number of visits per pole = 0.3). Instead, this group persistently clustered its choices among the normally baited intermediate ring of eight poles (75.9% of their choices were of this type, mean number of visits per pole = 3.4). This result suggests the Distal group was partly employing the arena's circular geometry to guide their choices in these rearranged environments. Because these rats had been trained in one sense to find their food at locations "between" landmarks, we also paid attention to any visits made to poles between the rearranged landmarks. An overall examination of the five best "between" poles from all three test sessions revealed that they were chosen infrequently, and only if they also happened to be located in the intermediate ring of poles. Even in the third test, where this "betweenness" cue was strongest, the Distal group still highly preferred to choose poles located in the intermediate ring of the arena.

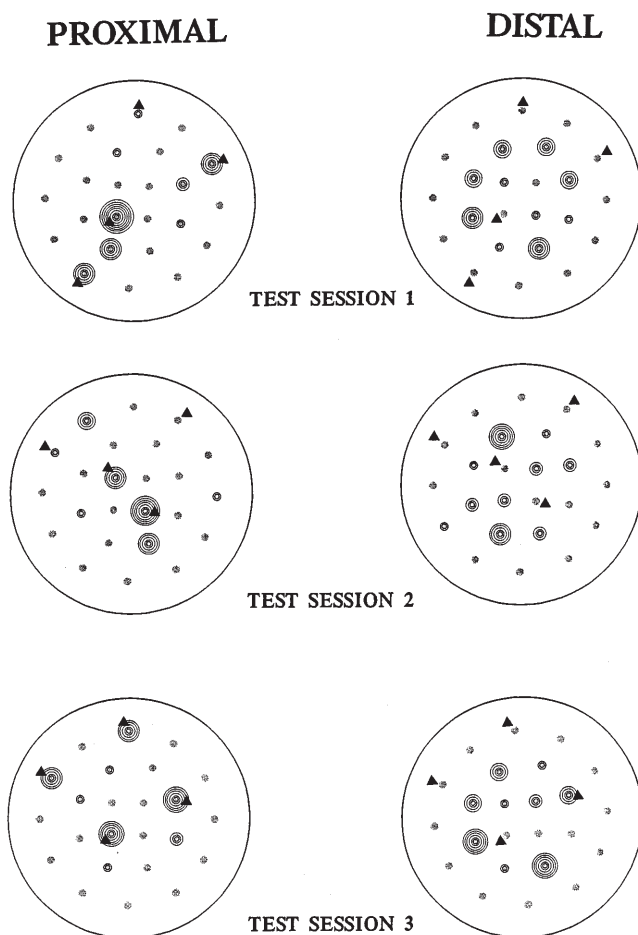


Fig. 3 Results from the three sessions of the landmark rearrangement test. The *triangles* represent the shifted locations of the landmarks. The total choices to each pole during these test sessions are represented by the *number of rings* drawn around each pole (except for those poles chosen only once)

Discussion

Important differences were found between the two groups in terms of their spatial search behavior and use of the arena and its objects as discriminative cues. Despite the manifestly identical visual appearance of the arena for each group, the latent spatial relationship between the objects and hidden goals influenced how these elements and their spatial relations were employed by the rats in their respective food searching tasks. The Proximal group very quickly solved their problem, apparently in large part by learning to directly approach the objects as if they were beacons. The Distal group learned its task more slowly than the Proximal group, although it did eventually reach a comparable level of performance (although they did take more time to complete these choices). The Distal group apparently located its food by using a combination of information derived from using the objects as spatial landmarks and the global geometry of the arena. They

also showed a discrimination of food quantity at each location that was not comparably demonstrated by the Proximal group.

The rats in the Proximal condition appeared to have used the objects as a set of spatially independent beacons, strongly tracking them about the arena as they shifted their location. This is not to say that these animals completely disregarded the global geometry of the arena. These beacons did appear to be weakly tied to some extent to the surrounding reference frame of the arena's geometry. This is suggested by this group's slightly greater tendency to choose shifted landmarks located in the center of the arena rather than the periphery (although this effect was small in comparison to the stronger global control exhibited by the Distal group). The majority of initial choices in the landmark removal tests were also directed at the intermediate ring of poles, and this possible control by global geometry in the absence of the objects may explain the still relatively efficient behavior of the rats in the removal tests. Nevertheless, when the objects/beacons were placed in direct conflict with the geometry of the arena, as in all of the rearrangement tests, it was clear that the former were by far the dominant cue, with these local stimuli attracting the rat's search behavior regardless of their global position in the arena.

The Distal group, on the other hand, clearly placed the object/landmarks within the larger spatial framework of arena, even to the point where local landmark information was overshadowed when placed in direct conflict with the global cues (rearrangement test 3; see also Cheng 1986). These results suggest the possible use of a two-step process to the Distal group's solution to finding the hidden food. The first step used the circular geometry of the arena to orient and initiate search in the spatially appropriate section of the arena, followed by the secondary use of the local landmarks to guide the final pole choices (see Brodbeck 1994; Spetch and Edwards 1987 for similar hierarchical views of spatial control). As mentioned, we did note that the Distal rats showed more orienting, rearing, and investigative behavior – generally taking less direct paths to the baited poles and pausing more often – than the Proximal group. This is reflected by the Distal group taking significantly longer than the Proximal to clear the arena. Brown and Cook (1986) found that these types of search behaviors increased in frequency and duration during the latter choices of rats tested in a 12-arm radial maze, presumably reflecting the greater difficulty of the radial maze at that point. Given the same kinds of behavior in the current setting and the slower acquisition, it suggests that more cognitive resources were required to solve the Distal than the Proximal version of the task.

Another possible source of difficulty for the Distal group may have come from a perceived instability of the landmarks within the arena. Beigler and Morris (1993, 1996) have recently demonstrated that the relative stability of landmarks is an important factor in the development of spatially controlled behavior. Because no attempt was made to disrupt the inertial navigation system of the rats

(for instance, by rotating them prior to their placement in the arena), they may have been able to sense a kind of trial-to-trial instability relative to a set of earth-based coordinates. Because the Distal group relied on the objects as spatial landmarks, rather than as non-spatial beacons, this factor might have been a greater problem for this particular condition.

The Distal rats also demonstrated a small reward size effect that was not shown by the Proximal group. The Distal group tended to retrieve the food in the numerical order of the largest to the smallest amount. Roberts and Ilersich (1989) previously found a similar reward size effect with rats when they were tested in the radial maze. The Proximal group showed no comparable knowledge regarding the locations of the different sized rewards. While these effects were small, their existence again points to the generally more complete representation of the arena and its contents shown by the Distal group.

Poucet (1993) has suggested that animals gradually build up their representations of space in a piecemeal fashion. As such, spatial behavior is initially directed by local place associations, which with experience become internalized and connected into increasingly larger and more integrated map-like structures of the environment. In many ways our two groups look like examples of each of these stages: with the Proximal group focused on a restricted local view of the objects and the Distal group developing a more integrated and richer representation of the entire environment and its component landmarks. If so, one question is: why did the Proximal group not develop a more complete description of the environment? One interesting possibility is that the immediate success provided by the beacons may have functioned to short-circuit any subsequent global integration process, perhaps in a manner similar to the development of blocking in compound stimulus conditioning paradigms (Kamin 1969). Consistent with this idea, Rodrigo et al. (1997) recently found in rats evidence for landmark blocking in the spatial domain when additional landmarks were added to an already learned Morris water maze task.

Even if the two groups engaged the same set of mechanisms in solving the task, the Proximal group's performance is inconsistent with the strong form of the global precedence hypothesis proposed by Cheng (1986) and Gallistel (1990). Instead our results are more like those of Collett et al. (1986). They found that gerbils use landmarks individually in computing distance and direction to a goal and that the most proximal landmark defines a goal's location, apparently in deference to directional information provided by multiple more distal landmarks. Only when the closer landmark was absent, or all landmarks were equidistant from the goal, did the gerbils determine search location according to the global geometry of the spatial cues. Our results suggest that even in a setting where rats are capable of complex spatial representations, they will rely on the "cognitive economy" of using simple absolute encoding strategies to solve visuo-spatial discriminations if not required to engage these more complex representations

(see Wright et al. 1989 for a similar effect in monkeys in a discrimination learning task).

Finally, it should be noted that in many respects our conditions and results are highly reminiscent of the “feature positive” effect observed in various types of discriminations (Crowell and Bernhardt 1979; Jenkins and Sainsbury 1970). This effect means that animals learn more readily to distinguish stimuli in which the critical feature is directly associated with reinforcement, rather than with non-reinforcement. Similarly, our Proximal condition (feature-positive in that the object marked poles always contained food) was learned more quickly than the Distal condition (feature-negative in that the object marked poles never contained food). Although it is often tacitly assumed in animal spatial research that landmarks only provide spatial information, this conditioning perspective suggests that spatial landmarks might also take on associative value. Thus, the proximal landmarks may not only have served as spatial beacons, but might also have taken on positive associative value due to their close proximity to food (Rescorla and Cunningham 1979). Likewise, the landmarks in the Distal condition may have taken on a negative associative value. How much any active avoidance of the landmarks affected the Distal group’s behavior cannot be determined from our tests, but the potential effects of the associative sign-tracking of visual features (e.g., Hearst and Franklin 1977) in spatial environments needs to be more systematically examined.

In conclusion these experimental outcomes indicate that the development by rats of complex, potentially map-like, representations of their surrounding environment is not an automatic outcome of spatial experience. Additional factors are involved that influence the relative priority of local and global information in spatial environments. The present study suggests that the proximity and positioning of a hidden goal to surrounding objects, landmarks, and global context is one such factor. Another is the relative stability of these landmarks to the hidden goals (Biegler and Morris 1993, 1996). Although our groups encountered identical visual environments, and in some sense identical spatial tasks, the latent geometric relations between the objects and goals had dramatically different influences on the eventual strategy used to find food in this environment. Besides their theoretical implications, these results also suggest a practical caution to the prevalent assumption in the behavioral neurosciences that popular spatial tasks, such as the water maze and radial maze, directly measure only spatial processing. Clearly that is not always the case. The finer-grain analyses of these tasks that can be provided by researchers in comparative cognition offer an important collaborative bridge to a more precise understanding of brain-behavior relations.

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References

- Biegler R, Morris RGM (1993) Landmark stability is a prerequisite for spatial but not discrimination learning. *Nature* 361: 631–634
- Biegler R, Morris RGM (1996) Landmark stability: further studies pointing to a role in spatial learning. *Q J Exp Psychol* 49B: 307–345
- Brodbeck DR (1994) Memory for spatial and local cues: a comparison of a storing and nonstoring species. *Anim Learn Behav* 22: 119–133
- Brown GS (1994) Spatial association learning by rufous hummingbirds (*Selasphorus rufus*): effects of relative spacing among stimuli. *J Comp Psychol* 108: 29–35
- Brown MF (1992) Does a cognitive map guide choices in the radial-arm maze? *J Exp Psychol Anim Behav Proc* 18: 56–66
- Brown MF, Cook RG (1986) Within-trial dynamics of radial-arm performance of rats. *Learn Motiv* 17: 190–205
- Cartwright BA, Collett TS (1983) Landmark learning in bees. *J Comp Physiol* 151: 521–543
- Cheng K (1986) A purely geometric module in rat’s spatial representation. *Cognition* 23: 149–178
- Collett TS, Cartwright BA, Smith BA (1986) Landmark learning and visuo-spatial memories in gerbils. *J Comp Physiol* 158: 835–851
- Crowell CR, Bernhardt TP (1979) The feature-positive effect and sign-tracking behavior during discrimination learning in the rat. *Anim Learn Behav* 7: 313–317
- Gallistel CR (1990) *The organization of learning*. MIT Press, Cambridge
- Greene CM, Cook RG (1997) Landmark geometry and identity controls spatial navigation in rats. *Anim Learn Behav* 25: 312–323
- Hearst E, Franklin SR (1977) Positive and negative relations between a signal and food: Approach-withdrawal behavior to the signal. *J Exp Psychol Anim Behav Proc* 3: 37–52
- Jenkins HM, Sainsbury RS (1970) Discrimination learning with the distinctive feature on positive or negative trials. In: Mostofsky D (ed) *Attention: contemporary theory and analysis*. Appleton-Century-Crofts, New York, pp 239–274
- Kamin LJ (1969) Predictability, surprise, attention, and conditioning. In: Campbell BA, Church RM (eds) *Punishment and aversive behavior*. Appleton-Century-Crofts, New York, pp 279–296
- Leonard B, McNaughton BL (1990) Spatial representation in rat: Conceptual, behavioral, and neurophysiological perspectives. In: Kesner RP, Olton DS (eds) *Neurobiology of comparative cognition*. Lawrence Erlbaum, Hillsdale, pp 363–422
- Milner AD, Goodale MA, Morton MC (1979) Visual sampling after lesions of the superior colliculus in rats. *J Comp Physiol Psychol* 93: 1015–1023
- O’Keefe J, Nadel L (1978) *The hippocampus as a cognitive map*. Clarendon, Oxford
- Olton DS, Samuelson RJ (1976) Remembrance of places past: Spatial memory in rats. *J Exp Psychol Anim Behav Proc* 2: 97–116
- Poucet B (1993) Spatial cognitive maps in animals: New hypotheses on their structure and neural mechanisms. *Psychol Rev* 100: 163–182
- Rescorla RA, Cunningham CL (1979) Spatial contiguity facilitates Pavlovian second-order conditioning. *J Exp Psychol Anim Behav Proc* 4: 152–161
- Roberts WA, Ilersich TJ (1989) Foraging in the radial maze: the role of travel time, food accessibility and the predictability of food location. *J Exp Psychol Anim Behav Proc* 15: 274–285
- Rodrigo T, Chamizo VD, McLaren IPL, Mackintosh NJ (1997) Blocking in the spatial domain. *J Exp Psychol Anim Behav Proc* 23: 110–118
- Sokal RR, Rohlf, FJ (1995) *Biometry*, 3rd edn. Freeman, New York

- Spetch M (1995) Overshadowing in landmark learning, Touchscreen studies with pigeons and humans. *J Exp Psychol Anim Behav Proc* 21:166–181
- Spetch M, Edwards C (1987) Pigeons', *Columba livia*, use of global and local cues for spatial memory. *Anim Behav* 36:293–296
- Stollnitz F (1965) Spatial variables, observing responses, and discrimination learning sets. *Psychol Rev* 72:247–261
- Suzuki S, Augerinos G, Black AH (1980) Stimulus control of spatial behavior on eight-arm radial maze in rats. *Learn Motiv* 11:1–18
- Tolman EC (1948) Cognitive maps in rats and men. *Psychol Rev* 55:189–208
- Vallortigara G, Zanforlin M, Pasti G (1990) Geometric modules in animals' spatial representations: a test with chicks (*Gallus gallus domesticus*). *J Comp Psychol* 104:248–254
- Wright AA, Cook RG, Kendrick DF (1989) Relational and absolute stimulus learning by monkeys in a memory task. *J Exp Anal Behav* 52:237–248