BRIEF COMMUNICATION

Searching in the Center: Pigeons (*Columba livia*) Encode Relative Distance From Walls of an Enclosure

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Pigeons (*Columba livia*) searched for food hidden in the center of a square enclosure. On occasional tests without food, the enclosure was (a) unchanged from training (control tests), (b) moved to different corners of the testing room (corner tests), or (c) doubled in size (expansion tests). The birds showed localized search in the center of the enclosure on control and corner tests. On expansion tests, some birds searched near the center of the enclosure, suggesting relative-distance encoding. Other birds searched at locations that maintained the training distance from walls, suggesting absolute-distance encoding. These results are consistent with previous studies on chicks (*Gallus gallus*) in similar enclosures and contrast with previous results on pigeons' responses to expansions of discrete landmark arrays.

The ability to remember places is important in everyday life for humans and other animals. Many of our daily routines, such as driving to work or walking to the store, depend on memory for locations. Inaccurate place memory, such as forgetting where we left our keys, can lead to frustration and inefficient behavior. For many animals, everyday survival can depend on the ability to remember where home is, where water is located, or where they have stored food.

Research has revealed various ways in which animals remember and locate a goal, including landmark-based search and orientation based on environmental geometry (see Cheng & Spetch, 1998). Several recent studies on landmark-based and geometry-based place finding have explored whether spatial search is based on absolute or relative spatial relations. An example of searching based on an absolute spatial relation would be learning that a goal is a particular absolute distance and/or direction from a landmark or wall. By contrast, when searching is based on relative spatial relations, the goal location is defined in terms of a set of landmarks or walls, and information from these spatial cues is used jointly in searching for the goal. Relative encoding is often described in terms of "rules." An example of relative encoding is learning a "middle rule" in which the goal is in the middle of a landmark array. With such rules, the spatial information is abstracted away from absolute metrics.

Evidence for use of absolute metrics has come from several studies in which a goal was hidden at a fixed location relative to an array of landmarks. For example, Collett, Cartwright, and Smith (1986) trained gerbils to find a goal that was hidden midway between and at a fixed distance south of two identical landmarks. The landmark array was moved within the search space across trials so that other cues could not indicate the goal location. Encoding of absolute metrics was indicated by expansion tests in which the landmarks were moved farther apart: Gerbils concentrated their search at two locations defined by the training vector from each individual landmark. Spetch, Cheng, and MacDonald (1996) found similar results for pigeons in a touch screen task. Pigeons also showed absolute encoding when the goal was in the center of a square array of four identical landmarks, both on the touch screen (Spetch et al., 1996) and the laboratory floor (Spetch et al., 1997). On array expansion tests, pigeons searched at locations that maintained the approximate training vector from individual landmarks. They showed no tendency to use a relative rule and search in the middle of the array. Squirrel monkeys (Sutton, Olthof, & Roberts, 2000) as well as marmoset monkeys and human children (MacDonald, Spetch, Kelly, & Cheng, 2003) also showed little or no evidence of using relative metrics. After learning to find a reward in the center of four identical landmarks, neither the monkeys nor the human children showed a consistent tendency to search in the center when the landmark array was expanded.

By contrast, adult humans showed almost exclusive use of relative spatial relationships when trained with similar landmark arrays (Spetch et al., 1996, 1997). On expansion tests, adult humans adjusted their distance from each landmark so as to maintain the same relative location to the entire array (e.g., to search in the center of the four-landmark array).

Clark's nutcrackers have also been shown to use relative rules (Kamil & Jones, 1997, 2000) when trained to find food based on

relative distances or bearings from two landmarks. The distance between the landmarks varied so that the birds could not solve the task on the basis of absolute landmark-to-goal relationships, but the goal could be found on the basis of a relative rule such as "midway between" the landmarks. The nutcrackers acquired relative rules and transferred to novel interlandmark distances. Although these findings initially suggested a qualitative difference in encoding processes between pigeons and nutcrackers, subsequent research has indicated that the differences are largely quantitative and that methodological factors (i.e., single- vs. multiple-exemplar training) play a large role. Pigeons that were given the same multiple-exemplar training with varying interlandmark distances also eventually acquired the relative-rule task, although they were less accurate than the nutcrackers (Jones, Antoniadis, Shettleworth, & Kamil, 2002; Spetch, Rust, Kamil, & Jones, 2003). Thus, use of a relative rule for landmark-based search is possible for pigeons but seems to be neither a preferred nor an easy strategy.

It is interesting to note that when nutcrackers were trained with fixed interlandmark distances to locate the center of a four-landmark array similar to that used by Spetch et al. (1997), the nutcrackers showed reliance on an absolute strategy during landmark expansion tests (Kippenbrock, Kelly, Templeton, & Kamil, 2003). Therefore, nutcrackers, like pigeons, appear to favor a strategy based on absolute metrics when given single-exemplar training.

Encoding of absolute or relative spatial information has also been investigated for geometry-based search. Many species use the geometric shape of a rectangular enclosure for directional orientation (e.g., rats: Cheng, 1986; humans adults and children: Hermer & Spelke, 1996; chicks: Vallortigara, Zanforlin, & Pasti, 1990; pigeons: Kelly, Spetch, & Heth, 1998; and fish: Sovrano, Bisazza, & Vallortigara, 2002). In these studies, the task is to remember which corner contains a reward. Evidence for use of geometry is provided by frequent "rotational errors" of choosing the opposite but geometrically equivalent corner. Kelly and Spetch (2001) trained pigeons in a rectangular enclosure and then tested them with transformations of scale (smaller rectangle) and shape (square) of the enclosure. Significant transfer was found to the smaller enclosure but not to the square enclosure, indicating encoding of geometry that was based at least partly on relative metrics.

Encoding of relative metrics was also found in chicks that were trained to find food buried in the center of a square enclosure (Tommasi & Vallortigara, 2000; Tommasi, Vallortigara, & Zanforlin, 1997). When tested in expanded enclosures, the chicks searched both at the center and at the absolute training distance from the walls. The center-directed searching by chicks contrasts with the lack of any tendency to search in the center of expanded landmark arrays by pigeons, gerbils, and monkeys. However, given that pigeons show relative encoding of the geometric shape of an enclosure, we hypothesize that the contrasting results likely reflect stimulus factors rather than species differences. Specifically, whereas discrete landmarks may encourage the learning of absolute vectors, the continuous nature of geometric surfaces may promote attention to relative metrics. If so, then pigeons should respond like chicks and show relative encoding of distance from the walls of an enclosure.

Method

Subjects

Six adult silver king pigeons (*Columba livia*) served as subjects. None of the birds had previous experience in searching for food within an enclosed arena. Birds 1, 2, and 4 had previous experience in searching for food in an open-field task with discrete landmarks; Bird 5 had experience in touch screen spatial tasks based on geometric shape; and Bird 6 had experience in an operant object-recognition task. Bird 3 was experimentally naive. The birds were kept at approximately 85% of their free-feeding weight by maple peas obtained during experimental sessions and supplemental feedings of pigeon pellets. They were housed in large individual cages on a 12-hr light–dark schedule (lights on at 6 a.m.).

Apparatus

The experimental arenas were located within a 2.9 × 3.3-m laboratory room. The training apparatus was a 70 × 70-cm wooden arena (height = 60 cm). The expanded test arena measured 140 × 140 cm and was 60 cm high. The walls of both arenas were uniformly painted white. Horizontally aligned fluorescent lights (46.5 cm long) were centered across the top (inside) of each wall. Ten layers of mesh fabric, sewn together with elastic, covered the arenas to provide an effective one-way screen when the lights inside the arena were on and the room lights were off. The elastic allowed a corner to be easily lifted for placement of the bird in the arena. The arena floor was covered with approximately 5 cm of wood chips. The food dish was a rectangular plastic (10 × 5 × 2-cm) container with a 2 × 2-cm hole that held maple peas. Behavior was recorded from a video camera mounted above the apparatus. White noise played through speakers in the room served to mask extraneous noises. Two opaque rotation boxes were located in opposite corners of the room.

Training

Pigeons were pretrained in their home cages to eat from the experimental food dish and to sweep away wood chips to uncover the maple peas. The birds then received one 10-trial session per day. Birds were transported to the experimental room in an opaque plastic container. Before each trial, the bird was disoriented by slow rotation (12 to 18 rotations per minute) in a randomly selected rotation box. The bird was then moved directly from the rotation box back into the opaque plastic transport container and placed into a randomly chosen corner of the arena. The arena lights were then turned on to start the trial.

The food container was located in the center of the arena. After the bird located and ate the food, the arena lights were extinguished and the bird was removed and placed into a rotation box. Before rotating the bird for the next trial, the experimenter refilled the food container and redistributed the wood chips to eliminate visual or olfactory cues. On initial trials, the food dish was completely uncovered. Once the bird ate within 30 s on two consecutive trials, the container was gradually buried over successive trials until it was completely hidden under 2–3 cm of wood chips.

Once a bird found the completely buried food within 30 s on all trials for two successive sessions, two nonreinforced trials were interspersed among eight reinforced trials in each session. On nonreinforced trials, the food dish was absent, and the bird was left in the apparatus for 1 min. Training continued until the bird met the following criteria for two successive sessions: (a) found food within 30 s on all reinforced trials and (b) searched in a 10 × 10-cm area in the center of the arena within 30 s on both of the unreinforced trials. We defined search responses as movement of the beak that resulted in visible displacement of wood chips.

Testing

Testing sessions contained eight reinforced training trials, one control trial in which the apparatus was identical to training, and one test trial. On

control and test trials, the food was absent, and the birds were videotaped for 4 min.

Two types of tests were presented. On corner tests, the training arena was moved to different corners of the larger test room to rule out the use of cues external to the enclosure. Expansion tests were conducted in a larger arena (140 × 140 cm), which was centered in the same room location that the smaller arena occupied on control tests. Each bird received eight control tests, four corner tests (one in each corner), and four expansion tests.

Data Analysis

Videotaped trials were played on a TV screen, and the location of each search response was marked on a transparent grid. For scoring, we followed the procedures used by Tommasi and Vallortigara (2000) so that our results could be easily compared with those reported for chicks (*Gallus gallus*). We partitioned the surface of the training arena into a 5 × 5 grid of cells that were 14 cm per side. For the expanded arena, we partitioned the surface into 15.56 × 15.56-cm cells forming a 9 × 9 grid.

The data were summarized in five ways: (a) overall search distributions, (b) individual search means, (c) distance of searches from center, (d) individual peak places of searching, and (e) proportion of searching in areas defined by the center or absolute distance from walls on the expansion tests. The first three ways of summarizing the data followed procedures used by Tommasi and Vallortigara (2000). In keeping with their methods, we used only the data from the first control trial, corner test, and expansion test for each bird. These summaries allowed a comparison of our results with those found for chicks. For the fourth and fifth data summaries, we used the data from all control and test trials. The fourth summary (peak place of searching) allowed a comparison of our results with previous results for pigeons on landmark expansion tests. For this summary, we followed the procedures used in the previous studies on landmark-based search by pigeons and humans (e.g., Spetch et al., 1996, 1997). The final summary allowed us to test whether the proportion of searching in center region or regions that maintained the training distance from walls was significantly above that expected by chance.

To determine the overall search distributions, we calculated and plotted the proportion of searches made in each grid area. For each grid cell, the proportion of search pecks in that cell made by each individual bird was calculated. These proportions were then averaged across birds. The range of mean values across cells (spanning from zero to the maximum for each type of test) was then partitioned into 10 intervals, and each cell was assigned a size that represented Levels 1–10 on the interval scale. To determine individual search means, we calculated the mean location of search pecks for individual birds in the two axes of the search space as well as the standard errors of these search pecks. To determine distance of searches from center, we measured the straight-line distance of each search peck to the center of the arena.

We calculated the individual peak place of searching using the iterated median procedure described by Cheng (1989). The iterated median procedure determines the middle of the highest region in a distribution. For each bird, we summed the search responses in each row and in each column of the scoring grid, using the data from all tests of a given type. The median of each of the two distributions was then determined. The median calculation was then iterated over the range in which the first median was centered. For example, if the first median was calculated over the range of 1–18 and the median was 6, then the next median calculation would include only units 1–11. This process was repeated until two consecutive calculations resulted in medians that differed by no more than 0.05 of a unit. The last value is taken to be the peak place.

Finally, we calculated the proportion of search pecks that fell in the center region and a region that would maintain the absolute training distance from walls and then conducted chi-square tests to determine whether searching in these regions differed from chance. For the center region, we used a 25 × 25-cm square area at the center of the search space. This area makes up 3.2% of the total arena; so, the expected proportion of searches in this region on the basis of random responding is .032. The absolute distance from the walls to the center in training was 35 cm. To define a region on the basis of this absolute distance, we specified a frame 25 cm wide centered at 35 cm from the wall. This frame makes up 35.7% of the arena; so, the proportion of searches in this region expected by chance is .357.

Results

In both the control and corner tests, the pigeons concentrated their search in the center of the arena. In the expanded arena, the pigeons showed more scattered searching, but a substantial portion of the searching was in or near the center area.

The overall search distribution data are shown in Figure 1A. The left graphs show the proportion of searches in each grid location
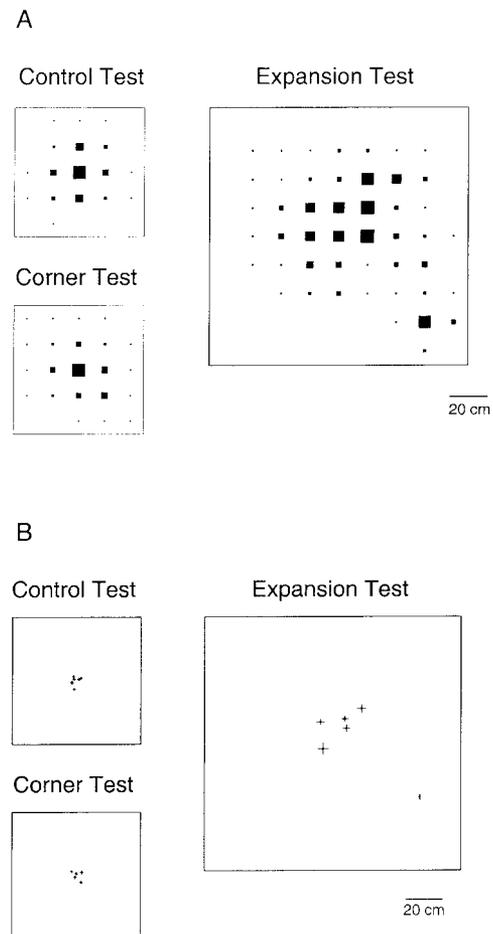

Figure 1. A: Proportion of searches in each area of the control, corner, and expanded enclosures, for the first test of each type averaged across the 6 birds. Larger squares indicate a higher proportion of searching behavior in that location. B: Mean and standard error of the mean of search pecks for each individual bird during the first control test, corner test, and expansion test trial. The center of each symbol indicates the mean location, and the lengths of the lines indicate the standard error in each axis of the search space.

during the control and corner tests, and the right graph shows the proportions on the expansion tests. These data are averaged across the 6 pigeons. These overall proportions show high proportions of searching in the center on control and corner tests. On expansion tests, the birds showed a high proportion of searching in locations in and near the center as well as some searching near two of the corners.

Figure 1B provides an indication of the search behavior of each individual bird during the first test session of each type. Each symbol shows the mean location of all search pecks for a bird, with the length of the lines indicating the standard error of the mean in each axis of the search space. The mean search location was near the center for 5 of the birds and nearer to a corner for 1 bird.

The mean distances of search pecks from the center of the arena on the first control test, corner test, and expansion test were 11.43 cm ($SEM = 0.71$), 11.74 cm ($SEM = 0.02$), and 32.23 cm ($SEM = 5.69$), respectively. The values are strikingly similar to the distances reported by Tommasi and Vallortigara (2000) for chicks on control ($M = 9.61$ cm, $SEM = 0.83$) and expansion tests ($M = 33.92$ cm, $SEM = 4.27$).

Figure 2 shows the calculated peak place of searching for each bird on control, corner, and expansion tests. These peak places are based on search behavior during all test trials of each type (eight trials for control tests, four trials for corner tests, and four trials for expansion tests). The peak places were very close to the center on control and corner tests for all birds. In the expanded enclosure, the peak place of searching was near the center for most birds but closer to a wall for 1 bird.

To determine whether individual birds were significantly more likely to search at the center or absolute distance from walls than expected on the basis of random search, we conducted chi-square tests to compare the observed proportion of searches that fell in the center or absolute distance regions with that expected by chance. Because two tests were conducted on the data from each bird, we set alpha to .025. The proportions of search pecks in the center for the 6 birds were .198, .171, .152, .044, .057, and .007. Chi-square tests ($df = 1$) indicated that the proportions for 4 birds (Birds 1, 2, 3, and 5) were significantly higher than the expected proportion (.032) based on random responding. The proportions of search

pecks in the region defined by the absolute distance were .358, .410, .416, .676, .742, and .550. The proportions for Birds 3, 4, 5, and 6 were significantly higher than the expected proportion (.357) based on random responding. Thus, Birds 1 and 2 showed significant proportions of searching in the center region only, Birds 4 and 6 in the absolute region only, and Birds 3 and 5 in both regions.

Discussion

The pigeons learned to accurately find food in the center of the training arena. They also localized their search in the center of the arena on corner tests, ruling out the use of cues external to the arena. On tests in the expanded enclosure, the pigeons showed less localized searching, but all birds searched more in the center region or at the absolute distance from the walls than expected by chance.

The pigeons' center-directed searching on expansion tests is congruent with recent studies of chicks in geometric enclosures (Tommasi & Vallortigara, 2000; Tommasi et al., 1997). Like the chicks, some of the pigeons searched mainly in the center, and some searched at locations that maintained the absolute distance from walls. The mean distance of search pecks from the center of the arena on expansion tests was strikingly similar for the pigeons and the chicks.

The pigeons' tendency to search in the center of the enclosure contrasts sharply with results found for pigeons on tests with expansions of a landmark array both on the touch screen (Spetch et al., 1996) and on the laboratory floor (Spetch et al., 1997). When trained to find food in the center of an array of discrete landmarks, pigeons do not search in the center when the array is expanded. Apparently, searching that is based on an array of discrete landmarks differs in an important way from searching that is based on surfaces of an enclosure. These findings and those of Kelly and Spetch (2001) suggest that pigeons spontaneously encode both relative and absolute metrics when searching on the basis of distances from walls or the geometric arrangement of walls. By contrast, pigeons spontaneously use absolute metrics almost exclusively when searching on the basis of discrete landmarks. Relational use of landmarks seems to be neither a preferred nor an easy strategy for pigeons (Spetch et al., 2003).

An examination of methodological considerations provides further support for the idea that surface geometry and discrete landmarks may encourage different forms of encoding. With the exception of studies on human adults, studies that have reported use of a relative strategy with discrete landmarks have used a multiple-exemplar training paradigm. Kamil and Jones (1997, 2000), for example, showed that nutcrackers used a relative strategy to encode the relationship between two landmarks and a central goal position when trained with several interlandmark distances. Although they are less accurate than the nutcrackers, pigeons also show some evidence of relational encoding after multiple-exemplar training with arrays of discrete landmarks (Jones et al., 2002; Spetch et al., 2003). However, in studies that have used single-exemplar training with discrete landmarks, expansion tests have not revealed a relational use of landmarks by birds (e.g., Spetch et al., 1996, 1997, and Kippenbrock et al., 2003). The interesting difference is that when birds are trained with continuous surfaces (instead of discrete landmarks), they show relational
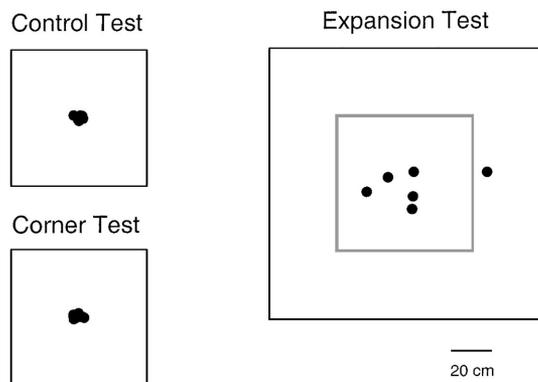

Control Test

Corner Test

Expansion Test

20 cm

Figure 2. Calculated peak places of searching for each of the 6 birds during all control, corner, and expansion tests. On expansion tests, the gray outline shows the locations that maintain the absolute distance from walls to the center of the training arena.

encoding even after single-exemplar training (Kelly & Spetch, 2001; Tommasi & Vallortigara, 2000; Tommasi et al., 1997; and our current study).

Our results suggest that searching on the basis of distances from surfaces or the geometric arrangement of walls may promote different encoding strategies than searching on the basis of discrete landmarks. A distinction between encoding based on discrete landmarks and encoding based on global surfaces may accord well with recent hemispheric specialization studies in chicks. Tommasi and Vallortigara (2001) trained chicks binocularly to find food in the center of a square arena and then tested them in larger and smaller arenas. If tested binocularly or with the left eye only, the chicks searched primarily on the basis of relative distance from walls. However, if tested with the right eye only, the chicks searched primarily on the basis of absolute distance from walls. Differences between eyes also emerged in whether priority was given to distance from walls or proximity to a local discrete landmark in the arena. After binocular training in which food was found in the center of the arena beside a discrete landmark, tests were given in which the landmark was moved, thereby placing the local landmark and the global arena cues in conflict. When tested binocularly or with the left eye, the chicks searched in the center of the arena, whereas when tested with the right eye only, they searched beside the landmark. Tommasi and Vallortigara suggested that the right hemisphere (driven by the left eye) may be concerned primarily with global aspects of a spatial environment and favors the use of relative distances, whereas the left hemisphere (driven by the right eye) is concerned with specific local cues and favors the use of absolute distances.

A preference for using absolute distance when searching on the basis of landmarks but relative distance when searching on the basis of surfaces may also have a functional basis. In nature, when an animal is searching on the basis of small discrete landmarks that are close to the goal, encoding of absolute distance may dominate because landmarks typically do not move in unison and because the spatial location of the goal would be unlikely to fall at a location that would allow a simple precise relational rule such as "in the center." However, estimation of absolute distance becomes less accurate the farther the landmark is from the goal; so, relative encoding of multiple distant landmarks may sometimes be required. Most natural surfaces provided by such environmental features as rows of trees or mountain ranges may typically be somewhat more distant to a goal, and surfaces may therefore encourage attention to relative spatial relationships. A tendency to encode relative spatial relationships among surfaces may persist even in a small-scale laboratory space in which the surfaces are close to the goal.

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