

BRIEF COMMUNICATION

Pigeons Encode Relative Geometry

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Pigeons were trained to search for hidden food in a rectangular environment designed to eliminate any external cues. Following training, the authors administered unreinforced test trials in which the geometric properties of the apparatus were manipulated. During tests that preserved the relative geometry but altered the absolute geometry of the environment, the pigeons continued to choose the geometrically correct corners, indicating that they encoded the relative geometry of the enclosure. When tested in a square enclosure, which distorted both the absolute and relative geometry, the pigeons randomly chose among the 4 corners, indicating that their choices were not based on cues external to the apparatus. This study provides new insight into how metric properties of an environment are encoded by pigeons.

Establishing a directional frame of reference is an essential step in many navigation and spatial search problems. Consider, for example, an animal that needs to remember the location of a goal, such as a nest or source of food. The animal may encode its distance and direction from a salient landmark, such as a tall tree, and then later use that landmark to locate the goal. Many studies have demonstrated such landmark-based searches in vertebrate and invertebrate species (see Cheng & Spetch, 1998; Collett & Zeil, 1998). However, an accurate match between a landmark-to-goal vector perceived during searching and one stored in memory requires the establishment of a stable directional frame of reference. This process is sometimes referred to as *determining heading, getting bearings, or getting oriented*.

Given that determining heading is fundamental to spatial search, it is not surprising that many animals seem well equipped to accomplish this step using various types of information. Celestial cues, such as the sun and stars, provide directional information for navigation by birds and insects, but other cues can be used as well (for reviews, see Able, 1991; Dyer, 1996). In smaller or enclosed spaces, heading may be determined by the configuration of landmarks or surface features (e.g., Suzuki, Augerinos, & Black, 1980; Kelly, Spetch, & Heth, 1998) or by the geometric shape of the environment (e.g., Cheng, 1986).

Determining heading from geometric shape is a particularly interesting process first demonstrated by Cheng (1986) in rats.

Cheng trained rats to search for food that was hidden in one corner of a rectangular enclosure. Distinctive features differentiated the corners. Rotating the rats prior to the trial disrupted inertial cues, and external room cues were blocked or masked. In a working-memory task, the rat was shown and allowed to eat a portion of food in one randomly selected corner, and was then removed. The food was then buried in the same corner, and the rat's task was to relocate it. Strong control by geometry was indicated by systematic rotational errors, in which rats confused the correct corner with the geometrically equivalent corner. In a reference memory task, food was hidden in the same corner on every trial, and the rats eventually used the features to distinguish between the geometrically equivalent corners. However, tests revealed that geometric shape dominated over features because the rats did not follow the correct feature when it was moved to a geometrically incorrect corner. Margules and Gallistel (1988) provided further evidence for the primacy of geometric cues in rats. Young children also attended to geometric shape to the exclusion of features in a disorientation task analogous to Cheng's working-memory task (Hermer & Spelke, 1994, 1996).

Pigeons (Kelly et al., 1998) and chicks (Vallortigara, Zanforlin, & Pasti, 1990) also encode geometric shape of an enclosure, but unlike rats they do not show dominance of geometric information when features and geometry are placed in conflict. Kelly et al. found that pigeons' weighting of geometry and features depended on initial experiences. Pigeons that were trained with distinctive features in the enclosure from the start of training (i.e., both features and geometry) showed primary control by the features. However, pigeons that were trained first without the features (geometry only) and then with the features added showed shared control by features and geometry.

Although species and experiential factors may alter the weighting of geometric and featural cues, it is clear that rodents, birds, and humans can use the geometric shape of an enclosed environment to determine heading. Thus, sensitivity to the geometric properties of an environment has considerable species generality. However, little is known about the mechanisms underlying the

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encoding of geometric shape or the form in which this geometric information is encoded.

Consider, for example, a case in which an animal in a rectangular environment finds food in a corner that has a 200-cm wall on the left and a 100-cm wall on the right. The geometric information could be encoded in terms of either or both of these absolute metrics. That is, when facing the goal, the animal could encode the length of the wall on its right or the wall on its left, or both. Even if only one of these absolute lengths is encoded, this information would specify the correct corner and its geometrically equivalent corner, and the information would not match that perceived at the other corners. Thus, encoding of absolute metrics, whether specified by visually perceived length of a wall or steps taken to travel along a wall, is one simple way in which geometric shape could be encoded. Another way is by attending to relative metrics (e.g., the correct corner has a longer wall on the left side than on the right side). That is, the animal might extract a shape that is independent of absolute metrics.

The question of whether geometric information is encoded as absolute or relative metrics can be addressed through size transformation tests, which preserve shape but alter absolute metrics. Of the previous studies on use of geometry for determining heading, only the Kelly et al. (1998) study with pigeons included a size transformation test. Unfortunately, this test (referred to as the *New Wall Test*) was conducted in the presence of distinctive features and did not provide a sufficiently sensitive test of whether geometric information is encoded according to absolute or relative metric properties.

On intuitive grounds, one might expect that encoding would be based on relative metrics, because such encoding requires less precision and is more flexible. Moreover, theoretical discussions of rats' encoding of geometry have assumed that metric relations, rather than absolute metrics, are encoded. For example, Gallistel (1990) assumes that relational learning underlies the rotational error shown by rats: "only the combination of a sense relation (left-right) and a uniquely metric relation (longer-shorter) renders one pair of diagonally opposite corners in a rectangle geometrically distinct from the other pair" (p. 199). However, this assumption has not been tested, and a strategy based on absolute metrics is possible given that only one size of rectangle is used in training. Moreover, one must be cautious in assuming that an animal will solve a task in the intuitively most likely fashion. Indeed, in some situations pigeons seem prone to using a seemingly more difficult strategy based on absolute information than one based on relational information. For example, in matching to sample, pigeons often do not learn a relational "same-as" rule (e.g., Wilson, Mackintosh, & Boakes, 1985a), although they can do so under certain conditions (Wright, 1997; Wright, Cook, Rivera, Sands, & Delius, 1988). Pearce (1991) found little evidence that pigeons could categorize stimuli in terms of whether bars were of similar or different heights, and he suggested that "when for humans there exists an obvious relational solution to a problem, pigeons are extremely reluctant to adopt it" (p. 157). Similarly, Wills and Mackintosh (1999) suggested that one interpretation of the previous result is that "pigeons are remarkably insensitive to the relationships between stimuli" (p. 32). Although they found some evidence of a relational process in pigeons' luminance discriminations, they suggested that it could reflect lower level sensory

contrast and does not necessarily imply learning of a conceptual relation (e.g., "brighter than").

Studies of rule learning in landmark-based spatial search have revealed another situation in which pigeons, and at least some other species, seem surprisingly likely to use absolute information rather than learning what seems to humans an obvious and simpler relational rule. When trained to find a hidden goal in the middle of an array of identical landmarks, adult humans learn an abstract middle rule, as revealed by expansion tests in which the landmarks are spread farther apart (Spetch, Cheng, & MacDonald, 1996; Spetch et al., 1997). Adult humans also learn a relational rule when the goal is located between and below two identical landmarks (Spetch et al., 1996). By contrast, pigeons (Spetch et al., 1996, 1997) and gerbils (Collett, Cartwright, & Smith, 1986) trained with similar landmark arrangements did not learn abstract relational rules but instead learned absolute spatial relationships between individual landmarks and the goal. Squirrel monkeys (Sutton, Olthof, & Roberts, 2000) also failed to learn a relative middle rule in a similar task.

However, a few results from other species have suggested some control by relative spatial information. Kamil and Jones (2000) trained Clark's nutcrackers to find food that was hidden at a fixed relative location from two landmarks that varied across trials in their interlandmark distance. The food was located at the midpoint between the landmarks or at a fixed distance or direction away from the landmarks. The nutcrackers learned a geometric rule as evidence by the ability to search at the appropriate relative location on transfer tests with new interlandmark distances. The contrast between these results and those found for pigeons could reflect training or species differences. Both are reasonable candidates because varying interlandmark distance provides training with multiple exemplars, which is known to enhance relational learning (Wright et al., 1988), and because differences in relational learning between Corvids and pigeons have been found in other tasks (Wilson, Mackintosh, & Boakes, 1985b). In another recent study, chicks were trained to find food hidden in the center of a square enclosed arena (Tommasi & Vallortigara, 2000). Transformations of the size of the arena revealed that the chicks learned both the relative and the absolute distance from the arena walls. To our knowledge, no other species have yet been tested on this task. Finally, place cell firing studies in rats have suggested strong sensitivity to absolute distances from walls and some control by relative distances (O'Keefe & Burgess, 1996). Whether these results are general across species and how they translate into search behavior remains to be determined.

None of the aforementioned rule-learning studies focused on use of absolute versus relative geometry for determining heading in the environment. In the landmark-based search studies, numerous external cues were available for orientating within the environment, and these were not controlled or investigated. In the study with chicks, orientation within the environment was not required and indeed was not possible because there were no directional cues provided by the shape or features of the enclosure, and external cues were blocked. In the study on place cell firing, cues external to the arena appeared to exert some directional control. We are not aware of any studies, in any species, that have addressed the question of whether animals attend to relative or absolute metrics when determining heading exclusively from the geometric shape of their environment.

Accordingly, we trained pigeons to locate a single reinforced corner in a rectangular enclosure with identical features at all corners. Steps were taken to eliminate inertial and external cues so that geometric shape of the enclosure was the only available cue. Once the pigeons learned the geometry, as evidenced by preferentially searching in the geometrically correct corners, the size or shape of the enclosure was altered on unreinforced test trials. If the pigeons had encoded only absolute geometry, then resizing the apparatus should have disrupted accurate search behavior. However, if the pigeons extracted the relative geometric properties of the enclosure, then they should have continued to search in geometrically correct corners despite resizing of the apparatus, but they should have been disrupted if the shape was changed.

Method

Subjects

Three Silver King pigeons (*Columba livia*), all experimentally naive in open field searching tasks, served as subjects. The birds were housed in large individual cages under a 12-hr light–dark cycle (with light onset at 6 a.m.). We maintained birds at approximately 85% of their free-feeding weights by feeding them maple peas during experimental sessions and Key Tee pigeon pellets after sessions. Water and grit were available ad lib in the home cages.

Apparatus

The apparatus was a uniformly white, large rectangular enclosure constructed to control for cue availability (similar to Kelly et al., 1998). The walls were made of 5-cm-thick Styrofoam covered with opaque white plastic. Thick white cloth sheets were used for the upper walls and for the suspended ceiling. Specific measurements of the entire apparatus are provided in Figure 1. Approximately 5 cm of aspen chip bedding covered the floor. A video camera was centered above the apparatus and was hidden behind the suspended ceiling so that only the lens of the camera was visible. Four identical tin containers (diameter, 8.5 cm; height, 3.5 cm) were located 20 cm from each corner of the apparatus and were secured to the floor with Velcro. To ensure that each corner was salient, identical glass bottles (height, 25 cm; width, 14 cm) were situated behind each container. The bottles were filled with yellow construction paper and had a brown strip around the middle. White noise was played through two speakers (randomly located along the four walls) to mask exterior noises.

General Procedures

Experimental sessions consisted of 10 trials and were conducted once per day, 5 days per week at approximately the same time each day for a given bird. Each pigeon was carried to the experimental room in an opaque plastic container and placed within one of two completely enclosed metal holding cages that were located in different ends of the testing room. The selected holding cage randomly alternated across trials. Before each trial, the pigeon was rotated while inside the holding cage for 1 min at approximately 12–14 rpm to eliminate use of inertial cues. The pigeon was removed from the metal cage into the plastic container and then placed into the apparatus according to a predetermined random entry position (one per wall).

The corner that provided food was constant across trials for a given pigeon but differed across the 3 pigeons. On each trial, the pigeon was given a maximum of 5 min to locate the reinforced tin or peck through the paper towel covering of any two tins. The first peck directed to any tin that broke the paper-towel covering was considered the choice on each trial.

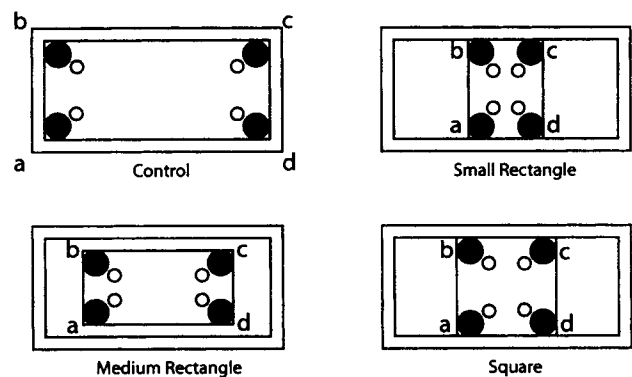
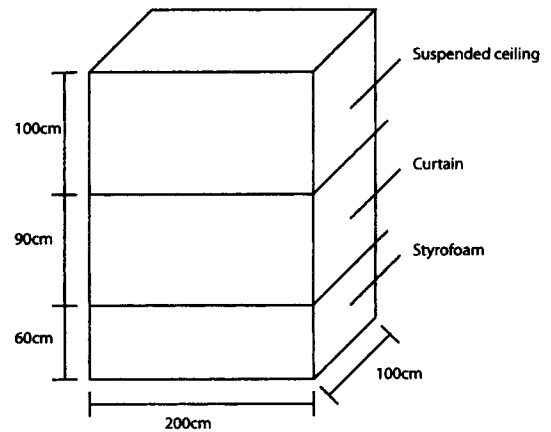


Figure 1. The top illustration shows the dimensions of the experimental apparatus. The bottom illustrations show an overhead view of the experimental setup for the control and test sessions. The darkened circles represent the landmark bottles, and the open circles represent the food containers. Letters a–d are labels for the four corners.

Once the pigeon pecked at two of the tins or 5 min elapsed, the room lights were extinguished, and the pigeon was removed from the apparatus and placed in a holding cage. The lights were then illuminated, the apparatus was prepared for a new trial, and the bird was rotated.

Between trials, all debris was removed from the bedding, and the four identical tins and bottles behind each tin were randomly rearranged. Periodically between sessions, the two speakers, the walls of the enclosure, the curtains, and the bedding were rearranged or replaced. These procedures were designed to eliminate or disrupt use of any subtle cues that might have provided nongeometric information.

Shaping Procedures

While in their home cages, pigeons were provided with tin containers filled with grit and a few maple peas. Once the pigeons were quickly eating from the containers, a piece of paper-towel covering was placed over the top and secured with an elastic band. The pigeons were required to peck through the paper towel to gain access to the food. Once the pigeons were readily pecking through the paper towel, shaping in the experimental apparatus began.

Experimental training was divided into five stages to progressively acclimatize the bird to the novel surroundings and train for accurate searching behavior. In the first stage, a single uncovered tin with four maple peas was placed in the positive corner. The pigeon was required to

approach and eat from the tin within 5 min. If the pigeon did not eat within the allotted time, it was removed from the apparatus. Once the pigeon successfully ate from the tin within the time limit on all 10 trials, Shaping 2 began. Shaping 2 was identical to Phase 1 except that identical-looking but empty tins were placed in each of the remaining three corners. If the pigeon ate from the reinforced tin within 5 min on each of the 10 trials, it was moved to Shaping 3. In Shaping 3, all of the tins were covered with paper towel, and the pigeon was required to peck through the paper-towel covering in order to obtain the hidden food. Successful completion of Shaping 3 required that the pigeon meet the requirements of Shaping 2 while maintaining 80% accurate choice responding. Because no cues were present to discriminate the positive corner from its geometrically equivalent corner, choices of the two geometrically equivalent corners were scored as correct choices in this accuracy calculation.

The fourth and fifth shaping phases were designed to prepare the birds for a reduction in the overall amount of reinforcement available during a session. In Shaping 4, 3 of the 10 trials were nonreinforced, and in Shaping 5, 5 of the 10 trials were nonreinforced. The criteria for successful completion of these phases were identical to those in Shaping 3 except that completion of Shaping 5 required that the pigeon maintain 80% accuracy over 2 consecutive days. Testing began upon completion of Shaping 5.

Testing

Three tests, which altered the structure of the experimental apparatus, were administered to determine whether pigeons were using the absolute or the relative geometry of the enclosure to locate the correct corner. All test and control trials were nonreinforced to eliminate any food-related cues. Control trials were visually identical to baseline trials but were nonreinforced. On test trials, the enclosure was altered to change the size or shape.

The control and three types of test trials occurred in mixed order and were interspersed randomly among reinforced baseline trials within each test session. Control and test trials were presented on randomly selected trials within each session with two constraints: a) they never occurred on the first trial and b) they never occurred on two consecutive trials. Each experimental session contained a maximum of two control trials and three test trials. To maintain accurate responding, some experimental sessions contained only one control trial and two randomly selected test trials.

Testing continued until each bird had completed a minimum of 68 control trials (1 bird received 72) and 18 trials of each test type. Occasionally a bird would fail to make a choice within the 5-min period on a test or control trial. When this happened, the trial was repeated on a later day. If accuracy during baseline trials of a session fell below 80%, or if a bird failed to complete any of the trials within the 5-min period, the bird was retrained for a minimum of 2 days following the criteria outlined for Shaping 5. One bird received a total of 12 retraining sessions, and another received 14 retraining sessions to maintain accuracy. Partway through testing, the experiment was interrupted for several days and a new researcher began testing the birds when the experiment resumed. Therefore, each bird was retrained to criterion with the Shaping 5 procedures before testing resumed. This required a range of 3 to 16 retraining sessions for the three birds.

The *Medium Rectangle Test* was a size transformation in which a replication of the experimental apparatus was constructed from the same material as the training apparatus but with length and width two thirds the size of the original (length 133 cm, width 67.7 cm; see Figure 1). This new apparatus was centered in the middle of the training apparatus. This medium rectangle perfectly preserved the relative geometry of the training enclosure, but the length of both the long and the short walls were changed. Moreover, length of the long wall of the medium rectangle (133 cm) was more similar in absolute length to the short wall (100 cm) than to the long wall (200 cm) of the original enclosure. Thus, search behavior based on absolute metrics should have been completely disrupted by this manipulation.

The *Small Rectangle Test* was a more drastic size transformation in which the short walls of the enclosure now became the longer walls. For this test, two identical walls were inserted 50 cm apart and parallel to the two short walls of the training apparatus, creating a new, much smaller enclosure (length 100 cm \times width 50 cm; see Figure 1).

The *Square Test* was designed to ensure that accurate choice of the geometrically correct corners did in fact depend on the geometric shape of the enclosure. The square test altered the shape of the enclosure and made all walls equidistant (see Figure 1). Two identical walls were inserted 100 cm apart and parallel to the two short walls. Thus, in the Square Test, all of the walls were identical to the short walls of the training apparatus and none of the corners could be distinguished on the basis of geometry. Thus, the birds should have chosen randomly whether they had encoded relative or absolute geometry.

During both size transformation tests, accuracy was scored according to relative geometry. For example, for a bird with *a* as the positive corner, *a* and *c* would be scored as correct choices on Control and Medium Rectangle Tests, whereas *b* and *d* would be scored as correct on Small Rectangle Tests (see Figure 1). On Square Tests, accuracy was scored according to the orientation of the corners in the test room. That is, *a* and *c* would be scored correct for a bird that had *a* as the positive corner. Choices were recorded manually during the sessions, and all control and test trials were videotaped. The video tapes were independently rescored for corner of first-choice peck by the researcher and by a student naive to the experimental predictions. No discrepancies were found.

Results

All birds progressed at a reasonable rate through the shaping procedures. Two birds required a total of 12 shaping sessions, and 1 bird required a total of 22 shaping sessions to complete all five shaping phases.

The overall pattern of test results indicated that the birds had encoded relative geometry. Figure 2 shows the overall accuracy in choosing the corners that were correct according to relative geometry on control trials and on each of the transformation tests. As expected, accuracy was very high on control trials, with almost all choices being made to the two geometrically correct corners. Accuracy remained high on the Medium Rectangle Test, in which relative geometry was preserved but absolute geometry was distorted. Accuracy decreased on the Small Rectangle Test and fell to

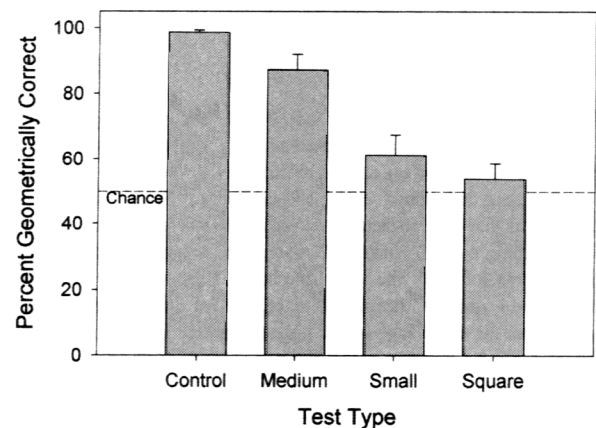


Figure 2. The mean percentage of responses to the geometrically correct corners are plotted for the control and three test conditions. Chance level is 50%.

chance on the Square Test. A repeated measures analysis of variance with test type as the factor revealed a significant effect of test type on accuracy, $F(3, 6) = 20.7, p < .001$. Newman-Keuls post hoc comparisons showed only the following differences to be significant: control versus small rectangle, control versus square, and medium rectangle versus square (all $ps < .01$).

Three types of evidence confirmed that the accurate choices on Control and Medium Rectangle Tests were controlled by geometry rather than extraneous external or internal cues associated with the positive corner. First, on Square Tests, which removed geometry, the birds chose randomly and did not preferentially choose the corner that was oriented the same way in the room as the positive corner during training. Specifically, the mean proportion of choices of the positively oriented corner was .22, which is not significantly different from chance level of .25, $t(2) = -0.43, p > .10$. Second, on the Control and Medium Rectangle Tests, the birds were not significantly more likely to choose the positive corner than the geometrically equivalent corner. The proportion of geometrically correct choices that were to the positive corner was not significantly above .5 for either the Control Tests, $M = 0.621, t(2) = 1.86, p > .10$, or the Medium Rectangle Tests, $M = 0.493, t(2) = -0.17, p > .10$. The third and perhaps most convincing piece of evidence is provided by an analysis of choices to the three noncorrect corners. If extraneous cues rather than geometry controlled choice of the positive corner, one would expect that incorrect choices would be randomly distributed among the three remaining corners, or might even favor the corner that is closest to the correct one. Therefore, we excluded choices of the positive corner and analyzed choices made to the remaining three corners. The proportion of choices made to the corner opposite to the correct one (i.e., the geometrically equivalent one) was significantly above chance (.33) during both the Control Tests, $M = 0.968, t(2) = 35.34, p < .001$, and the Medium Rectangle Tests, $M = 0.773, t(2) = 4.94, p < .05$. By contrast, a similar analysis revealed that on Square Tests, choice of the corner opposite to the positive one was not significantly above chance, $M = 0.400, t(2) = 1.13, p > .10$.

For the Small Rectangle Tests, the corners that were correct according to relative geometry were incorrect according to both absolute geometry and any extraneous cues associated with the positive corner. Although 2 birds made more choices to corners that were correct according to relative geometry, the third bird chose randomly on this test. Consequently, the mean proportion of choices of the corners that were correct according to relative geometry (.61) was not significantly higher than .5, $t(2) = 1.73, p > .10$.

Discussion

The pigeons in this experiment learned to locate hidden food on the basis of the geometric properties of an enclosed arena. When the size of the enclosure was reduced such that the absolute length of the long wall was made closer to that of the short wall in training (i.e., the Medium Rectangle Test), the birds continued to search in corners that were correct according to relative geometry. When the enclosure was made equilateral (i.e., the Square Test), the birds responded randomly, indicating that they had not encoded cues external to the testing apparatus but rather were relying on the geometry of the environment. Indeed, the lack of any significant

difference between the proportion of responses to the two geometrically correct corners and the significant preference for the geometrically equivalent noncorrect corner over the other noncorrect corners supports this conclusion.

The lower accuracy in choosing the geometrically correct corners during the Small Rectangle Test may suggest a qualification of the conclusion that encoding was based on relative rather than absolute geometry. However, we suspect that the lower accuracy is instead a reflection of performance problems in the very small search space. During test trials with the small rectangle, the birds frequently chose the tin container most near their point of entry.

The encoding of relative geometry in this task is particularly interesting for several reasons. Encoding of geometry in terms of relative metrics meant that the birds were sensitive to the relative lengths of the walls (e.g., at the correct corner, the wall on the left was longer than the wall on the right). Our study therefore demonstrates an instance of relational learning that occurred despite training with only a single exemplar (i.e., only one size of enclosure was used during training). This is interesting given the literature suggesting that pigeons are often insensitive to relational cues or favor strategies based on absolute learning. Our results are also surprising given the previous finding that pigeons encode landmark arrays in an absolute rather than a relative fashion (Spetch et al., 1996, 1997). Finally, our results provide empirical support for the assumption that geometric encoding is based on metric relations (Gallistel, 1990).

The contrast between our finding that pigeons encode geometry in terms of relative metrics and our previous findings that pigeons encode landmark arrays in terms of absolute metrics suggests that the form of the encoding may depend on the nature of the spatial information encoded. In the present study, pigeons encoded geometric information to orient themselves in the environment. All extraneous cues were removed, so that the directional heading could come only from the geometric shape. In previous landmark configuration studies (Spetch et al., 1996, 1997), many extraneous cues were present that could be used to establish a stable direction frame of reference. The landmark array was translated within the search space so that these external cues could be used for heading but could not be used for goal localization. However, the stable frame of reference allowed the learning of vectors from landmarks. One possibility, therefore, is that absolute metrics are typically encoded when using local landmarks to pinpoint a goal in a well-oriented search space, whereas relative metrics are encoded when using geometric shape to determine heading. Encoding of relative geometry to establish heading might be favored because it provides a flexible means of orienting within a search space regardless of the distance one is from the surfaces that make up the geometry. A strategy based on absolute metrics may be less efficient because the animal might need to travel to each corner to determine whether the absolute metrics match those stored in memory. On the other hand, absolute distance from local landmarks that are used to pinpoint a goal is likely to be important in many natural search situations.

Our results are also interesting in relation to the recent studies in which chicks found food in the center of an enclosed environment (Tommasi, Vallortigara, & Zanforlin, 1997; Tommasi & Vallortigara, 2000). In those studies, as in the present one, there were no external cues and no local landmarks that could be used to pinpoint the goal. On size transformation tests, the chicks spent a consid-

erable portion of time searching at the center of the altered environment, suggesting that they had encoded the relative distance from the walls. Unlike the present study, however, this encoding of the center did not require any directional determination. There was no need to, and no means of, orienting within the search space. Furthermore, searching in the center could be based on a simple rule of searching as far as possible from a wall. The center of the arena satisfies this rule for all walls, regardless of size. Thus, it is not clear whether the relative center rule learned by the chicks entailed a relational, comparison process.

In summary, our results show that pigeons encode relative metrics when using environmental geometry to determine heading. When the size of the environment was reduced but the relative geometric relations between the walls of the environment were maintained, the pigeons continued to distribute their choices among the two geometrically correct corners. This result indicates that the pigeons had extracted the relative geometric shape of the environment rather than encoding only the absolute metrics. The ability to encode the environmental shape using relative geometry may provide pigeons with a more flexible search mechanism than relying on the absolute metrics alone.

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