Use of Landmark Configuration in Pigeons and Humans: II. Generality Across Search Tasks

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Pigeons and humans searched for a goal that was hidden in varied locations within a search space. The goal location was fixed relative to an array of identical landmarks. Pigeons searched on the laboratory floor, and humans searched on a table top or an outdoor field. In Experiment 1, the goal was centered in a square array of 4 landmarks. When the spacing between landmarks was increased, humans searched in the middle of the expanded array, whereas pigeons searched in locations that preserved distance and direction to an individual landmark. In Experiment 2, the goal was centered between and a perpendicular distance away from 2 landmarks aligned in the left–right dimension. When landmark spacing was increased, humans, but not pigeons, shifted their searching away from the landmarks along the perpendicular axis. These results parallel those obtained in touch-screen tasks. Thus, pigeons and humans differ in how they use landmark configuration.

Many creatures remember places to return to by the use of visual landmarks. In this spatial search strategy, some kinds of spatial relationships between the goal and its surrounding landmarks are encoded and are later used to find the goal again (for reviews, see Collett, 1992; Gallistel, 1990). In many studies of landmark-based spatial memory, the landmarks defining the goal are shifted about from one trial to the next, thus forcing the subject to use the experimentally specified landmarks to locate the target. This method has demonstrated the use of landmarks in studies with insects (e.g., Cartwright & Collett, 1983; Tinbergen, 1972), birds (e.g., Cheng & Sherry, 1992; Spetch & Mondloch, 1993; Vander Wall, 1982), and rodents (e.g., Cheng, 1986; Col-

lett, Cartwright, & Smith, 1986; Suzuki, Augerinos, & Black, 1980). Transformation of the landmark array on unrewarded tests has been used to look for the underlying mechanisms by which creatures use landmarks (e.g., Cartwright & Collett, 1983; Collett et al., 1986; Suzuki et al., 1980).

In previous work (Spetch, Cheng, & MacDonald, 1996), we used the space on a computer monitor to study how humans and pigeons use the configuration of an array of landmarks. Consider a situation in which a hidden goal is located at a particular spot relative to an array of identical landmarks that moves about within the search space from trial to trial. Learning the location of the goal relative to a single landmark would not suffice because, without attending to the other landmarks, one could not determine in which direction from that landmark to search. Such tests reveal that species ranging from invertebrates (Cartwright & Collett, 1983) to humans (Spetch, Cheng, & MacDonald, 1996) can solve such a task. Transformations of the shape or size of the landmark array, however, have revealed striking differences in the way in which landmark configurations control the search behavior of different species.

Studies by Cartwright and Collett (1983) and by Collett et al. (1986) revealed that honeybees and gerbils respond differently to manipulations of the size of an array composed of identical landmarks. The honeybees were trained to find a goal that was located at a particular distance and direction away from a triangular-shaped array of three identical landmarks (Cartwright & Collett, 1983). On test trials, the landmarks were either spread farther apart (array expansion) or moved closer together (array contraction). The bees

adjusted their distance from the landmark array on these tests, searching farther away when the array was expanded and closer when the array was contracted. This adjustment of distance allowed the bees to maintain the same approximate compass directions from each landmark as in training. A similar study with gerbils produced a different pattern of results (Collett et al., 1986). The gerbils were trained with an array of two identical landmarks. The goal was between and a fixed perpendicular distance away from the imaginary line connecting the two landmarks. When the array was expanded by moving the landmarks farther apart, the gerbils did not adjust their distance from the landmark array; instead, they responded in the two locations that maintained the approximate training vectors from each of the landmarks. The gerbils appeared to use the configuration of the array to determine the direction from each landmark to search, but they appeared to use the landmarks singly in determining distance.

We recently found that pigeons and adult humans differ markedly in their use of landmark configuration to find a goal (Spetch et al., 1996). Both species were trained on a touch-screen search task (Spetch, Cheng, & Mondloch, 1992) in which the goal was an unmarked spot on the vertical surface of a monitor screen, and visual stimuli displayed on the screen served as landmarks. The touch frame recorded the location of search responses. In some studies by Spetch et al. (1996), the goal was in the center of a square array of four identical landmarks. The location of the landmark array and of the corresponding goal on the screen varied across trials. Both pigeons and humans readily used the configuration of the array to locate the goal accurately. However, when the landmark array was expanded on test trials (by moving each landmark diagonally outward from its normal position in the array), humans responded in the center of the expanded array, whereas pigeons responded in locations that maintained the approximate distance and direction from an individual landmark. In another experiment, the landmark arrangement was modelled after that used by Collett et al. (1986) for gerbils, in which the goal was between and below a horizontally aligned array of two identical landmarks. After training, the array was either expanded by moving the landmarks farther apart or contracted by moving them closer together. In response to these manipulations, humans, but not pigeons, adjusted their searching vertically. That is, the human participants searched farther from the imaginary line connecting the two landmarks when the array was expanded and closer to the line when the array was contracted, thereby preserving roughly the same triangular shape formed by the landmarks and the goal. The pigeons appeared to respond more like the gerbils, using both landmarks for determining the direction to search, but maintaining approximate training distances from an individual landmark.

These results suggest that pigeons and humans may process spatial configural information in fundamentally different ways, with humans abstracting a generalizable rule on the basis of the structure of the array (e.g., "the goal is in the middle" or "the landmarks and goal form a triangle") and with pigeons using the configural information only for

directional determination. However, before concluding that the differences observed by Spetch et al. (1996) represent fundamental between-species differences in spatial processes, it is important to rule out the possibility that the differences arose because of certain procedural artifacts. The present research, therefore, sought to replicate the results obtained by Spetch et al. using different kinds of search tasks.

Pigeons have two separate visual systems, a short-distance binocular frontal field and long-range monocular fields for each eye (for reviews, see Zeigler & Bischof, 1993). The touch-screen task presents stimuli to the frontal field of pigeons. In natural situations in which pigeons move through space in search of a food goal, both kinds of visual fields are likely called into play because stereoacuity breaks down beyond 20 cm for pigeons (McFadden, 1993). Therefore, it is important to show that results obtained with pigeons on the touch-screen task generalize to laboratory tasks in which pigeons move through space and in which stimuli are 20 cm or more from the target of search. Accordingly, we tested pigeons in a landmark-based search task developed by Cheng (1988), in which food is hidden under sawdust on the laboratory floor. Landmark arrays consisted of visually identical objects placed on the floor. This task differs from the touch-screen task not only in the visual system called into play but also in the size and orientation of the search space, in movement through space, and in the spatial contiguity of the goal and the food. If pigeons respond in a similar fashion in spite of these and other differences, it will provide added evidence that behaviors displayed in the touch screen are governed by general processes that transcend the specific characteristics of the search space and response requirements (see Spetch et al., 1992; Spetch & Wilkie, 1994).

We also assessed the generality of the results obtained with humans in the touch-screen task by designing search tasks in two very different settings. In one, humans searched for a hidden goal on a small search space presented on a table top. In the other, they searched for a goal in a much larger search space at an outdoor location. The outdoor setting, in contrast with both the touch-screen and table-top tasks, required that participants move through space to find the goal, much as pigeons move through space to find the goal in search tasks conducted on the laboratory floor.

Experiment 1

In Experiment 1, pigeons and humans were trained with a four-landmark array with the goal in the middle, modeled after that used by Spetch et al. (1996) and, then, were tested with expansions of the array. Both the table-top and outdoor settings were used for humans.

Method

Subjects. The pigeons were five Silver Kings, maintained at 85% weight with grain obtained during experimental sessions and with supplemental feedings of pigeon chow. They were housed individually in large cages with free access to water and grit. The

colony was on a 12-hour light–dark cycle (lights on at 6 a.m.). All subjects had extensive previous experience in the spatial search task, but had not previously seen the particular landmarks used in this research.

The human participants were undergraduates who participated for credit in their introductory psychology class. Eight participants (4 women), aged 18–23 years, served in the table top task and 12 participants (5 women), aged 19–42 years, served in the outdoor task.

Apparatus and procedure for pigeons. The birds were tested in a 300 cm × 330 cm room, with an observation window on one wall and a door on another wall. A wooden tray, 200 cm × 200 cm, with sides 5 cm high was centered flush against the wall that was opposite the door. The floor of the tray was lined with approximately 2 cm of wood chips. Forty-nine Velcro pieces, forming a 7 × 7 square, were fixed on the bottom of the tray, 25 cm apart. These were used to select landmark and goal locations, to secure the goal in place, and to divide the search space into bins for scoring. Start and finish boxes were centered flush against the wall with the door. Strings attached to openings on the boxes ran through a pulley system into the adjacent observation room so that the boxes could be opened and closed from that room. The search space was assigned a left–right dimension and an up–down dimension with the top of the space being the wall opposite the door. A video camera was centered above the search space.

The landmarks were four identical grit-filled bottles, 7 cm in diameter and 16.5 cm tall with black caps. The sides of the bottles were covered with yellow cardboard and marked with a horizontal stripe made from blue cloth tape. The goal was a bottle cap, 4 cm in diameter and 1 cm high. During initial training only, finding the goal was made easier by fixing it to the center of a 16-cm diameter margarine lid. In the training configuration, the landmarks were placed 50 cm apart, center to center, to form a square array. The goal was placed in the center of the landmark array. For each training trial, the goal location was selected randomly from the middle 25 locations of Velcro pieces, but the configuration of landmarks and goal remained identical across trials. For test and control trials, only the middle nine locations were used as the hypothetical goal locations.

All birds were experienced in the search task and had been trained to exit the start box and enter the finish box in response to the opening of the appropriate doors. The birds required three or four shaping sessions to find the food (10 maple peas) in the goal buried under approximately 2 cm of wood chips. The goal was placed in the larger container for the first 2 or 3 shaping sessions only.

The birds were then given 8 to 12 sessions of training followed by 5 sessions of testing. Each session consisted of 5 trials. Trials were set up with the bird in a start box. To begin the trial, the start box door was opened (by pulling a string from the observation room) until the bird exited into the search space. At the end of a trial, the door to the finish box, which was baited with eight maple peas, was opened until the bird entered the box. During the first 6 training sessions, the goal was present on all trials. For the remaining training sessions, the goal was absent on two of the five trials (randomly selected). During test Sessions 1, 2, 4, and 5, unrewarded tests were presented on Trials 2 and 4. During test Session 3 an unrewarded test was presented on Trial 3. On a test trial, the food and bottle cap were absent. The trial terminated after the experimenter counted 50 search pecks anywhere in the search space.

Three types of tests were given (3 of each). On control tests, the landmarks were spaced as in training trials. On right–left expansion tests, the landmarks were moved 50 cm farther apart than in

training in the right–left dimension only. On diagonal expansion tests, the landmarks were moved 50 cm farther apart than during training in both the right–left and the up–down dimensions. The three types of tests each occurred once in every block of three tests. The location of the hypothetical goal on test trials was selected randomly with the constraint that the same location not be used twice for a given type of test.

All tests were videorecorded, and the data were analyzed frame by frame. The location of the bird's head during each sweeping peck at the bedding was recorded on a transparency that contained a template of the search space. These data were then transferred into bins of 12.5 cm, and the place of peak searching for each bird in each test condition was extracted, following methods used by Cheng and Sherry (1992).

Apparatus and procedure for humans on the table-top task. The experiment was conducted in a small private room containing a video camera mounted on a tripod 30 cm from a table with a chair on either side to seat the participant and the experimenter. The search space was a rectangular grid, 58 × 50 cm marked onto a 72 × 57 cm sheet of white cardboard that was taped to the table top. The search space was assigned a left–right and an up–down dimension, with the part of the grid closest to the participant considered to be the bottom. The grid consisted of 720 squares of 2 × 2 cm (30 in the left–right dimension and 24 in the up–down dimension), each of which contained a 1 × 1-cm brown cardboard chip. The goal was a brown chip, visually indistinguishable from the others, but with an x marked on the underside. The landmarks were four identical black chess pieces (pawns), approximately 2 cm high and 1 cm in diameter. They were arranged in a square, with three grid spaces between landmarks and with the goal in the center. A black cardboard barrier, 55 cm high and 70 cm wide, blocked the participant's view of the search space while the experimenter prepared for each trial.

Upon arrival, the participant was read instructions that included the following information: He or she would perform a task and then complete a short questionnaire. The task would consist of finding the chip with the x on the underside. The experimenter would reveal its location on the first trial. On all subsequent trials, the participant would have four chances to find the x, and then the experimenter would reveal its location. A camera would record the choices but not the participant's face. The experimenter confirmed that the participant wished to participate before starting the experiment.

At the beginning of each trial, the experimenter placed the barrier between the participant and the search space and arranged the landmarks into a square array with the goal in the center. The absolute location of the array on the grid varied during each training trial according to a predetermined list. The locations were selected at random with the restriction that neither the landmarks nor the goal was less than two squares from the edge of the grid. The experimenter removed the cardboard to begin the trial.

On the first trial, the experimenter revealed the goal location by showing the participant the chip with the x. On all subsequent trials, the participant was allowed four choices to find the x. If the x was not found, the experimenter showed the participant where it was. Training trials continued until the participant found the x on the first choice for five consecutive trials.

The last trial was a test trial, in which the array was expanded by moving each landmark diagonally outward by two grid spaces, and none of the chips contained an x. The location of the landmark array on the grid varied across participants. After the participant made four choices, the experimenter told the participant that the x chip was not present on this trial.

The experimenter then left the room while the participant filled

out a questionnaire that asked participants to provide their age and gender and to "please tell us about any strategies you used to try to find the square with the *x*."

The experimenter recorded the participants' choices on templates of the grid and the landmark locations for each trial. Another experimenter later viewed the videotape to confirm the accuracy of the recordings. To summarize the results of the four choices made by each participant, we weighted each choice according to its order, assigning a weight of 4 for first choices, 3 for second choices, 2 for third choices, and 1 for fourth choices. For visual presentation of the pooled data across participants, we computed a value for each location on the grid that represented the sum of choices multiplied by their weights.

Apparatus and procedure for humans in the outdoor study. The experimental setting was a grassy field on the university campus, with a road on one side and a building on the opposite side. The space was arbitrarily assigned a left–right and an up–down dimension, with the road end designated as up and the building end designated as down. Prior to an experimental session, two experimenters (E1 and E2) measured off four, 6 × 6 m, square areas, placing a small marker (a golf ball marker) in each corner and in the center of each square. These markers were used to determine the placement of the landmarks, which consisted of four bright pink Styrofoam posts, 7 cm in diameter and 85 cm high ("pool noodles" cut in half and supported with a stainless steel rod), and the goal, which consisted of a nickel covered in green cloth tape. A thin stainless steel post with a flag at one end was used by participants to mark their selected location. To set up for the first trial, the landmarks were placed in the corners of one square, 6 × 6 m, randomly selected and the goal was placed at the center of the square on top of the ball marker.

At the beginning of the session, the participant was informed that the task involved searching for a small green object in the grass, and that the experimenter would reveal the location of this goal object on the first trial, but on all subsequent trials, the participant would be timed while he or she searched for the goal. The participant was instructed that, on finding the goal, he or she should place a flag next to the goal.

After confirming that the participant wished to participate, E1 showed the participant the goal location from the perimeter of the square. E1 then took the participant for a short walk away from the search space, then walked the participant back to 1 of 12 start locations at the perimeter of the square. The 12 locations consisted of the four corners and of two locations between each landmark. These locations were randomly selected for each training trial and for each participant. E1 then handed the participant the flag and told him or her to find the goal. E2 timed the trial until the participant picked up the goal marker and placed the flag in the ground. On all subsequent training trials, E1 took the participant on a walk, while E2 moved the landmarks and goal to another one of the premarked 6 × 6 m squares. The participant was then brought back to one of the 12 start locations and told to search for the goal.

Training consisted of a minimum of four trials and continued until a participant's search time was 10 s or less for two consecutive trials. The participant then read new instructions stating that the goal would now be present on only some of the trials. The participant was instructed to search for the goal but that if he or she could not find it within a reasonable time, to place the flag where the goal should be. The participant then started a test phase, which consisted of five or more trials that were each set up while the participant was taken for a walk. Three of the trials in this phase were tests. All the data presented are from these test trials. One test was a control, in which the landmarks were placed in a normal 6 ×

6 m square; one test was a left–right expansion test in which the landmarks were placed 12 m apart in the left–right dimension and 6 m apart in the up–down dimension, and one test was a diagonal expansion test in which the landmarks were placed 12 m apart in both dimensions. On both the control and the expansion tests, the goal and the ball marker in the center of the array were absent. To control for possible effects of start location, each participant started from the same place (one of the four corner locations) on each of their three tests. These four start locations were counterbalanced across participants, with three participants assigned to each corner. Each test was always separated by one or two review trials, which were identical to the preceding training trials and were not included in the data set. The order of exposure to the three tests was balanced across participants, with two participants assigned to each of the six orders. After the last trial, participants filled out a questionnaire that asked them to provide their age and gender and to indicate how many landmarks they used to find the goal. They were told that they could elaborate on the strategies they used, if they so wished.

After each test, E2 measured the distance of the flag from the two landmarks at the top of the search space. The law of cosines was later used to determine the *xy* coordinates of the participant's placement, relative to the center of the array.

Results

An alpha level of .05 was used for all statistical tests.

Pigeons. For the control and the expansion tests, data were collapsed into response distributions in both the left–right and up–down dimensions. Inspection of these response distributions suggested that the distributions were not always single peaked. To decide objectively when a distribution showed more than one peak, we identified which bin in the distribution had the highest number of pecks (primary mode) and, then, we determined whether any other bins had at least 50% of the pecks in the primary mode bin (secondary modes). If a secondary mode was separated from the primary mode by one or more bins that contained less than 50% of the pecks in the secondary mode, the distribution was said to have more than one peak. The iterated median procedure (see Cheng, 1989; Spetch et al., 1992) was used to calculate peak places for all single-peaked distributions. When multiple peaks were found, the distribution was divided at the lowest bin between the primary and secondary modes (with this lowest bin serving as the end bin for each portion of the distribution). The iterated median procedure was then used to calculate a primary peak for the portion of the distribution that contained the most pecks and secondary peak(s) for the other portion(s) of the distribution. This procedure revealed no multiple peaks for any birds in either dimension of the control tests or in the up–down dimension of the left–right expansion tests. Two birds (61 and 41) showed double peaks in the left–right dimension of the left–right expansion tests. For the diagonal expansion tests, two birds (809 and 41) showed double peaks in the left–right dimension and one bird (C221) showed a double peak in both dimensions.

Figure 1 shows the calculated peak places of searching for the five birds on the control and the test trials. The filled squares show the peaks calculated from single-peaked dis-
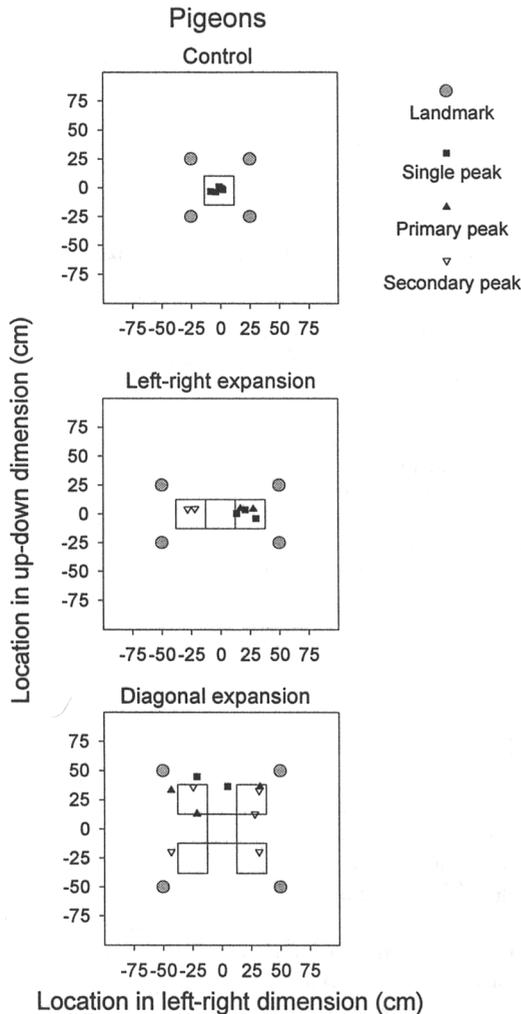
Pigeons

Control

Left-right expansion

Diagonal expansion

Location in up-down dimension (cm)

Location in left-right dimension (cm)

○ Landmark

■ Single peak

▲ Primary peak

▽ Secondary peak

Figure 1. Training array (control) and arrays used during expansion tests for pigeons in Experiment 1, drawn to scale. The outlined square at the center of the landmark array in the control diagram indicates the 25 × 25-cm area surrounding the goal during training. The absolute location of the goal and landmark array in the search space varied across trials. The outlined square areas in the test diagrams indicate theoretical goal areas on the basis of the center of the array or of vectors from individual landmarks. The gray circular symbols indicate the four landmarks, and the smaller symbols indicate calculated peak places of searching for individual pigeons. Black squares show peaks from single-peaked distributions, black triangles show the primary peaks from double-peaked distributions, and inverted white triangles show secondary peaks from double-peaked distributions. See text for details.

tributions and the filled triangles show the primary peaks from double-peaked distributions. The unfilled inverted triangles show the secondary peaks calculated for double-peaked distributions (it should be noted that one bird had three secondary peaks for the diagonal expansion tests because the response distribution was double peaked in both the up–down and the left–right dimensions).

Although search behavior on control tests was well centered in the array, the birds clearly did not concentrate their searching in the center of the landmark array on expansion tests. Instead, most of the peaks fell at locations that would maintain the correct distance and direction from an individual landmark (hereinafter referred to as individual landmark locations).

To provide statistical confirmation that pigeons searched more in individual landmark locations than in the center of the array, we compared the average number of search pecks made in the individual landmark locations (i.e., total number divided by 2 for the left–right expansion test and by 4 for the diagonal expansion test, to correct for opportunity) to the number of pecks made in the center location. This revealed that the birds searched significantly more in individual landmark locations than in the center location during both the left–right expansion tests, $F(1, 4) = 13.30$, and the diagonal expansions tests, $F(1, 4) = 18.17$. The average proportion of search pecks falling in individual landmark locations was also higher than that expected on the basis of random searching within a 125-cm² area (i.e., within the range of possible goal locations during training) during both the left–right expansion tests, $t(4) = 8.65$, and the diagonal expansion tests, $t(4) = 6.00$. The average proportion of search pecks falling in individual landmark locations was higher during the left–right expansion tests than during the diagonal expansion tests, $t(4) = 8.57$.

Humans: Table-top task. The test results are shown in the bottom panel of Figure 2. The sum of the weighted choices for each grid is indicated by the fill pattern or symbol, with empty squares having a sum of zero. There was a strong tendency to choose the chip in the middle of the expanded array. In fact, every participant chose the middle chip first, and none of the participants ever picked one of the four chips that would maintain the same absolute distance from one of the four landmarks as in training. On the questionnaire, seven of the eight participants used the word "middle" or "center" to indicate where the x was relative to the landmarks. The eighth participant stated that the x was an equal distance from each landmark. One participant also mentioned counting the squares from each landmark to the goal.

Humans: Outdoor task. Figure 3 shows the location at which the participants placed their flags on the control tests, right–left expansion tests, and diagonal expansion tests. These responses fell near the center of the array on all tests. On control tests, all responses fell within a 2 × 2 m area at the center of the array. On both types of expansion tests, 10 of the 12 responses fell within the 2 × 2 m area at the center of the array, and none of the 12 responses were within any of the 2 × 2 m areas that would maintain the same vectors from the landmarks as in training.

In response to the questionnaire, 9 of the 12 participants reported that they used all four landmarks, one participant reported using two landmarks, and two participants did not specify a number. Seven participants provided strategy information. Of these, five said they searched in the center or middle, one mentioned searching between the post, and one reported using the intersection of diagonal lines.
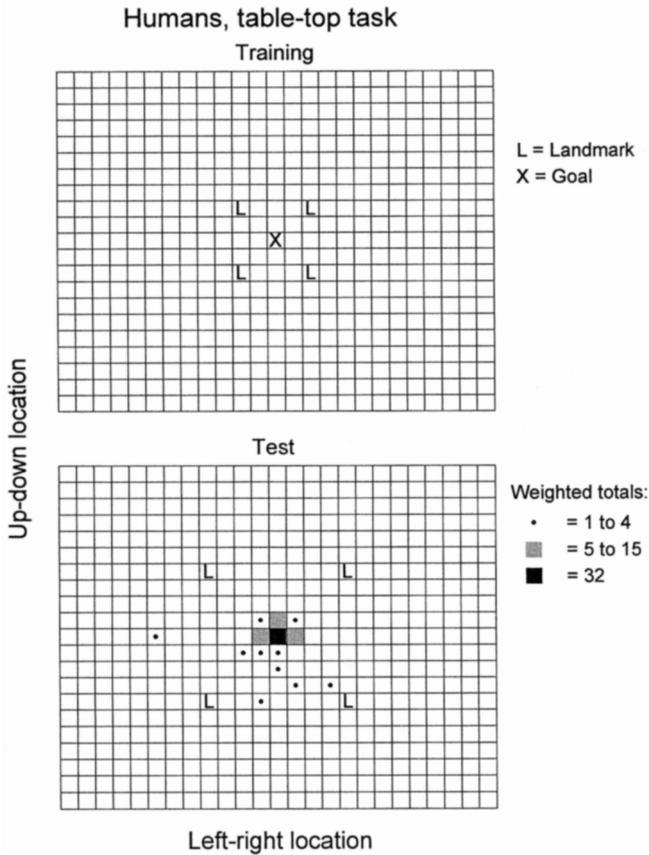
Humans, table-top task
Training

L = Landmark
X = Goal

Up-down location

Test

Weighted totals:
- • = 1 to 4
- ▨ = 5 to 15
- ■ = 32

Left-right location

Figure 2. Arrangement of landmarks (L) and goal (X) during training and test trials for humans in the table-top task of Experiment 1. The absolute grid locations of the goal and landmark array varied across trials. The summed responses of the 8 participants, weighted for choice order, are indicated by the fill patterns and symbols. Empty grid spaces are locations that were never chosen. See text for details.

Comparison between pigeons and humans. It seems clear from examining the figures that pigeons responded very differently from humans to expansions of the landmark array. To provide some statistical support for this observation, we transformed the peak place data from pigeons (using single peaks or primary peaks of the double-peaked distributions) and the response data from humans in the outdoor task into scores that represented absolute distance from the center of the array along the two dimensions. We scaled these scores as a proportion of the distance between landmarks, and then subjected them to a two-way analysis of variance (ANOVA), with species as a between-subjects factor and test type as a within-subjects factor. For the left–right and up–down dimensions, respectively, these analyses revealed significant main effects of species, $Fs(1, 15) = 53.23$ and 56.92, and of test type, $Fs(2, 30) = 18.23$ and 66.51. Most important, the interaction between species and test type was significant for both the left–right and the up–down dimensions, $Fs(2, 30) = 11.66$ and 62.21, confirming that the two species responded differently to expansion manipulations.

Discussion

The use of identical landmarks and variable goal locations required subjects to use the landmark array when searching for the goal. Both pigeons and humans were well able to solve this task, but their test results suggested different ways of using the configural information. Whereas humans appeared to learn a relational rule (goal is at the center), pigeons appeared to be restricted to the determination of direction in their use of the configural information. As a result, humans continued to respond at the center of the array when it was expanded, whereas pigeons showed no tendency to respond in the center of expanded arrays. Instead, they responded more often in locations that maintained approximately the training distance and direction from individual landmarks. These results replicate those found by Spetch et al. (1996) on the touch screen.
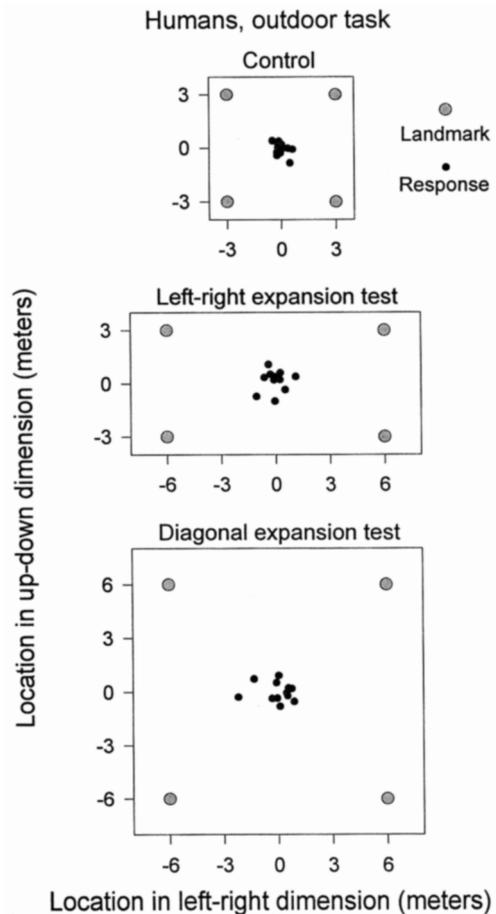
Humans, outdoor task
Control

3
0
-3

○ Landmark
• Response

-3 0 3

Location in up-down dimension (meters)

Left-right expansion test

3
0
-3

-6 -3 0 3 6

Diagonal expansion test

6
3
0
-3
-6

-6 -3 0 3 6

Location in left-right dimension (meters)

Figure 3. Training array (control) and arrays used during expansion tests for humans in the outdoor task of Experiment 1, drawn to scale, except for landmarks, which were smaller in diameter than shown. The location of the goal and landmark array in the search space varied across training trials. Each small black symbol indicates the response location of 1 participant. See text for details.

Experiment 2

In Experiment 2, pigeons and humans were trained with a two-landmark array, modelled after the arrangement used by Collett et al. (1986) with gerbils and by Spetch et al. (1996) in touch-screen studies with pigeons and humans. The landmarks were aligned in the left–right dimension of the search space, and the goal was between the landmarks but a perpendicular distance away from the line connecting the two landmarks. On tests, the landmarks were moved closer together or farther apart. On the basis of the pattern of results seen in the touch-screen task (Spetch et al., 1996), we expected the pigeons to keep the same perpendicular distance to the landmarks on all tests, behaving like gerbils (Collett et al., 1986). Humans were expected to shift their perpendicular distance from the array to preserve the triangular shape formed by the landmarks and the goal.

Method

Subjects. The pigeons were four White Kings, maintained at 85% weight by grain obtained during experimental sessions and supplemental feedings of mixed grain. They were housed as in Experiment 1, except that the colony was on a 14:10-hr light–dark cycle (lights on at 6 a.m.). The birds had extensive prior experience in spatial search tasks, but had not previously seen the landmarks used in this research. The humans were eight undergraduates (four women), aged 18–20 years, who participated for credit in their introductory psychology class.

Apparatus and procedure for pigeons. The birds were tested in a 428 cm × 262 cm room with an observation door and a window at one end. Centrally located in the room was a 122-cm^2 piece of Masonite, 0.3 cm thick. At the center of the Masonite board were attached nine pieces of Velcro forming a 3 × 3, with neighboring Velcro pieces 12.5 cm apart (center to center). These were the locations at which the goal, a bottle cap 4.8 cm in diameter and 1 cm deep, might be attached. The entire room except the area near the door was covered with wood chips. The search space was assigned a left–right dimension and an up–down dimension with the top of the search space being the wall opposite the observation door. A video camera was suspended above the search space.

Two identically constructed bottles filled with clear water served as landmarks. They were 9 cm in diameter, 22.5 cm tall, and tapered at the top. In the training configuration, the bottles were placed 30 cm apart, edge to edge. The goal was centered between the two landmarks and 15 cm perpendicular from the line segment connecting the two bottles (see top graph in Figure 4). Each day, the location of the goal varied across the nine possible locations, but the configuration of landmarks and goal remained identical from day to day.

All the birds were familiar with the task required of them. It took only three sessions of preliminary shaping, following the shaping procedures used by Cheng and Sherry (1992), to train the birds to find food (four large grains consisting of corn and various legumes) located in the bottle cap that was completely covered with approximately 2 cm of wood chips. Trials were set up with the bird under the cover of an opaque box. The bird was covered and released with the room lights off. A dim 7-W light in the adjoining observation chamber and the glow of the monitor used for video-recording allowed the experimenter to see the bird in the dark.

The birds were then given 10 sessions of training and 15 sessions of testing. Each session consisted of five trials. During training, each trial was a rewarded training trial. During testing, one of Trials 3, 4, or 5 (selected at random) was an unrewarded test trial. On a test trial, the food and bottle cap were absent. A template with 10-cm distances marked along the principal axes was videorecorded (on a Panasonic AG7300 VCR) for a few seconds. The search behavior of the bird was then videorecorded for 60 s from the first peck, after which the test terminated.

Three types of tests were given (5 of each). On control tests, the landmarks were spaced 30 cm apart, as in training trials. On expansion tests, the landmarks were spaced 45 cm apart, and on contraction tests, the landmarks were spaced 15 cm apart (see Figure 4). In each 3-day block, the three types of tests were given.

The videorecorded data were analyzed frame by frame, and the location of place of peak searching for each bird in each test condition was extracted, following methods used by Cheng and Sherry (1992).

Apparatus and procedure for humans. The experimental setting was the same as for the table-top task of Experiment 1, except that there was no video camera in the room. The search space consisted of a 46 × 30-cm sheet of paper on which two identical landmarks were placed (the chess pawns used in Experiment 1). A new sheet of paper was used for each trial. On all training trials, the landmarks were spaced 11.5 cm apart, center to center. The goal area, in which participants attempted to place their mark, was 1.8 × 1.8 cm. The goal was centered between the two landmarks in the left–right dimension and was below them (i.e., closer to the participant) in the up–down direction. The perpendicular distance from the center of the goal to an imaginary line connecting the centers of the two landmarks was 5.75 cm. The location of the landmarks and corresponding goal area on the paper varied across training trials with the constraint that neither goal nor landmarks were less than 4 cm from the edge of the paper. On tests, the landmarks were not less than 12 cm from either edge of the paper in the up–down dimension.

On arrival in the laboratory, the participant was read instructions that provided the following information: He or she would perform a task and then fill out a brief questionnaire. The task would involve trying to mark a dot in the correct location on a sheet of paper. On the first trial, the participant would first be shown the correct location, but on all subsequent trials, the location would not be shown prior to a response. After some, but not all trials, feedback would indicate whether the placement was accurate. The experimenter confirmed that the participant wished to participate before starting the experiment.

On the first trial, the experimenter placed the paper that served as the search space on the table and placed the two landmarks in locations marked on the paper. She then removed the landmarks and placed some tracing paper (feedback sheet) on top of the search space. The feedback sheet contained marks for the landmark locations and an outline of the goal location. The experimenter aligned the feedback sheet with the search space, placed the landmarks in their marked locations, and told the participant to study the goal location. She then removed the feedback sheet, placed the landmarks on the search sheet, and asked the participant to mark with a dot the place where he or she thought the goal was. She then placed the feedback sheet back on the search sheet to indicate the accuracy of the participant's response.

For Trials 2 to 12, the experimenter placed a new search sheet on the table, put the landmarks in the marked locations, and asked the participant to mark the place where he or she thought the goal was. Feedback was provided on Trials 2, 3, 4, 5, 7, 8, 10, and 12. On Trials 6, 9, and 11, the feedback sheet was not presented, and the participants were told, after they responded, that it was a no-feedback trial.
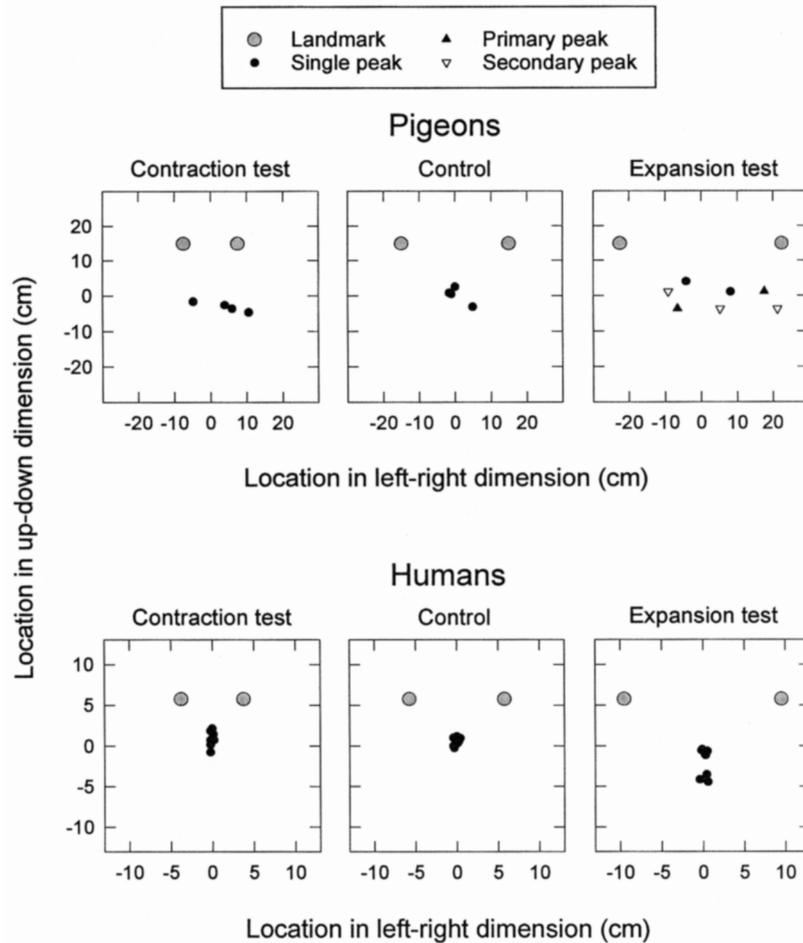
Figure 4. Training array (control) and arrays used during expansion and contraction tests for pigeons (top panel) and humans (bottom panel) of Experiment 2. The diagrams are drawn to scale, except for the diameter of the landmarks. The gray circular symbols indicate the locations of the two identical landmarks, and the smaller symbols indicate the calculated peak places of searching for individual pigeons or the response locations for individual humans. For pigeons, black circles show peaks from single-peaked distributions, black triangles show the primary peaks from multiple-peaked distributions, and inverted white triangles show secondary peaks from multiple-peaked distributions. See text for details.

Trials 13, 15, and 17 were tests. On one test (control), the landmark array was the same as during training; on another test (expansion), the landmarks were farther apart (19 cm); and on the third type of test (contraction), the landmarks were closer together (7.5 cm). The order of tests varied across participants. After all tests, the participant was told that it was a no-feedback trial. Trials 14 and 16 were baseline trials with feedback.

After the last trial, the experimenter left the room while the participants filled out a questionnaire, which asked about age, gender, and any strategy used.

Results

An alpha level of .05 was used for all statistical tests.

Pigeons. The place of peak searching for individual birds are shown in the top of Figure 4. Using the same criterion as in Experiment 1, multiple peaks were found only in the left–right dimension during the expansion tests, with one bird showing a double peak and one bird showing a triple peak. All other distributions were single peaked. Single peaks are shown with circular symbols, primary peaks from multiple-peaked distributions are shown with filled triangles, and secondary peaks are shown with unfilled inverted triangles. Birds varied unsystematically across conditions on the axis parallel to the two landmarks (left–right dimension) and did not shift their location of searching on the perpendicular axis (up–down). Mean locations of peak searching (using single and primary peaks only) were 3.96 cm right and 3.01 cm down from the goal on contraction tests, 0.59 cm right and 0.11 cm up from the goal on control tests, and 3.77 cm right and 0.56 cm up from

the goal on expansion tests. Within-subject ANOVAs on these data revealed no significant difference across conditions in either the left–right dimension, $F(2, 6) = 0.19$, or the up–down dimension, $F(2, 6) = 2.35$.

Humans. The bottom graphs in Figure 4 show the location of participants' dots on the three types of tests. Responses were well centered between the two landmarks in the left–right dimension on all tests. However, the perpendicular distance of participants' dots from a line connecting the center of the two landmarks differed significantly across test conditions, $F(2, 14) = 14.44$. Subsequent multiple comparisons (Newman–Keuls) indicated that participants searched significantly farther from the landmarks on expansion tests than on either control or contraction tests. The difference between control and contraction tests failed to reach significance. On expansion tests, the participants' shift in distance relative to control trials (mean = 2.53 cm away from the landmarks) was significantly greater than 0, $t(7) = 4.83$, and was not significantly different from the shift expected on the basis of shape preservation (3.75 cm), $t(7) = 2.01$. On contraction tests, the participants' shift in distance (mean = 0.36 cm closer to the landmarks) was not significantly greater than 0, $t(7) = 0.86$, and was significantly less than expected on the basis of shape preservation (2.0 cm), $t(7) = 4.00$.

Responses to the question about strategy were variable, with two participants reporting that they used triangulation, two participants reporting that they tried to preserve the shape formed by the landmarks and the goal, three participants reporting that they tried to maintain the correct distance from the landmarks, and one participant reporting that she memorized the location.

Comparison between pigeons and humans. To provide statistical confirmation that pigeons and humans differed in their response to expansions of the landmark array, we analyzed the location of responses in the up–down dimension for the two species. For this analysis, we scaled the location of pigeons' peak places (using single and primary peaks only) and the location of the humans' responses as a proportion of the distance between landmarks. A two-way ANOVA, with species and test type as factors, revealed no significant main effect of species, $F(1, 10) = 0.09$, or of test type, $F(2, 20) = 3.00$. However, the interaction between species and test type was significant, $F(2, 20) = 10.10$, confirming that the two species responded differently to the array manipulations.

Discussion

On the whole, the results of Experiment 2 are consistent with those obtained by Spetch et al. (1996) in the touch-screen task. In response to expansions or contractions of the two-landmark array, pigeons showed unsystematic variation in their search locations in the dimension parallel to the shift and no shift in searching in the perpendicular dimension. By contrast, the humans' responses were well centered between the two landmarks in the parallel dimension on all tests, but their distance from the landmarks in the perpendicular dimension varied across tests.

The pigeons' response to expansion and contraction differed slightly from that of gerbils in Collett et al.'s (1986) study. The gerbils searched primarily at the locations dictated by the training vectors of the two landmarks. The pigeons searched at various spots along the dimension parallel to the landmark shifts. Both patterns may be understood as weighted averages of the dictates of the two training vectors. The gerbils alternately weighted the training vectors 1, 0 and 0, 1, whereas some of the pigeons appeared to use an intermediate weight for each vector. Use of intermediate weights would lead to search, at various places along the line segment connecting the locations dictated by the training vectors of the two landmarks. This form of vector averaging has been found in similar studies of landmark-based spatial memory in pigeons, both on the laboratory floor (Cheng, 1988, 1989, 1990; Cheng & Sherry, 1992) and on the computer monitor (Spetch et al., 1992). In these studies, the goal was near an edge. When a nearby landmark was shifted parallel to the edge, the birds also shifted their searching along the parallel dimension, to varying extents, but they did not shift their searching in the perpendicular dimension.

The pattern for humans differed slightly from that found on the analogous touch-screen task (Spetch et al., 1996). There, the participants searched closer to the landmarks along the perpendicular axis when the array was contracted. In Experiment 2, we found no significant difference along the perpendicular axis between the control and the contracted arrays. Why this difference is found is unclear. In both the touch-screen and the table-top task, however, humans searched farther from the landmarks along the perpendicular axis when the array was expanded.

General Discussion

With both the two-landmark and four-landmark arrays tested in the present research, pigeons and humans responded differently to expansions or contractions of the spacing between landmarks, suggesting that they used configural information in different ways. The pattern of results in this article replicated those found previously with comparable arrays presented on the touch screen. These results, therefore, appear to reflect fundamental differences in the way in which pigeons and adult humans use the configuration of a landmark array to find a goal.

Pigeons readily learned to find a goal that was hidden in a particular spot relative to an array of either two or four identical landmarks. The use of variable goal locations in the search space required that the pigeons attend to more than one landmark to find the goal, but they did not use the shape of the configuration to determine where to search, as the humans did. In some cases, they appeared to use only one of the landmarks to determine where to search. On the surface, this finding seems inconsistent with the requirement of the task that pigeons need to attend to more than one landmark to find the goal. One explanation of this paradoxical pattern of results is to divide the search process into a landmark matching process and a search place matching process.

The landmark matching process identifies landmarks; it matches landmarks in the current world, delivered by perception, with recorded landmarks stored in the landmark-based spatial memory. When all the landmarks individually appear to be identical, and the array shifts about in absolute space—the conditions holding in these experiments and their touch-screen counterparts (Spetch et al., 1996)—the pigeon is forced to use the configuration of the array to identify landmarks. Neither the individual characteristics of the landmark nor their positions in absolute space can supply the requisite information.

The pigeons do not, however, have to use the configuration for search place matching and, in fact, the data indicate otherwise. Search place matching is based on vectors from individual landmarks. Sometimes, the distance and direction (vector) from a single landmark dictate search place matching; sometimes the vectorial dictates of more than one landmark are averaged (in a weighted fashion). In any case, vectors govern search place matching, and Cheng (1994, 1995) presented evidence that the distance and direction components of the vectors are separately encoded and calculated. Search place matching is decidedly not based on the shape or configuration of the landmark array. Instead, the pigeons appear to use the configuration of the array to identify individual landmarks (e.g., the top right landmark) and, then, apply the search matching process to one or more of the identified individual landmarks. The results seen here with pigeons are also similar to those obtained with gerbils (Collett et al., 1986) and marmoset monkeys (MacDonald, Spetch, & Cheng, 1996), suggesting the possibility that they reflect a general characteristic of landmark use in nonhuman vertebrates.

Human participants, by contrast, showed no tendency to try to maintain the training distance from landmarks when the array was expanded; rather, they chose locations that preserved the shape formed by the goal and the landmark array. In the conceptual scheme outlined earlier, the search matching process is based on the configuration or shape of the array. The matching process "follows" geometric expansions and contractions, which preserve shape but not distances, and abstracts away from absolute distances. Various versions of geometric rules that participants verbalized are consistent with this hypothesis. We do not take this to mean that adult humans do not sometimes use distances in search place matching. Pilot studies in which young children were found to behave more like pigeons and gerbils than like adult humans (MacDonald et al., 1996) suggest otherwise. It is just that, in the case of conflict, shape takes precedence over any individual distance measure (and in our manipulations, the participant cannot match the distance to all landmarks).

The way in which pigeons and other animals appear to use landmark configuration makes some ecological sense when one considers natural situations in which landmarks might be used to locate a goal. In nature, it may sometimes be necessary to use the configuration of an array of similar looking landmarks (e.g., a group of similar looking trees) to identify landmarks that bear particular relationships to the goal. However, it is difficult to imagine a natural situation in which it would be beneficial for an animal to match the shape of a landmark configuration but not distances of the landmarks to the goal. In fact, the tendency of adult humans to match shape rather than distances may be a reflection of map-reading experience. Map reading requires a transformation of scale, which preserves shapes, directions, and relative distances but does not preserve absolute distances.

For both species, the similarity of the results obtained on the laboratory floor, on the table top, and outdoors with those obtained on the touch screen suggests that the different patterns of results found with the two species reflect differences in the perceptual and cognitive processes of the species and not artifacts of any particular method of study. The processes in each species hold across differences in size and orientation of the search space, movement allowed in the space, how much of the space can be taken in at one glance, and the many other variables that differ between the two tasks. The fact that pigeons showed similar results on the touch-screen monitor and on the laboratory floor also suggests that the pattern of performance is not attributable to the visual system that the birds were using. The touch-screen monitor is likely to be viewed binocularly, whereas on the laboratory floor, the distances to landmarks would force the use of monocular vision. Nevertheless, we have no direct confirmation of this difference. It has been suggested that pigeons normally prefer the right eye for learning visual discriminations (Güntürkün, 1985; von Fersen & Güntürkün, 1990). A possible test for the use of binocular vision is whether performance transfers across eyes (Goodale & Graves, 1982; Sherry, Krebs, & Cowie, 1981). If the birds are trained on a visual task with one eye doing the viewing and then tested with the other eye doing all the viewing, typically, transfer is found when the birds used the binocular system, but not when they used the monocular system. Such tests might be done on the touch-screen tasks to determine whether binocular vision is indeed used.

In spite of the differences found between humans and pigeons on the tasks here and their counterparts on the touch screen (Spetch et al., 1996), we should not overlook many similarities between the two species. Both species can learn to use the configuration of an array of landmarks to search for a goal. Both species give more weight to landmarks that are nearer rather than farther to the goal (Cheng, 1989; Spetch, 1995; Spetch & Wilkie, 1994). In both species, an additional landmark can overshadow the control exerted by another landmark (Spetch, 1995).

Even in the aspect in which the two species differ lies an underlying similarity. Humans and pigeons both use metric properties, that is, distances and directions, in determining where to search; but it appears that, in search place matching, different metric properties are used. On expansion tests, pigeons matched both distance and direction but to only one or sometimes two landmarks. Humans matched the directions to all landmarks but not the distances. This last strategy amounts to matching by shape. Using shape is using configuration in a strong sense. In other experiments, humans transfer perfectly to the middle of an array even when all the individual elements in the array have been changed, whereas pigeons show no transfer when the elements are

changed in this fashion (Spetch et al., 1996). Thus, humans show a stronger use of configuration than do pigeons.

Shape and vectors are both metric properties of space. Both species thus use metric properties for search place matching, but they prefer to rely on different metric properties. The use of metric properties in one way or another in landmark-based spatial memory has been found in every species in which the underlying mechanisms has been investigated. Models relying on metric properties have been proposed for insects (Cartwright & Collett, 1983; Wehner & Räber, 1979), rodents (Cheng, 1986; Collett et al., 1986), birds (Cheng, 1994, 1995; Cheng & Sherry, 1992; Spetch et al., 1992), and young children (Hermer & Spelke, 1994). The evidence suggests that any creature that relies on landmark-based spatial memory encodes and uses metric properties.

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