Landmark use by pigeons in a touch-screen spatial search task

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Pigeons obtained food by pecking at an unmarked target location on a video screen equipped with a touch-sensitive frame. The target area was located near the top edge of the screen in Experiment 1 and near the left edge of the screen in Experiment 2. On baseline trials, a graphic landmark was located below and left of the target (Experiment 1) or below and right of the target (Experiment 2). In both experiments, baseline search distributions showed a single peak and were roughly symmetrical about the target area in both horizontal and vertical dimensions. On occasional test trials, the landmark was shifted horizontally, vertically, or diagonally by 1.5 cm or 3 cm. In both experiments, landmark shifts in the dimension parallel to the nearest edge produced systematic shifts in the peak place of search. Landmark shifts in the dimension perpendicular to the nearest edge produced inconsistent (Experiment 1) or relatively small (Experiment 2) shifts in peak place. The magnitude of the behavioral shift was always less than the magnitude of the landmark shift and was not consistently greater when the landmark was shifted by 3 cm than when it was shifted by 1.5 cm. These results demonstrated that pigeons can accurately locate an unmarked target area in a two-dimensional vertical arena and that their use of landmarks for spatial localization is similar in several respects to that found in open-field spatial search tasks.

Many organisms pilot their way back to desired locations by the use of visual landmarks. Some aspects of the spatial relationships between the goal and the surfaces and objects that surround it are encoded and later used to seek the goal. Landmarks are used both to get to the vicinity of the goal over long distances and to pinpoint the goal once the animal is in its vicinity. Gallistel (1990, ch. 5) gives numerous examples of such piloting. The most convincing experimental strategy for demonstrating that an animal uses landmarks in spatial search is to systematically shift landmarks surrounding a goal. If the animal then systematically shifts its searching behavior in space, this indicates that it is relying on the shifted landmarks. Variants of this method have been used to show that landmarks are used by rats (Cheng, 1986; Suzuki, Augerinos, & Black, 1980), gerbils (Collett, Cartwright, & Smith, 1986), hamsters (Etienne, Teroni, Hurni, & Portenier, 1990), nutcrackers (Vander Wall, 1982), pigeons (Cheng,

1988, 1989, 1990; Spetch & Edwards, 1988), octopuses (Mather, 1991), ants (Wehner & Raeber, 1979), bees (Cartwright & Collett, 1982, 1983; Dyer & Gould, 1983; von Frisch, 1977), and digger wasps (Tinbergen, 1972).

In a series of recent studies on spatial localization (Cheng, 1988, 1989, 1990; Cheng & Sherry, in press), pigeons were trained to find food buried below the surface of a 1.2- or 1.6-m-square arena. The goal was located at a constant location near an edge of the arena, and a single arrangement of landmarks surrounding the goal was used. Objects placed in the arena or a stripe on the wall served as landmarks. The birds in this task pecked at the ground in search of the hidden food. Occasionally, a test trial was given in which the food was absent. Videotape records showed that the search distribution (of head positions over space) was symmetrical about a single peak, along dimensions both parallel and perpendicular to the wall. The spread of the distribution (ratio of width to height) was a constant proportion of the distance to the nearest landmark (Cheng, 1990). On tests where landmarks were shifted, the birds systematically changed their positions of search. Specifically, if a landmark was shifted by x cm in directions parallel or perpendicular to the edge nearest the goal, the bird shifted the peak position of searching by 0 to x cm in the direction of landmark shift,

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but it did not shift in the orthogonal direction. However, shifts of a landmark in a diagonal direction away from the edge nearest the goal did not cause the birds to shift their place of peak searching in the direction of the landmark shift (Cheng, 1990; Cheng & Sherry, in press). Instead, they shifted farther in the direction parallel to the nearest edge than in the perpendicular direction. In these studies, the fact that the peak place of searching shifted systematically when the landmark was shifted indicated that the birds used the landmarks for localization. However, the fact that search behavior often did not shift the full extent of the landmark suggested that behavior was also controlled by unshifted landmarks (Cheng, 1988).

The work presented here represents a first attempt to train pigeons in an analogous task on a different surface namely, the vertically placed surface of a video monitor. The video screen provided a two-dimensional (2-D) spatial arena, and a specific area near the edge of the screen served as the target. Computer-generated graphic stimuli displayed at various locations on the screen served as landmarks. Pigeons were rewarded with food for pecking at the target. The location of pecks was registered by a touch frame that emitted a grid of infrared beams: Whenever one or more beams was interrupted, a signal was sent to the computer to indicate the coordinates of the interruption.

The touch-screen task provided a differently oriented search space (vertical vs. horizontal), different kinds of landmarks (computer-generated patterns vs. objects), and a different spatial scale from that provided in open-field tasks. We wanted to determine whether pigeons can learn to use graphic landmarks to locate a position and to examine the nature of the search distribution obtained. The experiments also tested whether control by landmarks within this spatial arena would be similar to control by landmarks in the open-field setting (Cheng, 1988, 1989, 1990).

In our experiments, the target area was near a horizontal edge of the video screen in Experiment 1 and a vertical edge in Experiment 2. A rectangular graphic stimulus located near the target served as a landmark. In both experiments, the target was nearer to the edge of the screen than was the landmark. On occasional unrewarded tests, the landmark was shifted by a small extent vertically (up or down), horizontally (left or right), or diagonally (combinations of equal vertical and horizontal shifts). These tests are analogous to those that have been conducted in the open-field task.

EXPERIMENT 1

Method

Subjects

The subjects were 3 experimentally naive White Carneaux pigeons from 1-2 years old. Each bird was maintained at 80% to 85% of its free-feeding weight by 45-mg Noyes pigeon pellets obtained during experimental sessions and by supplements of mixed grain in the home cage. The birds were housed individually in large cages in a colony maintained on a 12:12-h light:dark cycle. Water and grit were freely available in the home cages.

Apparatus

The apparatus consisted of a standard rectangular pigeon chamber (BRS/LVE) with a large opening cut into one end wall. A color monitor (Zenith 1490) with an attached touch frame (Carroll Touch 1490 Smart Frame) was placed against the opening. A thin sheet of Plexiglas covered the video screen so that the pigeons could not directly touch the screen, and a spacer of approximately 1.6 cm was used to separate the touch frame from the monitor surface. A food cup was centered on the wall below the screen, and a small lamp located above the food cup was turned on during food presentations. A Colbourn pellet dispenser, attached to the top of the chamber, dispensed 45-mg pellets through an attached tube into the food cup. To prevent the birds from attempting to perch on the tube, food cup, or touch frame, a metal panel was inserted 3.5 cm from the end wall to act as a barrier. A rectangular hole 8 cm wide and 6 cm high provided access to the food cup. Above this, a large opening 27.5 cm wide and 15 cm high provided access to all except the bottom 5 cm of the video screen.

A microcomputer located in an adjacent room was used to control the experimental contingencies and record the peck coordinates in units of approximately 1.5 cm. Programs were developed with Turbo Pascal (Borland, Inc.) and used routines provided by Carroll Touch and a tachistoscopic display procedure developed by Finley (1989).

General Procedures

Sessions were run 5 or 6 days per week at approximately the same time. Sessions lasted either until all trials were completed or for a maximum of 1 h. The monitor screen was kept clean by wiping it with window cleaner at the beginning of each running day and between sessions as needed.

Training

Magazine training. Each pigeon was given Noyes pellets in its home cage until the pellets were readily consumed. Then, each bird received two or three sessions of magazine training in the chamber. During these sessions, the screen was illuminated with a light gray background, which provided dim chamber illumination. Initially, the food cup was filled with mixed grain, and the lamp above it was turned on until the bird ate all the food. Next, the bird received several trials in which 10 food pellets were dispensed and the lamp was turned on until the bird ate them. Subsequently, the bird received several trials, separated by 60-sec intervals, in which two pellets were dispensed and the food cup was illuminated for 4 sec. These trials were continued until the birds reliably consumed the pellets within these 4-sec periods.

Initial peck training. Each pigeon next received a number of sessions in which food presentations were preceded by the presentation of a graphic target marker (a filled yellow circle 2.0 cm in diameter) on the center of the screen against the light gray background. If the bird pecked at a 2.0-cm-square area containing the target marker within 8 sec, or if 8 sec elapsed without a peck, the target marker was removed (the gray background remained) and food was presented. After a 60-sec intertrial interval (ITI), the target marker was presented again. After a bird made several pecks at the target marker, a response requirement (a single peck in the target area) was initiated, and the ITI was reduced to 5 sec. Over the next two sessions, the location of the target on the screen that would serve as the target area (see Figure 1).

Target peck training. During this phase, the landmark stimulus, a blue bar approximately 1.2 cm wide and 2.4 cm high, was introduced in the location shown in Figure 1. In addition, a frame around the spatial arena was introduced by drawing a dark gray graphic border approximately 1.2 cm wide around the perimeter of the screen (see Figure 1). A fading procedure was used to establish pecking to the target location in the absence of the target marker but in the presence of the landmark. Over a number of ses-



Figure 1. Diagram of the video display presented during baseline and control trials of Experiment 1. The target is not visible to the birds. The graphic frame was a dark gray border drawn around the perimeter of the display screen.

sions, the target marker and the target area were decreased to about $1.5 \text{ cm} \times 1.5 \text{ cm}$ (1 unit width $\times 1$ unit height). Then, the target marker was faded by changing the graphics fill pattern and was further reduced in size until it was eventually eliminated. The rate at which the birds proceeded through these steps was determined by their behavior: Correct pecks incremented a counter by 5 counts. whereas incorrect pecks decremented the counter by 1 count. When the counter increased by 50 counts, the bird was moved to the next step; if the counter decreased by 25 counts, the bird was moved back to a previous step. Typically, the birds pecked at the landmark during their first exposures to the faded target marker, and consequently they moved back and forth between the various steps several times before finally proceeding to the condition in which the target marker was absent. They remained in this condition until they were able to complete an entire session of 100 trials without the counter decrementing enough to require a return to an earlier condition. Trials were separated by a 5-sec ITI, during which the screen was darkened. The birds received between 12 and 18 sessions of training during this phase.

Baseline training. This phase was identical to the last condition of the preceding phase, except that the bird was required to make two, three, or four consecutive pecks to the target location to obtain food; the peck requirement was randomly selected on each trial. This requirement was instituted to prevent the birds from producing food by simply sweeping their beak across the general area of the target, a behavior observed during the previous training phase (see also Morrison & Brown, 1990), and to accustom the birds to making several pecks to obtain food in preparation for the subsequent test phase. To adapt the birds further to conditions used during testing, the last few baseline sessions included 10 control trials randomly intermixed with the 90 standard baseline trials. On control trials, the stimulus conditions were identical to the baseline trials, but pecks at the target location did not produce food. The trial ended 10 sec after the first peck no matter how the bird behaved. Birds 2367, 2774, and 8935 received 20, 9, and 19 baseline sessions, respectively.

Landmark Tests

Following baseline training, each bird was given several test phases, each separated by a return to baseline training conditions for a few sessions. Birds 2367 and 2774 were exposed, in order, to all of the test phases described below. Bird 8935 began the experiment at a later time and was not exposed to Test Phase 1, but proceeded through the remaining test phases in the same order as the other birds. During each test phase, control and landmark-shift test trials were randomly interspersed among reinforced baseline trials within each session. On all control and landmark-shift trials, food was never presented, and the trial was terminated 10 sec after the first peck no matter how the bird behaved.

Test Phase 1: Landmark shifts. This phase consisted of 18 sessions, each containing 6 control trials and 12 trials with landmark shifts, interspersed among 82 baseline trials. On control trials, the landmark was in its normal location. On shift trials, the landmark was shifted by one or two 1.5-cm units left, right, up, down, left and down, or right and down.

Test Phase 2: Landmark shifts. During this test phase, each session contained 1 control trial and 8 trials with landmark shifts, interspersed among 91 baseline trials. Each shift trial contained a different direction of landmark shift: up, down, left, right, up and right, down and right, up and left, or down and left. During the first 14 sessions of this test phase, all shifts were by 2 units. During the next 7 sessions, all shifts were by 1 unit.

Test Phase 3: Landmark removal and top-border manipulations. Each of the eight sessions during this phase contained 2 control trials, 2 trials in which the landmark was absent, 2 trials in which the top graphic border was absent, and 2 trials on which the top border was doubled in width (so that it extended approximately 1.2 cm farther into the search arena). These test trials were randomly mixed within 92 reinforced baseline trials and were designed to determine whether the landmark was necessary for accurate searching and whether search location was controlled by the local edge provided by the graphic border at the top of the arena.

Test Phase 4: Landmark shifts. This phase replicated Test Phase 2, with the only difference being that sessions during which the landmarks were shifted by 1 unit were alternated with sessions during which they were shifted by 2 units. Each bird received five sessions with 1-unit shift tests and five sessions with 2-unit shift tests.

Data Analysis

Peak places in both the horizontal and vertical dimensions were calculated in all phases by using a formal procedure that determines the middle of the highest region in a distribution. First, the median of the distribution was calculated. To ensure that this median represented the middle point of the highest region in the distribution. the median calculation was iterated by calculating it over the region in which the previous median was centered. Thus, if the first median was calculated over the range of 1-17 units and gave a median unit of 5, the next calculation would be over the range of 1-9 units. This process was repeated until two consecutive iterated medians differed by less than 0.05 of a unit. The last value of the median was taken to be the peak place of the distribution. Justification for such a procedure is given in Cheng (1989) and in Roberts (1981). A measure of the spread of the distribution about the peak was provided by calculating the interquartile range. This was defined as the distance from the peak place, minus 25% of the total pecks in the distribution that remained after the last iteration, to the peak place plus 25% of the total pecks in this distribution.

Results and Discussion

Performance on the landmark-shift tests was qualitatively similar across Test Phases 1, 2, and 4. Because Bird 8935 did not participate in Phase 1, only results from the second two landmark-shift phases are presented. An analysis of variance (ANOVA) on peak places from Phases 2 and 4 revealed no significant effect of test phase, and therefore the peck distributions from these two phases were combined for all subsequent analyses. Figure 2



Figure 2. Search distributions along the horizontal and vertical dimensions for each bird on baseline trials in Phases 2 and 4 of Experiment 1. T represents the center of the target location in each dimension.

shows the distribution of pecks in the horizontal and vertical dimensions for individual birds, pooled across all baseline trials from Phases 2 and 4. In both dimensions, the birds consistently pecked most in the vicinity of the target, and their search distributions were roughly symmetrical, similar to the distributions found in open-field tasks (Cheng, 1988, 1989). Figure 3 provides a 2-D plot of search distributions for each bird. Search density in each 1.5-cm-square spatial location is shown with respect to the percentage of maximum pecks, with darker squares representing more dense search. Search behavior is centered around the target location and is somewhat more localized in the vertical dimension than in the horizontal dimension.

Figure 4 provides a 2-D plot of the mean peak places of the 3 birds on test trials for the 1-unit (top graph) and the 2-unit (bottom graph) shift test sessions. The arrows attached to the data points indicate the direction in which the landmark was shifted. The T in the center of each figure indicates the center point of the target area on control (and baseline) trials. The eight surrounding T locations correspond to the eight types of landmark shifts and indicate the location at which the center of the target would be if the shifted landmark provided the only cue. Downward or leftward shifts are indicated by negative numbers, and upward or rightward shifts are indicated by positive numbers. Several features of these data should be noted. First, with one exception (the condition in which the landmark was shifted 2 units up and 2 units left), leftward shifts in the landmark produced leftward shifts in peak location, and rightward shifts in the landmark produced rightward shifts in peak location, relative to control trials. The 1-unit shifts in particular show three clear clusters of data points that differ in the horizontal but not in the vertical dimension. Second, the magnitude of the shifts in peak location was never as great as the magnitude of the landmark shift. Third, horizontal shifts were



Figure 3. Two-dimensional search distributions for each bird on baseline trials in Phases 2 and 4 of Experiment 1. The density of search in each 1.5 cm square location is shown with respect to the percentage of maximum pecks.



Figure 4. Peak place of search in two dimensions on landmark shift and control tests of Phases 2 and 4 of Experiment 1. The T connected to each point shows the center of the target location relative to the shifted landmark.

not consistently larger in response to 2-unit shifts than to 1-unit shifts. Fourth, systematic shifts in peak place were not evident in the vertical dimension. For the 1-unit shifts, search place changed very little as a function of vertical landmark shift, whereas 2-unit shifts of the landmark tended to result in downward shifts of peak place regardless of whether the landmark was shifted up or down. Finally, diagonal shifts of the landmark generally produced less systematic change in search peaks than did horizontal shifts.

The data on peak place in the horizontal and vertical dimensions were analyzed with separate ANOVAs with the three factors being horizontal location of the landmark (left, baseline, right), vertical location of landmark (up, baseline, down), and magnitude of landmark shift (1 or 2 units). In the horizontal dimension, a main effect of the horizontal location of the landmark was found [F(2,4)]

45.09, p < .01, but a main effect of the vertical location of the landmark was not found [F(2,4) = 0.31]. Thus, search behavior shifted in the direction in which the landmark was shifted, but not in the orthogonal direction. There was also a significant interaction between vertical and horizontal placement of the landmarks [F(4,8) =4.02, p < .05, reflecting the smaller response to diagonal landmark shifts than to horizontal landmark shifts alone. The main effect of magnitude of landmark shift (1 or 2 units) was not significant, nor did magnitude of landmark shift interact significantly with either the vertical or horizontal position of the landmark $(p_{\rm S} > .1)$. Thus, 2-unit shifts did not produce a larger shift of peak place than did 1-unit landmark shifts. The three-way interaction between magnitude, horizontal placement, and vertical placement approached significance [F(4,8) = 3.42, p =.065], because the two-way interaction between vertical and horizontal placement was greater for the 2-unit shifts of the landmark.

In the vertical dimension, the only significant effect revealed by the ANOVA on peak places was a two-way interaction between the magnitude of the shift and the vertical placement of the landmark [F(2,4) = 8.17, p < .05]. This reflects the fact that the 2-unit shifts of the landmark produced a downward shift in peak place, whereas 1-unit shifts did not.

In general, these results parallel those found in the openfield search task. That is, shifts of the landmark in the direction parallel to a local edge (i.e., the horizontal dimension) produced systematic shifts in search behavior, whereas shifts in the dimension perpendicular to the nearest local edge did not lead to orderly shifts in search behavior. The one anomalous result observed was the tendency of the birds to show downward shifts in peak place when the landmark was shifted upward by 2 units. One possibility is that shifting the landmark up to this extent may have induced the birds to disregard the landmark as an indicator of where to search.

On tests in which the landmark was shifted diagonally, search behavior appeared to shift more in the horizontal dimension than in the vertical dimension (see the top panel of Figure 4). To determine whether the difference between the two dimensions was significant, we calculated for the four diagonal shift tests the extent to which the horizontal and vertical peak places shifted in the direction of the landmark shift, relative to peak places on control trials (shifts in the opposite direction of the landmark shift received negative scores). These scores were then divided by the magnitude of the landmark shift so that they represented the extent of behavioral shift as a proportion of the landmark shift. These data were then analyzed with a repeated measures ANOVA with shift magnitude (1 or 2 units), shift direction (up and left, up and right, down and left, down and right), and dimension (horizontal and vertical) as factors. The analysis revealed a significant main effect of magnitude of shift [F(1,2)] =24.66, p < .05], reflecting the fact that behavior shifted proportionally more in the direction of the landmark shifts for the 1-unit tests than for the 2-unit tests. There was



Figure 5. Interquartile range of the distributions on landmark shift and control tests of Phases 2 and 4 of Experiment 1.

also a significant interaction between magnitude of shift and direction of shift [F(3,6) = 9.52, p < .02], which presumably reflects the fact that search behavior shifted away from the landmark shift for 2-unit upward diagonal shifts. However, the main effect of dimension failed to reach significance [F(1,2) = 9.52, p > .05], and dimension did not interact significantly with any other factor (all ps > .2).

Figure 5 shows the mean interquartile range, the measure of spread about the peak, under each landmark shift condition. In general, interquartile range tended to increase when the landmark was shifted, and in particular when the landmark was shifted by 2 units. An ANOVA on the horizontal interquartile range revealed a significant interaction between vertical landmark placement and magnitude of the shift [F(2,4) = 11.024, p < .05]. No other effects reached the .05 level of significance. In the vertical dimension, interquartile range was significantly affected by vertical placement of the landmark [F(2,4) = 7.062, p < .05] and by horizontal placement of the landmark [F(2,4) = 7.415, p < .05]. In addition, there was a significant three-way interaction between vertical placement, horizontal placement, and shift magnitude [F(4,8) = 6.223, p < .02].

Table 1 shows the results from Test Phase 3, in which the landmark was removed or in which the top border was removed or extended farther into the arena. On tests in which the landmark was removed, the mean peak place of searching was below and to the right of control trials; this difference approached significance in both the horizontal dimension [t(2) = 3.61, p = .076] and the vertical dimension [t(2) = 3.80, p = .070]. The tendency to peck lower than normal when the landmark was removed is consistent with our speculation that the lower peak places in response to 2-unit upward shifts of the landmark may have reflected a tendency to disregard the landmark.

Manipulation of the top border had no consistent effects on peak places of search in either dimension, suggesting that this graphic border was not an important stimulus despite the fact that it was the closest edge to the target. This is surprising, because in the open-field search task, nearer landmarks are given more weight (Cheng, 1989). One possibility is that a 2-D graphic edge is not as salient as the 3-D frame surrounding the monitor itself.

EXPERIMENT 2

The results of Experiment 1 indicated that pigeons can learn to accurately search for an unmarked location on a video screen and that search could be guided in part by a graphic landmark. These results are similar to those obtained in open-field tasks in which search for unmarked locations was guided by nearby landmarks (Cheng, 1988, 1989). Also similar to results obtained in open-field tasks (Cheng, 1990; Cheng & Sherry, in press) was the finding that the landmark exerted greater control when shifted along the dimension parallel to the nearest edge than when shifted along the dimension perpendicular to that edge. However, in Experiment 1, the vertical dimension and the perpendicular dimension with respect to the edge were

Table 1	
Top-Border Manipulation and Landmark-Removal Tests in E	xperiment 1

•	Horizontal		Vertical	
	Peak Place	Interquartile Range	Peak Place	Interquartile Range
Control	-0.08	1.52	-0.24	0.92
No landmark	1.20	2.34	-0.69	1.12
Top border removed	-0.11	1.98	-0.34	1.12
Top border extended	-0.14	1.47	-0.15	0.76



Figure 6. Diagram of the video display presented during baseline and control trials of Experiment 2. The target is not visible to the birds. No graphic border was provided in this experiment.

confounded. Thus, the lack of clear control by landmark shifts along the perpendicular dimension could be due to the availability of other salient cues, such as proprioceptive cues, that may guide search in the vertical dimension. Although the tendency observed in Experiment 1 to peck lower in response to removal or 2-unit vertical shifts of the landmark argues against exclusive control by proprioceptive cues, there remains a lack of evidence that search behavior in the vertical dimension can be systematically guided by a graphic landmark. Experiment 2 was designed to provide such evidence by using an arrangement in which the nearest edge to the target was along the vertical dimension (see Figure 6). If landmark shifts along the dimension parallel to the edge cause the greatest shifts in search behavior, then with this arrangement vertical landmark shifts should control search behavior more effectively than horizontal landmark shifts.

Method

Subjects

The subjects were Birds 2367 and 2774 from Experiment 1, two Silver King pigeons that had previously served in a timing experiment conducted in standard operant chambers (Birds 241 and 242), and one experimentally naive Silver King pigeon (Bird 243). All birds were housed and maintained as described in Experiment 1.

Apparatus

For this experiment, we used a custom built touch-screen chamber that was 44 cm high, 32 cm deep, and 74 cm wide (inside dimensions). A Zenith 1492 color monitor with attached infrared touch frame (Carroll Touch, 1492 Smart Frame) was placed against an opening centered in the back wall of the chamber. This opening was 10 cm from the raised grid floor of the chamber and provided access to the entire surface of the monitor. Spacers were used to recess the touch frame by approximately 3 cm from the opening and to separate the frame from the monitor by approximately 1.6 cm. Two Gerbrands pigeon grain feeders were mounted on the back wall, one on each side of the monitor. The feeder openings began 8.5 cm from the sides of the monitor opening in the horizontal dimension and were centered with the monitor opening in the vertical dimension. Lamps located within each feeder were used to illuminate feeder presentations. The control equipment was the same as that described in Experiment 1.

Training

Magazine and initial peck training. All pigeons were first given several sessions of magazine training until they reliably and rapidly ate from either feeder. Each bird then received several sessions of autoshaping in which a target marker (a 3-cm-diam yellow circle) was presented on the center of the screen against a dark grav background and followed by 6-sec access to food. For this and all subsequent phases, the left or right food hopper was randomly selected for each food presentation. If the bird pecked in the 3-cm-square area containing the target marker, the target marker was extinguished and food was presented immediately. Otherwise, the target marker was extinguished and food was presented 8 sec after stimulus onset. Once a bird began to peck at the target marker, a number of changes were instituted over the course of several sessions. First, the location of the target and marker was moved in three steps to the intended target location (see Figure 6). Second, the temporal parameters were gradually changed until the ITI was only 5 sec, and the target marker remained on until a peck occurred. Each bird remained in this phase until it reliably completed all scheduled trials in a session.

Target localization training. In this phase, the landmark was introduced and the target marker was gradually eliminated. The landmark was a green rectangle, approximately 1.2 cm high \times 2.4 cm wide, located below and to the right of the target (see Figure 6). Over successive sessions, the target marker and target area were gradually reduced in size until the target area was approximately 2.3 cm square; then, the target marker was further reduced in size and faded, and finally completely eliminated. These changes were instituted in steps, as described in Experiment 1, with transitions between steps determined by each bird's behavior.

Baseline training. In this phase, the target marker was never presented. Trials began with presentation of the landmark on the dark gray background and lasted until each bird had made a criterion number of consecutive pecks on the unmarked target area of the screen. The criterion number varied across trials in a randomly determined order. During the first few sessions, the criterion was 1, 2, or 3 consecutive pecks. Once performance stabilized, the criterion was changed to 2, 3, or 4 consecutive pecks. When the peck criterion was reached, the screen was blackened and one of the hoppers was raised for 6 sec. After a 5-sec ITI, the screen was illuminated with the dark gray background, and the landmark was presented to initiate another trial. Baseline training continued until performance was stable and accurate.

Landmark Tests

Landmark-shift tests. During this phase, two types of test sessions were presented in alternation until each had occurred 10 times. The two types of test sessions differed only in the magnitude of landmark shifts: During 1-unit shift tests, the landmark was shifted approximately 1.5 cm, whereas during 2-unit shift tests, the landmark was shifted approximately 3.0 cm. During both types of tests, 91 of the 100 trials in each session were reinforced baseline trials that were identical to those presented at the end of baseline trials that were identical to those presented at the end of baseline trials were test trials in which the landmark was shifted horizontally (left or right), vertically (up or down), or in one of the four resulting diagonal combinations of a vertical and horizontal shift. On both control and landmark-shift test trials, the trial terminated without reinforcement 8 sec after the first peck.

Landmark-removal tests. Following the landmark-shift test phase, each bird was given a few sessions on the baseline procedure and then given 10 test sessions in which the landmark was removed on occasional test trials. During these sessions, 96 trials were reinforced baseline trials, 2 trials were control trials with the landmark in the baseline location, and 2 were test trials with the landmark removed. During control and test trials, the trial terminated without reinforcement 8 sec after the first peck.

Results and Discussion

Figure 7 shows the distribution of pecks in the horizontal and vertical dimensions during the baseline trials, collapsed across all test sessions. As in Experiment 1, the peak of the distribution for each bird fell in the target area, and the distributions were roughly symmetrical in the two dimensions. Figure 8 is a 2-D plot of baseline peck distributions for each bird and shows that search is centered in the vicinity of the target.

Figure 9 shows the mean peak places calculated for control and shift-test trials, with the arrows indicating the direction in which the landmark was shifted. The locations marked with a T indicate the center points of the hypothetical target locations based on the shifted landmark. Several features of these data should be noted. First,



Figure 7. Search distributions along the horizontal and vertical dimensions for each bird on baseline trials of Experiment 2. T represents the center of the target location in each dimension.

vertical shifts produced systematic shifts of peak place in the vertical dimension only, as can be seen for the three clusters of data points corresponding to upward, control, or downward shifts of the landmark. Second, behavior shifted approximately half of the distance of the 1-unit landmark shifts, indicating joint control by the shifted landmark and other cues. Third, 2-unit landmark shifts did not produce a consistently larger shift of peak place than did 1-unit shifts. Finally, horizontal shifts of the landmark tended to shift peak place in the horizontal dimension but not in the vertical dimension. However, these shifts in peak place produced by horizontal landmark shifts were neither as large nor as systematic as were the vertical shifts in peak place produced by vertical landmark shifts.

The data on peak place were analyzed with separate within-subject ANOVAs for the horizontal and vertical dimensions, as described in Experiment 1. In the horizontal dimension, only the main effect of horizontal location of the landmark reached significance [F(2,8) = 6.71, p < .02]; in the vertical dimension, only the main effect of vertical location of the landmark was significant [F(2,8) = 93.34, p < .0001]. Thus, behavior shifted in the horizontal dimension only when the landmark was shifted horizontally, and in the vertical dimension only when the landmark was shifted vertically.

On tests in which the landmark was shifted diagonally, search behavior appeared to shift more in the vertical dimension than in the horizontal dimension. To determine whether the difference between the two dimensions was significant, we calculated and analyzed the proportional extent of the shift in behavior produced by each of the four diagonal shift tests as described in Experiment 1. The ANOVA on these measures revealed a significant main effect of dimension of shift [F(1,4) = 43.02, p < .01], indicating a greater shift in the vertical than in the horizontal dimension. No other effects were significant (all ps > .1).

Figure 10 shows the mean interquartile range under each landmark-shift condition. In the horizontal dimension, the range was affected only by horizontal placement of the landmark [F(2,8) = 5.084, p < .05]. The ANOVA on interquartile range in the vertical dimension revealed no significant effects.

Removal of the landmark had little systematic effect on peak places; t tests comparing peak places on control and landmark-removal test trials failed to reveal any significant difference in either the horizontal dimension [control tests, M = -0.01; landmark-removal tests, M = -0.07; t(4) = 0.3138, p > .50] or in the vertical dimension [control tests, M = -0.07; landmark-removal tests, M = -0.02; t(4) = 0.300, p > .50]. The interquartile range of the search distribution was generally larger in the absence of the landmark, but this difference also failed to reach significance in either the horizontal dimension [control tests, M = 0.91; landmark-removal tests, M = 1.25; t(4) = 1.22, p > .25] or the vertical dimension [control tests, M = 0.78; landmark-removal



Figure 8. Two-dimensional search distributions for each bird on baseline trials of Experiment 2. The density of search in each 1.5 cm square location is shown with respect to the percentage of maximum pecks.

tests, M = 1.14; t(4) = 1.92, p > .10]. Thus, despite the significant effect of shifting the landmark, the birds located the target area with reasonable accuracy in the absence of the landmark.

In open-field studies, Cheng (1990) found that the spread of pigeons' search distributions in a given dimension is a constant proportion of the perpendicular distance from the nearest landmark or edge to the goal (i.e., that Weber's law holds). The Weber fraction calculated for two different experiments was .817 and .367 (Cheng, 1990). To provide a rough comparison, we calculated each bird's spread of searching in the horizontal dimension for the control trials from the three test series of this experiment (i.e., from the 1-unit shift, the 2-unit shift, and the no-landmark test series), using the procedure described in Cheng. Weber fractions were computed by dividing the spread by the distance from the center of the target area to the nearest edge. The Weber fractions calculated for individual birds ranged from .573 to .973, and the mean fractions from the three test series were .761, .668, and .783. Thus, the relative spread of the search distribution appears similar to that obtained in open-field tasks. Further research with varied target-to-landmark distances is needed to determine whether Weber's law holds in the touch-screen task.

GENERAL DISCUSSION

The present results demonstrated that pigeons can learn to accurately localize an unmarked target area on a video screen. Search distributions on baseline trials were characterized by a single peak in the vicinity of the target and were roughly symmetrical about the peak. In both experiments, the graphic landmark exerted good control of searching behavior within one dimension, as indicated by the systematic shifts in peak place of searching produced when the landmark was shifted along that dimension. Searching shifted in the direction of the landmark shift and not in the orthogonal dimension. Although comparisons across the two experiments must be made with caution because of differences in procedural and apparatus details, it is worth noting that in both cases the dimension that exerted good control was the one parallel to the nearest edge (horizontal in Experiment 1 and vertical in Experiment 2). The landmark exerted less control in the dimension perpendicular to the nearest edge, as indicated by the smaller (Experiment 2) or inconsistent (Experiment 1) shifts in peak place that resulted when the landmark was shifted in the perpendicular dimension. Similar results were obtained with diagonal shifts of the landmark; searching generally shifted more in the dimen-



Figure 9. Peak place of search in two dimensions on landmark shift and control tests of Experiment 2. The T connected to each point shows the center of the target location relative to the shifted landmark.

sion parallel to the nearest edge than in the dimension perpendicular to the nearest edge.

In all cases, the shift in peak place was of smaller magnitude than the shift of the landmark, and 3.0-cm shifts did not produce consistently larger shifts in peak place of searching than did 1.5-cm shifts. These results indicate joint control by the shifted landmark and the unshifted cues. The use of unshifted cues also seems apparent from the reasonably accurate search behavior obtained when the landmark was completely removed, particularly in Experiment 2. It is not clear which unshifted cues the birds might have used, but several possibilities exist. For example, although the pigeons did not appear to use the graphic border provided in Experiment 1, the frame provided by the opening in the chamber surrounding the monitor surface could provide salient cues. Proprioceptive cues might also be quite salient in this task. It is also possible that the birds created their own landmarks by leaving marks on the screen from their pecks. Although we cannot completely rule out this latter possibility, we think it was an unlikely source of control for several reasons. First, although the screen was sometimes dusty after sessions, we did not detect any specific marks that could provide cues about the location of the target area. Second, the screen was frequently wiped clean just before a session. Therefore, if there were peck-generated landmarks that were not detectable to a human observer, they could only be available to guide behavior on later trials of the session and would only be created if the bird pecked accurately in their absence. They also could not have provided an exclusive source of control, because then the reliable effects of landmark shifts would not be expected. Finally, we have recently begun a study in which the target area varies from trial to trial and is determined solely



Figure 10. Interquartile range of the distributions on landmark shift and control tests of Experiment 2.

on the basis of graphic landmarks that move across trials. This arrangement precludes control by proprioceptive cues or peck-generated landmarks. Our preliminary results indicate that target localization in this situation is also very accurate.

In several respects, the results obtained in the present study are quite similar to those obtained in the open-field search task (Cheng, 1988, 1989, 1990). In the open-field task, search distributions are also symmetrical about a single peak, and the ratio of the spread of peak searching to the distance from the target to the nearest landmark is similar to that found here. Shifts of a nearby landmark in dimensions parallel or perpendicular to the nearest edge produce shifts in place of searching in the direction of the landmark shift but not in the orthogonal direction (Cheng, 1988, 1989). Peak place of searching generally shifts only part way toward the target associated with the shifted landmark, indicating control by unshifted landmarks. These characteristics of landmark use provided support for the vector sum model (Cheng, 1988, 1989). According to this model, a goal is localized by a weighted average of vectors from various landmarks to the goal. When one of these landmarks is shifted, searching should shift in the direction in which the landmark is shifted but not in orthogonal directions. Moreover, searching will generally shift only part of the distance of the landmark shift because of averaging with unshifted landmarks.

Certain features of the present findings are consistent with other recent results from the open-field search task. For example, shifts of a landmark in the direction parallel to the nearest edge generally produce larger or more systematic shifts in open-field search behavior than do shifts in the direction perpendicular to the edge (Cheng & Sherry, in press). Diagonal landmark shifts do not consistently produce shifts in searching that are along the line in which the landmark is shifted (Cheng, 1990; Cheng & Sherry, in press). These latter results cannot be accommodated by the vector sum model because according to that model, place of peak searching must shift along the line connecting the target of the shifted landmark and the target of the unshifted landmark-thus, in the direction of the landmark shift. Cheng and Sherry suggested that in addition to, or perhaps instead of, vector summation, the perpendicular distance of the target from a nearby edge is used in calculating where to search. Some hints that pigeons in the touch-screen task might also be using the perpendicular distance to an edge is found in the top panel of Figure 4. Here, it is shown that the birds shifted systematically parallel to the edge (horizontally) but maintained approximately the same perpendicular distance to the edge (searched at the same vertical position) under all landmark shifts.

It is interesting that the results obtained in the present study provide the same pattern of support and disconfirmation of the vector sum model found in the open-field search tasks. Our touch-screen video task differs in a number of potentially important ways from the open-field task. In our task, the arena is considerably smaller than that

provided by the typical open-field arena and is oriented vertically rather than horizontally. In the open-field task, the subject moves through space to localize and approach the goal, whereas our task provides a top view of the entire arena, and very little movement of the body is reouired to move through the space. Our landmark was 2-D rather than 3-D, and in our task food was delivered from locations other than the target at which the birds pecked. Search behavior in the present task (pecks on the screen) produced no detectable change in stimulus conditions. whereas search behavior in the open-field task displaces bedding that could provide stimulus support for later search. Although further experiments may vet reveal some differences, the findings that baseline patterns of search behavior are similar and that landmark use shows similar characteristics within these two very different tasks suggest that the processes governing spatial search and landmark use may have considerable generality.

Touch-screen systems like those used in the present research offer the advantages inherent in the use of automated equipment, yet are more flexible than standard operant chambers (Morrison & Brown, 1990; Pisacreta & Rilling, 1987). Many stimuli, including dynamic ones, may be presented, and time and location of responses over the entire video screen can be recorded. The use of touchscreen systems have allowed or facilitated investigations of texture discriminations (Cook, 1992), visual search (Blough, 1989), and concept learning (Wright, Cook, Rivera, Sands, & Delius, 1988). The present results suggest that they may also provide a valuable complementary tool for the study of spatial search.

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