

Control of Pigeons' Spatial Search by Graphic Landmarks in a Touch-Screen Task

Marcia L. Spetch and Michael V. Mondloch

Pigeons learned to peck an unmarked 2-cm² target area, defined by 4 visually distinct graphic landmarks, on a color monitor with an attached touch frame. The configuration of landmarks and target area was constant during training, but their location on the screen varied across trials. The presence, relative location, and features of the landmarks were manipulated on probe trials. Most birds showed control by only 1 or 2 of the landmarks, and some birds displayed surprisingly accurate search with a single landmark. For individual birds, landmark-removal tests were very consistent with landmark-shift tests in indicating which landmark or landmarks controlled search. However, the dominant landmark varied across birds. Manipulation of landmark color and shape revealed that control was based exclusively on color.

Many organisms use visual landmarks to locate, remember, and return to desired spatial locations. Spatial information available from visual landmarks may be encoded during initial exposure or visits to a given location, and remembered spatial relationships can then guide search during subsequent attempts to return to that location. Experimental tests in which landmarks are shifted or removed have provided convincing demonstrations that visual landmarks can control spatial search in a variety of animals, including rodents (Cheng, 1986; Collett, Cartwright, & Smith, 1986; Etienne, Teroni, Hurni, & Portenier, 1990; Suzuki, Augerinos, & Black, 1980), birds (Cheng, 1988, 1989, 1990; Cheng & Sherry, 1992; Spetch & Edwards, 1988; Vander Wall, 1982), cephalopods (Mather, 1991), and insects (Cartwright & Collett, 1982, 1983; Dyer & Gould, 1983; Tinbergen, 1972; von Frisch, 1953; Wehner & Raeber, 1979). Considerable recent research has been devoted to understanding the processes by which organisms derive distance and directional information from visual stimuli (e.g., Cheng, 1989; Cheng & Sherry, 1992). Gallistel (1990) provided an excellent discussion of research on piloting by landmarks in animals.

Most real-world locations contain or are surrounded by numerous stimuli that might be encoded as landmarks for later spatial search. In many natural settings it may be adaptive for animals to encode spatial information from several sources. This would allow accurate localization even if one or more of the sources of information was not available when

the animal returned to the location (Balda & Turek, 1984; Spetch & Edwards, 1988). For example, when searching for home, pigeons appear to derive directional information from the sun when it is available but can derive directional information from other sources on overcast days (Keeton, 1974). In a laboratory spatial memory task, pigeons appeared to encode the location of a goal in terms of both its absolute location in the room and its position within a local array of cues and could use either source of information on a test trial (Spetch & Edwards, 1988). Encoding spatial information from several sources may also improve the precision of spatial search, because each source of information is likely to be inaccurate to some degree (Cheng, 1992). Bees, for example, show more precise goal localization when the goal is defined by a triangular array of landmarks than when it is defined by a single landmark (Cartwright & Collett, 1983), presumably because positioning by crossed bearings allows the animals to pinpoint the goal more accurately than positioning on the basis of a single landmark. Studies of landmark-based search also suggest that pigeons encode the relationship between the goal and more than one landmark (e.g., Cheng, 1988). Thus, pigeons may often encode spatial information from several sources, either because it improves precision or because it provides the flexibility that would be required to search under conditions in which a particular source of spatial information is unavailable. It seems likely, however, that some selectivity of encoding might occur when a goal location is surrounded by several potentially adequate landmarks.

The present investigation explored how control of pigeons' spatial search is allocated among multiple visual landmarks. The situation we explored is one in which a target area was surrounded by four landmarks. Each landmark was visually distinct and close to the target area. During the training period, all four landmarks were present on every search trial, and the spatial relations among the four landmarks and the target area were held constant. During testing we manipulated the presence or location of individual landmarks to determine the extent to which the pigeons had encoded, and the extent to which they relied on, the spatial information provided by each landmark.

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This investigation of control by multiple landmarks was conducted in a touch-screen spatial search task. In this task the surface of a color monitor served as a two-dimensional search space. An infrared touch frame surrounding the monitor recorded the location of pigeons' pecks. Graphic stimuli displayed on the monitor served as landmarks. In a recent study (Spetch, Cheng, & Mondloch, 1992) we demonstrated that pigeons will use graphic stimuli as landmarks and that control by graphic landmarks in the touch-screen task is remarkably similar in several respects to control by landmarks in open-field search tasks. Those results, together with the growing literature demonstrating the value of touch-screen technology for the study of behavioral and cognitive processes in animals (e.g., Blough, 1989; Cook, 1992; Morrison & Brown, 1990; Pisacreta & Rilling, 1987; Wright, Cook, Rivera, Sands, & Delius, 1988), encouraged us to use the touch-screen task to further investigate landmark-based search in pigeons.

Experiment 1

The tests conducted in the present study involved shifting or removing the landmarks. These tests were directed at three specific questions. First, when trained to locate a target area that is surrounded by several close and reliable landmarks, how much of the spatial information do pigeons encode? Second, if the encoding is selective, will the same landmark or landmarks be favored by all subjects? Consistency among the subjects would suggest that pigeons have a uniform preference for certain features in their selection of landmarks. In our study, all four landmarks were distinct in color and shape. In addition, one of the four landmarks was asymmetrical, one was closer to the target area, and one was farther from the target area than the remaining landmarks (see Figure 1). A consistent preference for one of these landmarks would provide an indication of the relative importance of these characteristics. On the other hand, lack of consensus about which landmark is best would suggest that none of these characteristics (within the range we manipulated) was particularly critical. Finally, if encoding was selective, would landmark-shift tests be consistent with the landmark-removal tests in indicating the degree to which particular landmarks controlled a bird's search?

Method

Subjects

Six adult Silver King pigeons were maintained at approximately 85% of their free-feeding weights by food obtained during and after experimental sessions. All birds were new to the touch-screen search task but were experienced at pecking keys in standard operant chambers. Bird C271 had also served in an open-field spatial memory study prior to this experiment. All birds were housed in large individual cages under a 12-hr light/dark cycle. Sessions were conducted from 1 to 7 hr after light onset. Water and grit were available ad libitum in the home cages.

Apparatus

Birds C242, C207, C271, and B329 were tested in a modified rectangular pigeon chamber (BRS/LVE) with a large opening cut

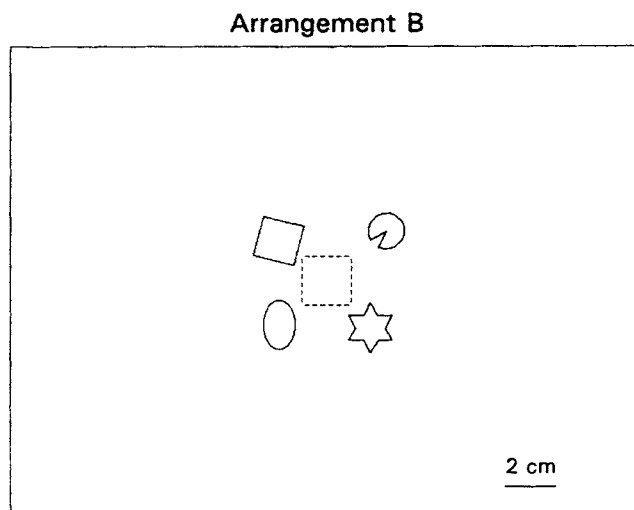
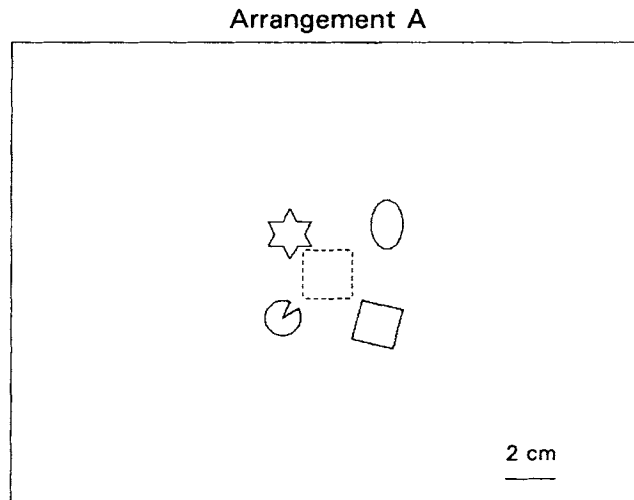


Figure 1. Diagram showing the two training configurations of the 2-cm² target area and four surrounding graphic landmarks. (The dashed square around the target is not displayed for the birds. The four landmarks are distinctly colored. Note that the location on the screen of the target area and the surrounding array of landmarks is not always in the center as depicted here but instead varies across trials. In Experiment 1, 3 birds were trained with Arrangement A and 3 with Arrangement B. In Experiment 2 all birds were trained with Arrangement A.)

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, and a spacer of approximately 1.6 cm separated the touch frame from the surface of the monitor. A Plexiglas food cup was centered on the wall below the screen, and a small lamp beneath the cup illuminated 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.

The remaining 2 pigeons were tested in a large custom-built chamber, 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 horizontally and were centered vertically with the monitor opening. Lamps located within each feeder were used to illuminate food presentations. Photocells in each hopper measured head entries into the hopper and were used to limit eating times.

Microcomputers located in an adjacent room controlled experimental contingencies and recorded peck coordinates in units of approximately 1 cm². Programs were developed in Turbo Pascal (Borland, Inc.).

Search Space and Stimuli

The search space was a rectangular area (approximately 26 cm × 20 cm) on the surface of the color monitors. Two arrangements of four graphic stimuli were constructed as shown in Figure 1. Birds C242, C207, and B488 were trained with the arrangement shown in the top diagram, and the remaining three birds were trained with the arrangement shown in the bottom diagram. The dashed outline of the 2-cm² target area is shown for illustrative purposes only. The four landmarks were distinctly colored. In both arrangements, the star was green, the ellipse was coral, the pie was blue, the rectangle was dark red, and the background color on the monitor was dark grey. The location on the screen of the entire array of landmarks and the corresponding target area varied from trial to trial, so that no fixed location on the screen served as the target area. The location of the center of the target area was randomly selected on each trial within three constraints. First, the target location was only placed in locations that allowed room for all landmarks. Second, we did not use the lowest two target locations that were possible given the first constraint, because some birds had difficulty meeting the response requirement during the initial training phase on trials in which the target area was low on the screen. Finally, to ensure that the target area always contained the same number of possible response coordinates, the center of each target location was always midway between two infrared beams in both dimensions.

General Procedures

Sessions were conducted at approximately the same time each day, 5 or 6 days per week. Sessions lasted until all scheduled trials were completed or for a maximum of 1 hr. The monitor screen was cleaned with window cleaner at the beginning of each day and between sessions as needed.

Training

Each bird was initially trained to eat from the food hoppers or pellet dispenser and then given several sessions of autoshaping. Each autoshaping trial began with illumination of a target marker (a 2-cm diameter solid yellow circle centered in the target area). The location of the target varied across trials as described above. The four landmarks surrounding the target area were displayed in a dim fill pattern that made them much less salient than the target marker. The target marker remained illuminated for 8 s or until a peck in the target area was recorded; then a food reward was presented (two 45-mg pellets or 2 s of eating time from a randomly selected food

hopper). Trials were separated by a 60-s intertrial interval (ITI) during which the monitor was illuminated with the dark grey background but no graphic stimuli were present.

Once a pigeon was pecking on at least 80% of the trials, it was moved to a training procedure in which a response in the target area was required to terminate the trial and produce the food reward. The ITI was initially 30 s and was reduced over subsequent sessions to 15 s and then to 5 s. The salience of the graphic landmarks was then gradually increased over sessions by changing the fill patterns from dim to solid. Next, the target marker was faded out within and between sessions by gradually changing its fill pattern from solid to empty at a rate that depended on each bird's accuracy. This training phase continued until the bird completed an entire session with an empty target fill pattern (i.e., with the target marker absent).

During the next phase of training the response requirement was gradually increased over sessions. First, the number of pecks required to the target area was increased from one to four. Then, a consecutive peck requirement was added such that the last two pecks had to be in the target area. Pecks outside the target area reset the consecutive peck counter. Finally, the consecutive peck requirement was increased again so that the last three pecks had to all fall within the target area. This requirement ensured that the bird could not trigger reinforcement by simply sweeping its beak around in the general vicinity of the target area.

During a final phase of training, the density of reinforcement for meeting the response requirement was decreased from 100%, to 80%, and finally to 50% in preparation for testing. On nonreinforced trials, completion of the response criteria resulted in initiation of the ITI. Thus, by the end of training all birds were accustomed to responding to the target area several times each trial and to receiving food reinforcement only 50% of the time that they met the response criteria. Each bird remained on the baseline 50% reinforcement condition for a minimum of five sessions and advanced to the test phase only after it completed at least 80 trials on each of the last two sessions.

The training phase lasted for 40 to 90 sessions. Bird C204 proceeded the fastest and Bird C207 proceeded the slowest through training.

Testing Procedures

During all test sessions, 50% of the trials were reinforced baseline trials. The remaining trials consisted of nonreinforced baseline trials, control trials, and test trials. Control trials were visually identical to baseline trials with all four landmarks present in their normal positions. On test trials, the presence or relative location of one or more of the landmarks was manipulated. On both control and test trials, the trial terminated without reinforcement 8 s after the first peck recorded anywhere on the screen.

Each bird was exposed to eight types of test sessions that differed in how the landmarks were manipulated. Two of these entailed landmark-removal tests in which the presence of certain landmarks was manipulated: During *three-absent* tests only one of the four landmarks was present on each test trial, and during *one-absent* tests one of the four landmarks was absent on each test trial. The remaining six types of test sessions were landmark-shift tests in which one of the landmarks was shifted outward from its normal location in the array. The landmarks were shifted by approximately 1 cm (1-unit shift tests) or 2 cm (2-unit shift tests) horizontally (horizontal-shift tests), vertically (vertical-shift tests), or both horizontally and vertically (diagonal-shift tests).

Each test session included four types of test trials that differed in which landmark was manipulated. Each block of trials within the test session contained one trial of each test type and one control trial

interspersed among the baseline trials. The order of trials was randomly selected within blocks. During the first series of test sessions for the birds in Arrangement A, each block of trials contained five reinforced baseline trials and no nonreinforced baseline trials. Ten trial blocks were scheduled for each session. During the second series of tests for birds in Arrangement A, and during all tests for birds in Arrangement B, a lower test-trial density was used in which each block of trials included eight reinforced baseline trials and three nonreinforced baseline trials. In this case, six trial blocks were scheduled in each session.

For birds in Arrangement A, each test session type was presented twice at the high test-trial density and once at the low test-trial density, resulting in a total of 26 scheduled test trials of each type. Arrangement B birds received 4 test sessions of each type at the low test-trial density, for a total of 24 scheduled trials of each type. A single baseline session with 50% reinforcement followed each high test-trial density session. With the low test-trial density sessions, 5 baseline sessions with 50% reinforcement followed 16 consecutive test sessions. Each type of test session was presented once in each block of 8 test sessions, and the order within blocks was randomly determined.

Data Recording and Analysis

Peck coordinates were recorded in units of approximately 1 cm². For each trial this resulted in an 18 × 25 unit matrix. Because the target location varied across trials, all units were defined in relation to the target. The variable target location resulted in some units that were only rarely available. For example, a response unit far to the left of the target would be available if the target were near the right edge of the monitor but not if the target were near the left edge of the monitor. To adjust for the differential availability of the response units, we weighed all data by dividing the number of responses in each unit by the number of times the unit was available. Thus, all data presented are shown in terms of location relative to a moving target, and all data are weighted according to opportunity to respond in each particular location. Because very few pecks occurred at a far distance from the target area, and to simplify the data analysis and presentation, all pecks that fell farther than 8 units from the target were treated as having fallen in the 8th unit. Finally, all response distributions are shown as the proportion of total weighted pecks that fell in each response unit.

On single-landmark tests in which it seemed possible that the birds might not know which direction from the landmark to search, we excluded trials in which the landmark fell close enough to one edge that pecking a target distance away in a wrong direction was not possible. Thus, the response distributions shown for these tests are based on trials in which it was always possible for the bird to peck a target distance away on all sides of the single landmark presented. It should be noted, however, that this exclusion did not appear to change the response distributions in any important way.

Inspection of the response distributions generally provided a very clear indication of a bird's accuracy in locating the target. However, to provide an additional quantitative measure, an accuracy score was computed for each bird in each condition by determining the proportion of total weighted pecks that fell in the four target units. For shift tests, we calculated two accuracy scores, one based on the proportion of pecks that fell in the target area in relation to the shifted landmark and one based on the proportion of pecks that fell in the target area in relation to the unshifted landmarks. Although it was physically possible for the birds to peck in each of the 450 units available on the screen, only 209 units served as possible target areas during training (units near the edges of the screen never served as target areas because they did not allow room for all landmarks).

Thus, the proportion of pecks expected to fall within the 4 target units on the basis of chance was only .019. However, it seemed possible that somewhat higher levels of accuracy might be achieved if the birds learned a proximity rule. That is, the birds might learn to peck in the general vicinity of the landmarks, even if they did not learn the direction of the target area from a given landmark. To provide a very stringent assessment of accuracy, we therefore used a 6 × 6 unit area (approximately 6 cm²) for our estimate of chance-level responding. Four target units out of 36 possible units yielded a chance level accuracy of .11. To provide some ancillary statistical support for our conclusions about which conditions resulted in accurate search behavior, one-sample Z-tests for proportions (with $n = \text{pecks}$) were conducted for each bird in each condition to determine whether the obtained accuracy score was significantly above .11.

For landmark-shift tests, we used the iterated median procedure described in Cheng (1989) and Spetch et al. (1992) to compute the peak place of searching in both the vertical and horizontal dimensions. These peaks were based on the weighted response distributions. For tests of statistical significance, alpha was set at .05.

Results

Responding on control trials of all tests was very localized, and accuracy was well above chance level for all birds.

Landmark-Removal Tests

The three-absent and one-absent tests indicated that control was not distributed equally among the four landmarks. Instead, each bird showed considerable selectivity of control, and some birds showed almost exclusive control by a single landmark. However, the birds differed in which landmark(s) exerted the best control.

Accuracy scores on the control and four types of test trials of the three-absent and one-absent tests are shown for each bird in Table 1. Values marked with an asterisk are significantly above the .11 chance level according to the Z test.

Table 1
Proportion of Pecks in Target Area for Landmark Removal Tests of Experiment 1

Trial type	Birds					
	C242	C207	B488	C271	C204	B329
Three-absent test						
Control	.42*	.68*	.40*	.49*	.61*	.79*
LM1 alone	.00	.10	.02	.03	.00	.32*
LM2 alone	.02	.06	.08	.00	.06	.03
LM3 alone	.05	.18*	.30*	.49*	.16	.29*
LM4 alone	.41*	.07	.07	.03	.42*	.02
One-absent test						
Control	.39*	.69*	.52*	.48*	.66*	.71*
LM1 absent	.44*	.24*	.59*	.40*	.70*	.26*
LM2 absent	.24*	.59*	.48*	.45*	.68*	.70*
LM3 absent	.42*	.54*	.24*	.09	.54*	.55*
LM4 absent	.04	.59*	.27*	.43*	.05	.73*

Note. LM = landmark. Numbers that are significantly above chance according to Z test are indicated with an asterisk; see text for details.

Figures 2 to 7 show an individual bird's response distributions from these tests. These response distributions are pooled across all test sessions of a given type and are shown in both side view and top view form. The height of the distribution as seen from the side view indicates the proportion of weighted pecks falling in each unit and provides an indication of how peaked the distribution is. Units containing less than 0.001 of the weighted pecks are plotted as empty units. The top views of the response distributions are shown in the same orientation as the actual touch screen and plot only units containing at least 5% of the total weighted pecks, or in other words, the units plotted are ones in which there is a concentration of responding. The top views provide an indication of the location of peak responding. In both views, the intersection of the two zero lines indicates the center of the target area, and the views show 8 units (approximately 8 cm) on either side of the target center.

Because the birds differed in which landmark(s) exerted the greatest control of accurate search, we discuss the results for each bird individually.

Bird C242 (Arrangement A). The three-absent tests showed excellent control by LM4 (the rectangle) and showed poor control by the other three landmarks when presented alone, suggesting that Bird C242 had encoded the target location primarily in terms of the fourth landmark (see Figure 2). The results of the one-absent test were consistent with this conclusion: Response accuracy was completely disrupted, particularly in the horizontal dimension, when LM4 was absent. Little disruption of accuracy is seen when any other single landmark is absent.

Bird C207 (Arrangement A). The three-absent tests did not suggest complete dominance by any single landmark. Searching was not very accurate with any of the single landmarks, although responding appeared to be more localized when either of the top two landmarks (LM1 or LM2) were presented alone than when either of the bottom two landmarks were presented alone (see Figure 3). However, the localized responding when LM1 and LM2 were presented alone was not centered on the target and therefore did not generate accurate search (see Table 1). During the one-absent tests, search remained accurate when any single landmark was removed, although some disruption in accuracy was seen when LM1 was absent. Thus, the overall profile for this bird suggested that none of the single landmarks exerted exclusive control but that LM1 exerted more control than any of the other individual landmarks.

Bird B488 (Arrangement A). The three-absent tests suggested that this bird had encoded the target location primarily in relation to LM3 (see Figure 4). Bird B488 searched more accurately when LM3 was presented alone than when any other landmark was presented alone. Nevertheless, Bird B488 did not depend exclusively on LM3 for accurate search because removal of LM3 during the one-absent tests reduced but did not eliminate accurate search (see Figure 4 and Table 1). Thus, LM3 appeared to be a dominant, but not an essential, landmark for Bird B488.

Bird C271 (Arrangement B). As can be seen in Figure 5 and Table 1, Bird C271 achieved far more accurate localization on tests with LM3 alone than with any of the other

landmarks presented alone. In fact, search accuracy with LM3 alone was as high as that achieved on control trials. During the one-absent tests, Bird C271 searched accurately when either LM1, LM2, or LM4 was removed but failed to search accurately, particularly in the vertical dimension, when LM3 was removed. Thus, Bird C271 appeared to have encoded the target area almost exclusively in terms of LM3.

Bird C204 (Arrangement B). The three-absent tests indicated that C204 had encoded the target location primarily in terms of LM4 (see Figure 6 and Table 1). Search was far more localized and accurate when LM4 was presented alone than when any of the other landmarks were presented alone. During the one-absent tests, removal of LM1, LM2, or LM3 did not disrupt search accuracy, whereas removal of LM4 resulted in scattered and inaccurate search, particularly in the horizontal dimension. Thus, LM4 clearly was the dominant landmark for this bird.

Bird B329 (Arrangement B). During the three-absent tests, this bird searched accurately with LM1 alone and with LM3 alone (see Figure 7 and Table 1). In sharp contrast, search was very scattered when either of the right two landmarks were presented alone. During the one-absent tests, Bird B329 searched accurately in all cases in which a single landmark was removed, although some disruption was seen when LM1 was absent. Thus, it appears that Bird B329 encoded spatial information about both LM1 and LM3 but relied slightly more on LM1.

To rank the four landmarks on the basis of their combined control on the one-absent and three-absent tests, we used the average of the accuracy when the landmark was presented alone on three-absent tests and the disruption in accuracy when that landmark was absent (i.e., control accuracy minus accuracy on one-absent tests for that landmark). According to this measure, the highest ranked landmark was LM4 for Bird C242, LM1 for Bird C207, LM3 for Bird B488, LM3 for Bird C271, LM4 for Bird C204, and LM1 for Bird B329. The lowest ranked landmark was LM1 for Bird C242, LM2 for Bird C207, LM1 for Bird B488, LM2 for Bird C271, LM1 for Bird C204, and LM4 for Bird B329.

Landmark-Shift Tests

The results of the landmark-shift tests were highly consistent with those of the landmark-removal tests in indicating which landmarks exerted the most control for individual birds. The 1-unit and 2-unit shift tests showed a similar pattern of results. For economy, we therefore report only the results of 2-unit shift tests, in which there was no overlap between the target area defined by the shifted landmark and that defined by the unshifted landmarks. Table 2 shows the proportion of pecks that fell in the target on control trials as well as the proportion of pecks that fell in either target (the target as defined by the shifted landmark or the target as defined by the unshifted landmarks) on test trials for the 2-unit vertical-, horizontal-, and diagonal-shift tests. A higher proportion of pecks in the target area defined by the shifted landmark than in the target area defined by the unshifted landmarks was seen in 15 in-

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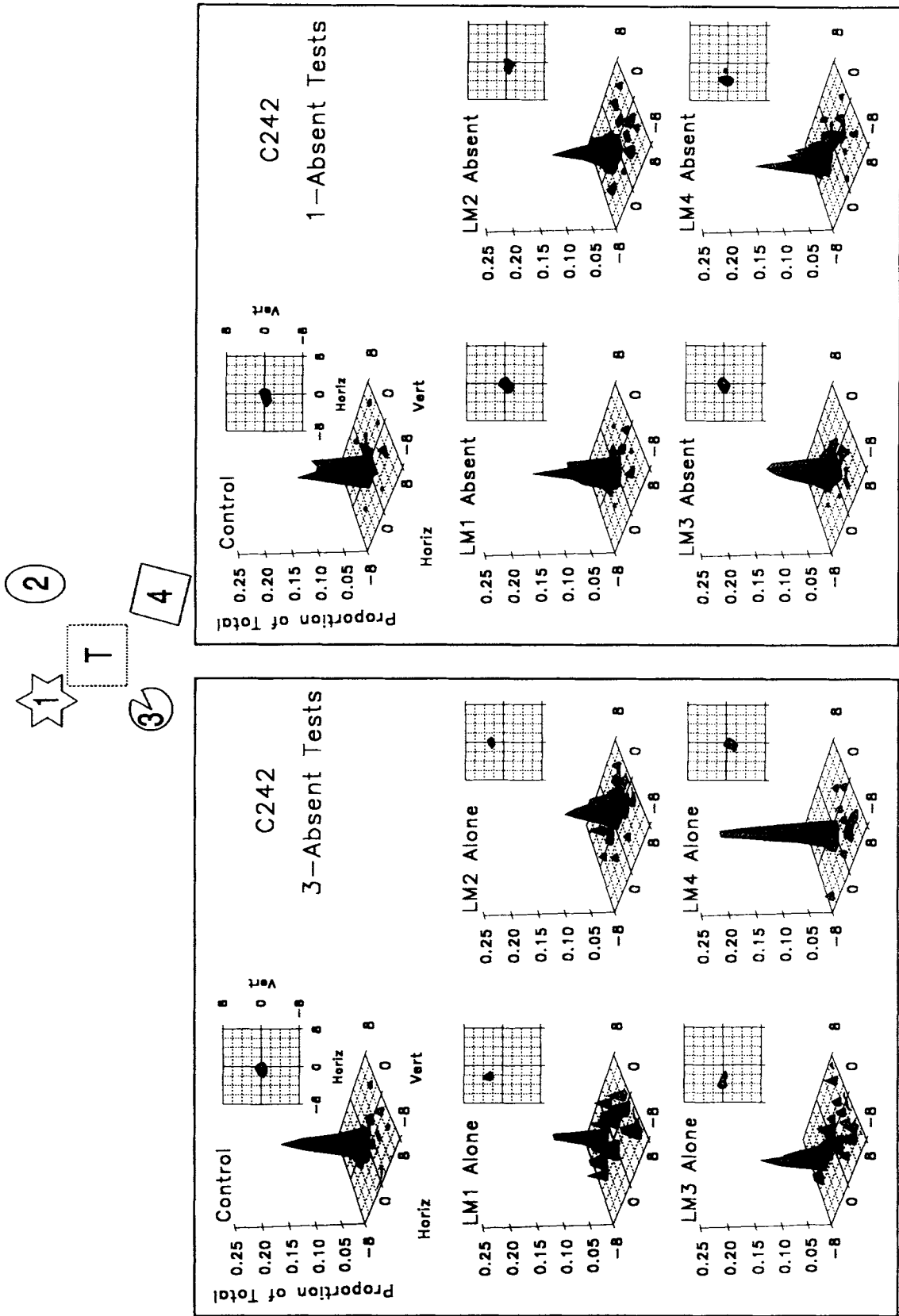


Figure 2. Response distributions on control and test trials from the three-absent and one-absent tests of Experiment 1 for Bird C242. (The diagram at the top shows the arrangement of Landmarks [LMs] 1 to 4 in relation to the target area [T] on baseline and control trials. Horiz = horizontal; Vert = vertical. See text for details.)

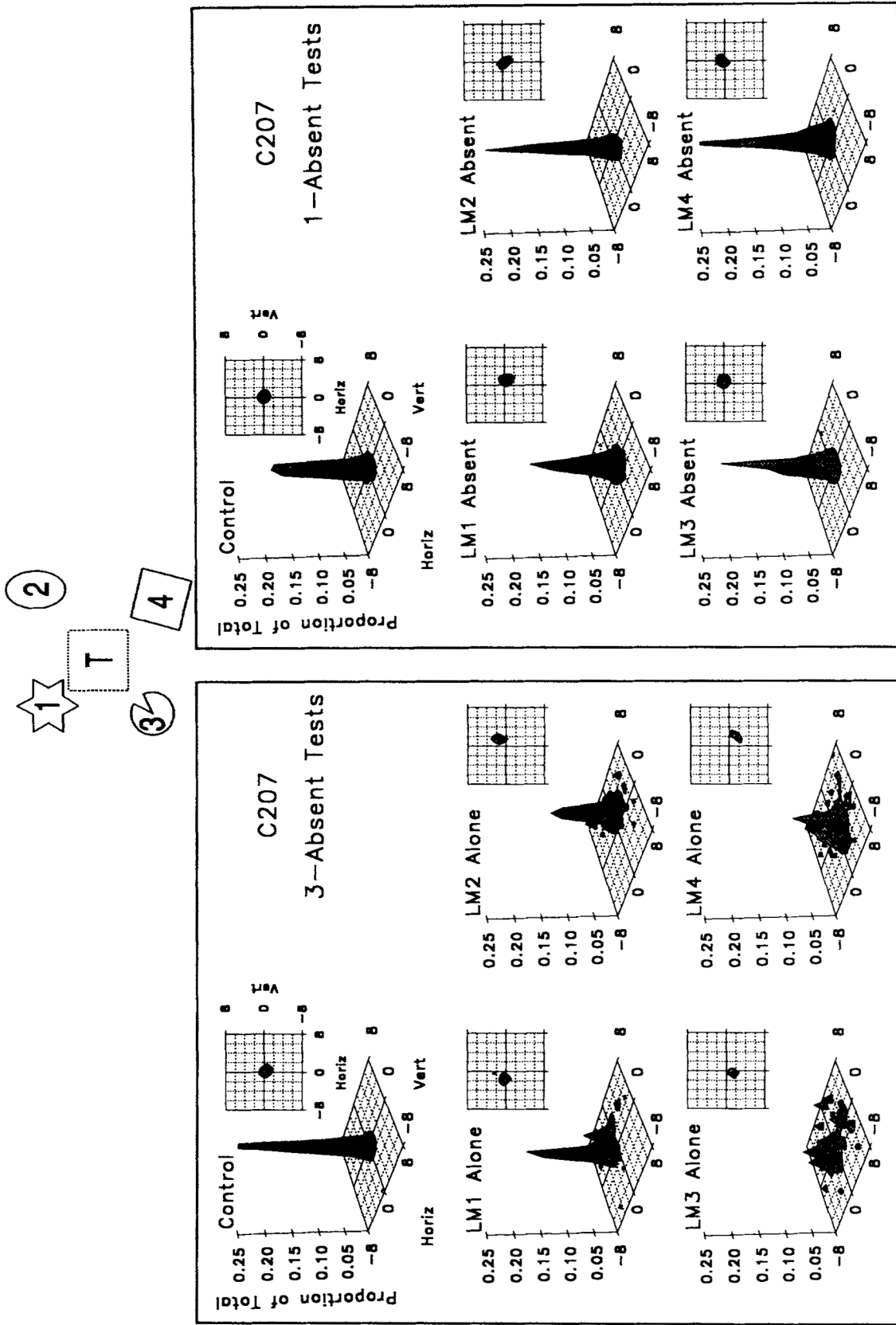


Figure 3. Response distributions on control and test trials from the three-absent and one-absent tests of Experiment 1 for Bird C207. (The diagram at the top shows the arrangement of Landmarks [LMs] 1 to 4 in relation to the target area [T] on baseline and control trials. Horiz = horizontal; Vert = vertical. See text for details.)

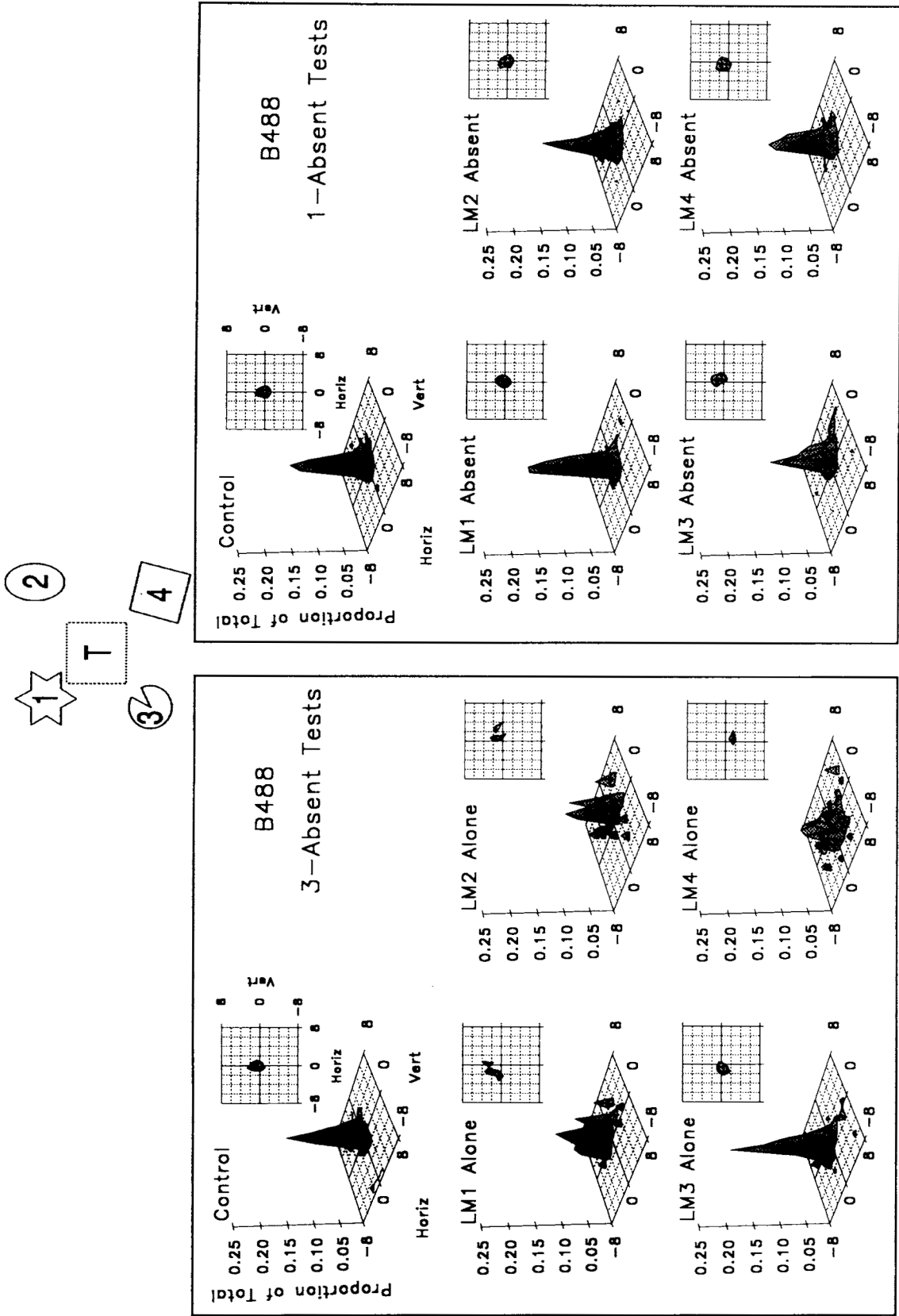


Figure 4. Response distributions on control and test trials from the three-absent and one-absent tests of Experiment 1 for Bird B488. (The diagram at the top shows the arrangement of Landmarks [LMs] 1 to 4 in relation to the target area [T] on baseline and control trials. Horiz = horizontal; Vert = vertical. See text for details.)

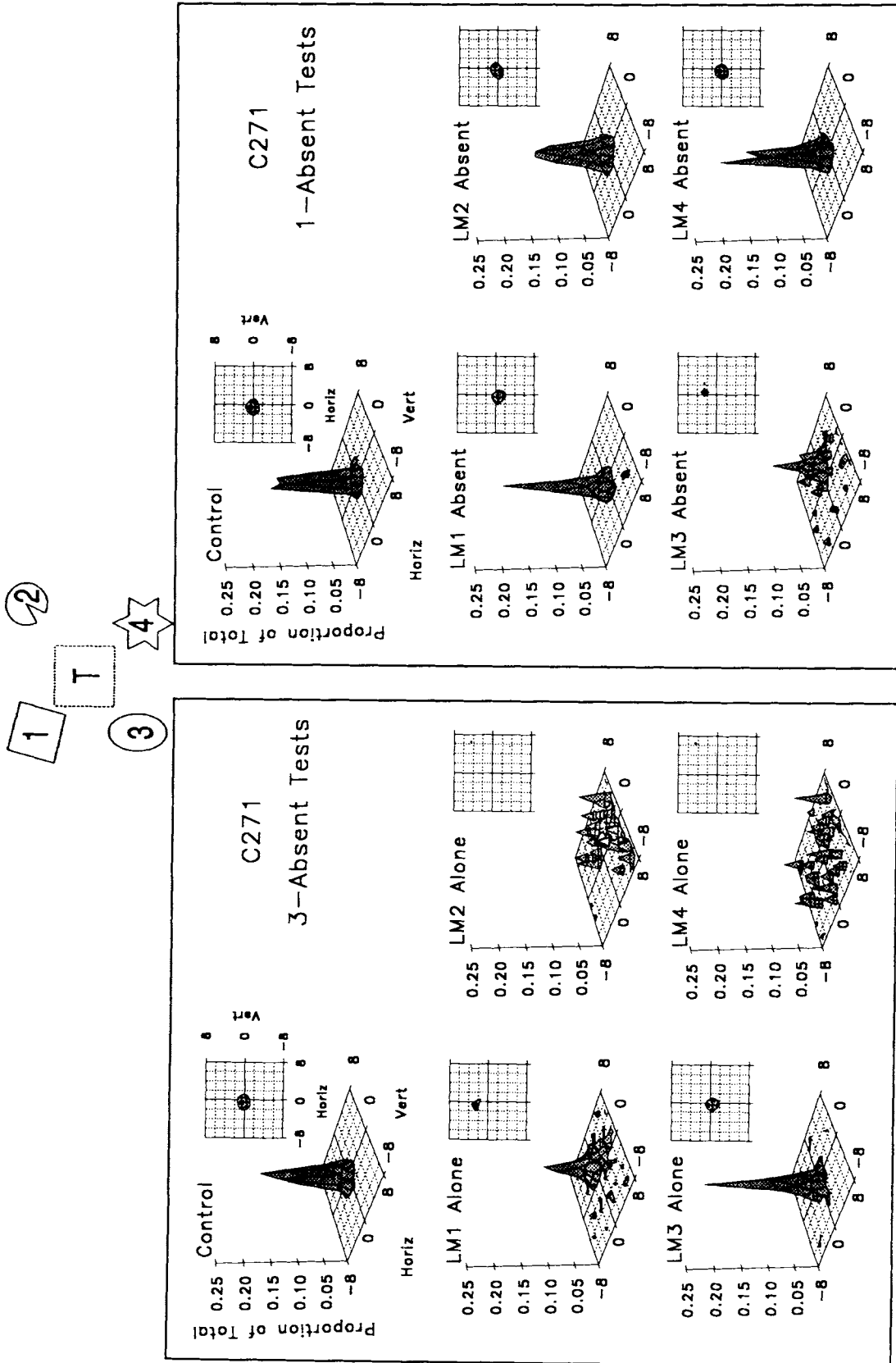


Figure 5. Response distributions on control and test trials from the three-absent and one-absent tests of Experiment 1 for Bird C271. (The diagram at the top shows the arrangement of Landmarks [LMs] 1 to 4 in relation to the target area [T] on baseline and control trials. Horiz = horizontal; Vert = vertical. See text for details.)

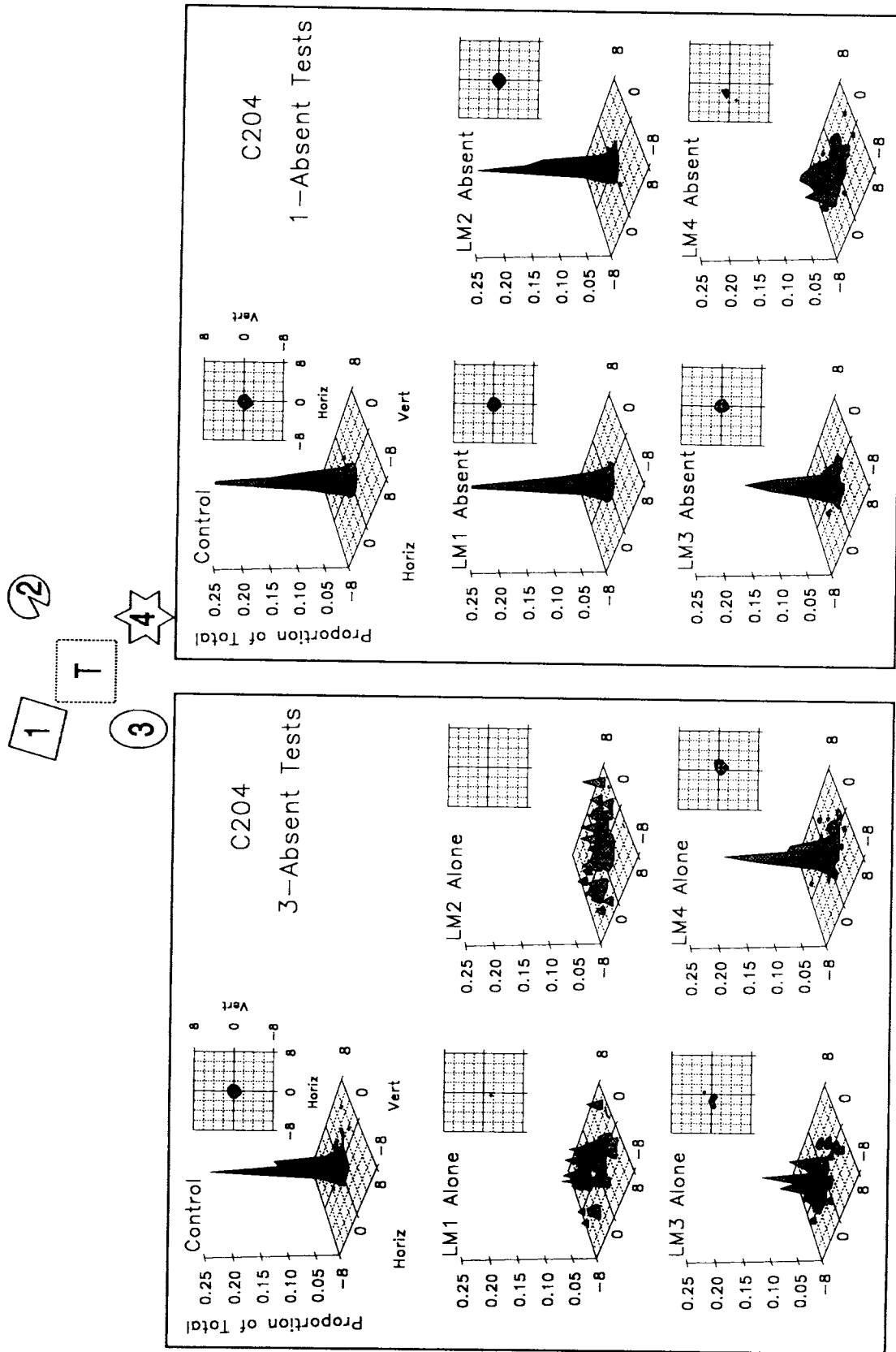


Figure 6. Response distributions on control and test trials from the three-absent and one-absent tests of Experiment 1 for Bird C204. (The diagram at the top shows the arrangement of Landmarks [LMs] 1 to 4 in relation to the target area [T] on baseline and control trials. Horiz = horizontal; Vert = vertical. See text for details.)

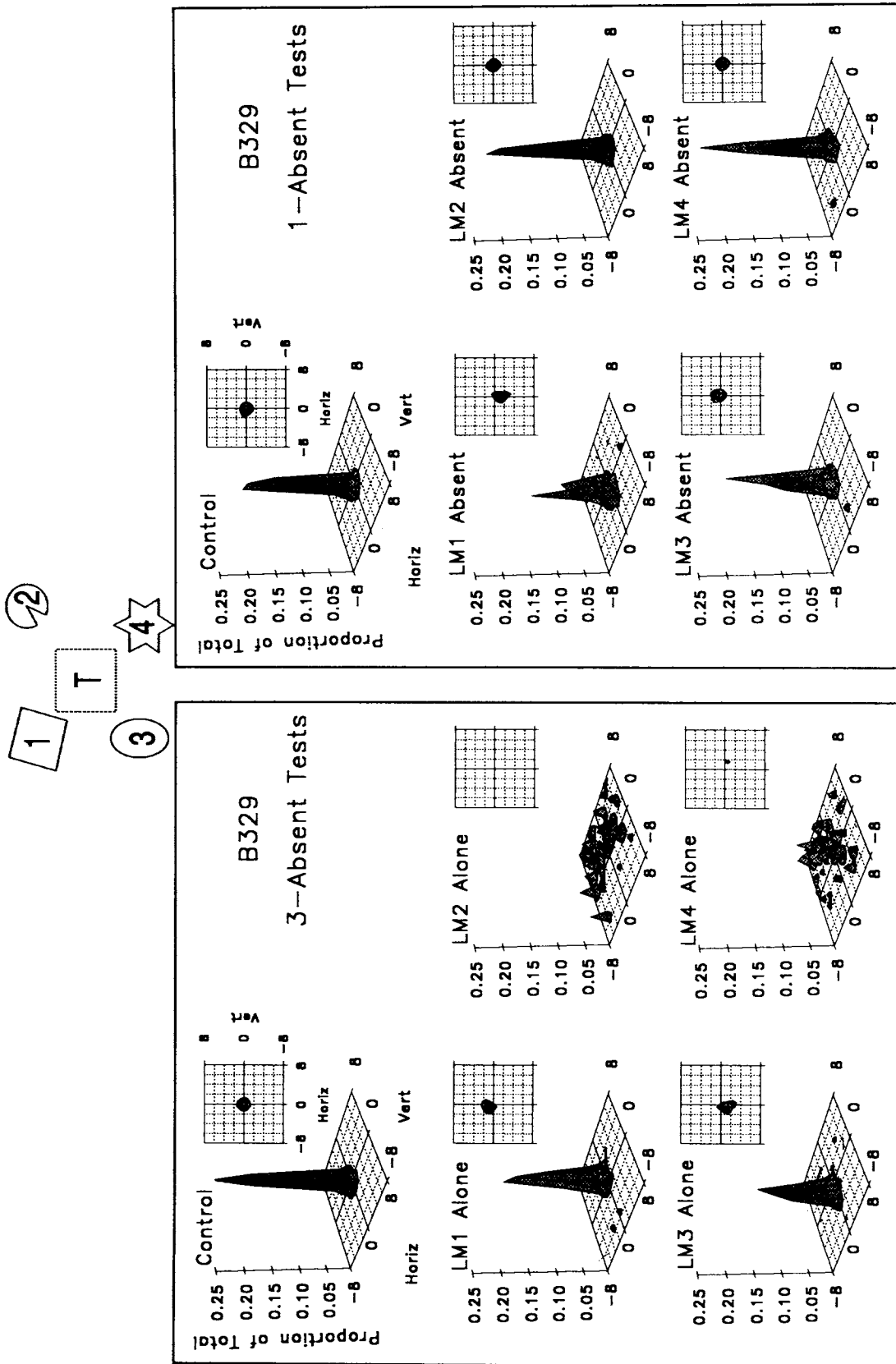


Figure 7. Response distributions on control and test trials from the three-absent tests and one-absent tests of Experiment 1 for Bird B329. (The diagram at the top shows the arrangement of Landmarks [LMs] 1 to 4 in relation to the target area [T] on baseline and control trials. Horiz = horizontal; Vert = vertical. See text for details.)

Table 2
Proportion of Pecks in Target Area for Two-Unit Shift Tests of Experiment 1

Trial type	Target	Bird					
		C242	C207	B488	C271	C204	CB329
Vertical test							
Control		.33*	.67*	.43*	.47*	.68*	.76*
LM1 shift	LM1	.06	.63*	.25*	.14	.02	.35*
	Unshifted	.56*	.17*	.31*	.36*	.68*	.28*
LM2 shift	LM2	.04	.08	.26*	.07	.05	.10
	Unshifted	.42*	.70*	.37*	.46*	.68*	.68*
LM3 shift	LM3	.05	.06	.08	.34*	.12	.15*
	Unshifted	.44*	.70*	.44*	.18*	.66*	.50*
LM4 shift	LM4	.25*	.07	.05	.08	.61*	.04
	Unshifted	.23*	.58*	.39*	.41*	.13	.75*
Horizontal test							
Control		.40*	.75*	.48*	.54*	.71*	.71*
LM1 shift	LM1	.25*	.26*	.08	.28*	.14	.49*
	Unshifted	.45*	.38*	.53*	.34*	.66*	.26*
LM2 shift	LM2	.01	.06	.08	.03	.04	.01
	Unshifted	.48*	.72*	.50*	.60*	.70*	.80*
LM3 shift	LM3	.26*	.10	.30*	.43*	.09	.32*
	Unshifted	.44*	.75*	.26*	.16*	.65*	.38*
LM4 shift	LM4	.46*	.22*	.10	.01	.59*	.04
	Unshifted	.23*	.59*	.33*	.56*	.13	.64*
Diagonal test							
Control		.32*	.68*	.45*	.51*	.67*	.73*
LM1 shift	LM1	.03	.35*	.07	.05	.00	.40*
	Unshifted	.39*	.20*	.44*	.41*	.74*	.21*
LM2 shift	LM2	.00	.01	.03	.01	.01	.01
	Unshifted	.42*	.71*	.44*	.48*	.62*	.73*
LM3 shift	LM3	.07	.01	.10	.38*	.01	.17*
	Unshifted	.30*	.69*	.30*	.09	.69*	.45*
LM4 shift	LM4	.28*	.02	.06	.00	.55*	.00
	Unshifted	.10	.62*	.41*	.49*	.04	.73*

Note. LM = landmark. Numbers that are significantly above chance according to Z test are indicated with an asterisk; see text for details.

stances. In each of these instances the shifted landmark was the one that was ranked highest according to the landmark-removal tests.

The calculated peak place of searching also indicated that search tended to shift in the direction of shifted high-ranked landmarks but not in the direction of shifted low-ranked landmarks. To determine the extent to which responding shifted toward a landmark, we computed the difference between the peak place on shift test trials and the peak place on control trials. We assigned a positive value if the difference was in the direction of the landmark shift and a negative value if the difference was in the opposite direction from the landmark shift. These scores were calculated for the horizontal dimension on the horizontal-shift tests and for the vertical dimension on the vertical-shift tests. The scores were calculated for both dimensions on diagonal-shift tests in which the landmark was shifted both horizontally and vertically. The mean shift in the peak place in response to 2-unit (approximately 2 cm) shifts of the highest-ranked and lowest-ranked landmarks are shown in Figure 8, with values above zero indicating a shift toward the shifted landmark and values below zero indicating a shift away from it. Clearly, search behavior shifted substantially when the highest ranked landmark was

shifted but not when the lowest ranked landmark was shifted. Two-tailed *t* tests comparing the scores of the 6 birds to the expected value of zero indicated that in all four cases peak place shifted significantly in the direction of the shifted highest ranked landmark [horizontal shifts, horizontal peaks: $t(5) = 5.99$; vertical shifts, vertical peaks: $t(5) = 6.32$; diagonal shifts, horizontal peaks: $t(5) = 4.97$; and diagonal shifts, vertical peaks: $t(5) = 5.49$] but not in the direction of the shifted lowest ranked landmark.

Discussion

Although the pattern of responding clearly differed between the birds, several striking commonalities emerge when one considers the full set of data. First, response distributions from control trials (which were never reinforced) were typically strongly peaked and centered at the target. Thus, responding was very accurate when all four landmarks were present in their normal positions; it was certainly well above the level expected if the birds had learned to peck in the general vicinity of the landmarks but had not learned the direction of the target from each landmark. Because the target position on the screen varied

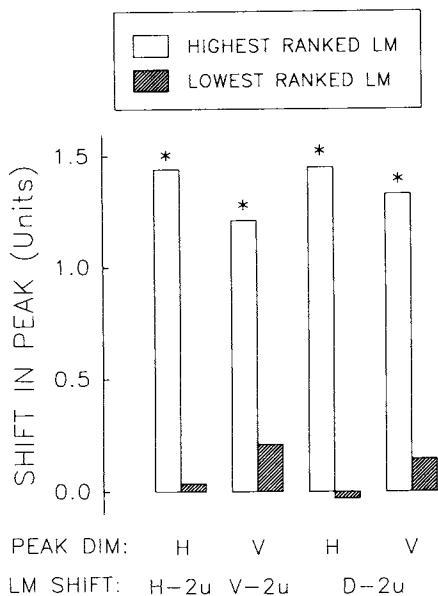


Figure 8. Mean shift in units of peak place of searching in the direction of a landmark (LM) shift for the highest and lowest ranked landmark during the 2-unit horizontal (H), vertical (V), and diagonal (D) shift tests of Experiment 1. (Values above zero indicate that peak place shifted in the same direction as the landmark shift, whereas values below zero indicate that peak place shifted in the opposite direction. The asterisks denote mean shift scores that are significantly different from zero according to two-tailed *t* tests [$p < .05$]. DIM = dimension. See text for details.)

across trials, accurate responding could not be based on proprioceptive cues, peck-generated marks on the screen, or distance from the edges of the monitor. Instead, accurate responding depended on one or more of the landmarks. Second, the three-absent and one-absent tests indicated that accurate responding was not controlled equally by the four landmarks. Most birds appeared to be controlled primarily by one or at most two of the landmarks as indicated by their ability to search accurately when the landmark was presented alone and as shown by the disruption in accuracy produced by removal of the landmark. Third, the extent to which search behavior shifted in the direction of a shifted landmark was highly consistent with the control it exerted during the landmark-removal tests. Thus, for individual birds, the results of the three-absent and one-absent tests were congruous with those of the landmark-shift tests in indicating which landmark best controlled responding.

Three of the birds (C207, B488, and B329) did not show a complete disruption of search accuracy during any of the one-absent tests; these birds did not depend on any individual landmark exclusively. The other three birds (C242, C271, and C204) showed a substantial disruption of search accuracy during one of the one-absent tests; these birds seemed to depend heavily on a single landmark. More research is necessary to discover the factors that determine whether one or more landmarks are relied on.

Despite the fact that each bird displayed selectivity in the encoding of the spatial information, there was clearly little

consensus among birds about which was the "best" landmark. Among birds exposed to Arrangement A, Bird C242 showed the best control by LM4 (the rectangle), Bird B488 by LM3 (the pie), and Bird C207 by LM1 (the star). Among birds exposed to Arrangement B, Bird B329 displayed the best control by LM1 (the rectangle), Bird C204 by LM4 (the star), and Bird C271 by LM3 (the ellipse). Thus, each of the four graphic stimuli appeared to be weighted most heavily by at least 1 of the birds. This idiosyncratic preference for particular landmarks suggests that the various shapes and colors of the graphic stimuli used did not result in one stimulus being uniformly more salient or informative than another. Assuming that each bird is capable of displaying control by each of the graphic stimuli used, the selectivity of control observed in the present study suggests the possibility that the development of control by one of the landmarks may have overshadowed control by the other landmarks. Although further research is needed to demonstrate overshadowing effects in this task, it is interesting to note that reciprocal overshadowing between intramaze and extramaze cues has been demonstrated for rats' spatial memory in the radial maze task (March, Chamizo, & Mackintosh, 1992).

The only apparent consistency among the birds in the selectivity of their control by the four landmarks is in which landmark was least likely to control accurate search. None of the 6 subjects showed strong control by LM2 (the ellipse in Arrangement A and the pie in Arrangement B), and several of the subjects displayed virtually no control by the landmark in this position. It is interesting to note that for both arrangements LM2 was the farthest landmark from the target area. Although additional research that tests a wider range of values than used in the present investigation is needed, this result suggests that the effectiveness of a graphic stimulus as a landmark may be determined more by its distance to the target area than by its visual features. Distance to the goal is an important determinant of the weight given to a particular landmark in open-field spatial search by pigeons, presumably because nearer landmarks provide more accurate guidance of search (Cheng, 1989). Gerbils (Collett et al., 1986) and honeybees (Cheng, Collett, Pickard, & Wehner, 1987) also appear to weigh landmarks according to distance to the goal.

Perhaps the most surprising result of the present research was the complete lack of disruption of search accuracy shown by 2 of the birds (C242 and C271) when three of the four landmarks were removed. These birds searched as accurately with one of the single landmarks as they did on control trials, and they were unable to search accurately when that landmark was absent. Apparently, these birds encoded the target area in relation to one landmark only and failed to use the spatial information provided by the other three landmarks. This seems surprising because use of the other landmarks would seem to allow more precise localization through use of crossed compass bearings (Gallistel, 1990). The lack of disruption seen when their three nonpreferred landmarks were absent also suggests that the configuration of the four landmarks was not of critical importance for these birds. This is surprising because the configuration of landmarks has been identified as an important controlling variable in other spatial

tasks (e.g., Spetch & Honig, 1988; Suzuki et al., 1980) and because the particular arrangement we used, in which the target area was surrounded by four nearby landmarks, would allow a seemingly simple strategy of responding roughly in the center of the array of landmarks. That no decrement in accuracy was seen when three of the landmarks were missing indicates that these 2 birds did not rely on, or even benefit from, this strategy.

Another interesting finding was that the pie was not the preferred landmark for all pigeons; in fact, it was not the preferred landmark of any of the 3 birds that displayed the most selective control (C242, C271, and C204). This suggests that the asymmetry this landmark afforded was not of great benefit in target localization and that the pigeons did not rely exclusively on features of the landmark itself to determine "which direction is which" (see Cheng, 1992). Because at least some of the pigeons also did not rely on relationships among the four landmarks to determine which direction was which, it appears that this information was derived at least partially from proprioceptive cues or from cues external to the stimulus display.

Experiment 2

Experiment 1 revealed that when birds were trained with four landmarks that provided reliable spatial information about a target area, they did not encode all of the information available but instead seemed to attend to only one or two of the landmarks. Although none of the birds displayed very strong control by the farthest landmark, there was little consistency among the birds about which of the three nearer landmarks was the best. Hence, the selective processing of only one or two landmarks did not appear to reflect inherent differences in salience of the graphic stimuli. Instead, it appeared that the birds had processed only as much information as was needed to search accurately. Indeed, in Experiment 1 all four landmarks were always present on all reinforced trials. Perhaps encoding would be far less selective if this were not always the case. Accordingly, in this experiment, birds that had initially been trained with all four landmarks as in Experiment 1 were given additional training with each of the six possible pairs of the four landmarks. This training provided variability in the stimulus conditions associated with reinforcement and precluded reliance on any single landmark for accurate search. Shift tests with each pair of landmarks were then conducted to determine the weighting given to individual landmarks. Control by single landmarks was also measured to assess the extent to which control by the four landmarks was selective.

Experiment 2 also included tests to determine what feature(s) of individual landmarks (i.e., color or shape) were important. In one test, individual landmarks were rotated from their normal orientation. We were particularly interested in whether rotation of the asymmetrical landmark would produce a shift in search location. In another test, individual landmarks were presented in the color of the landmark opposite to them. This would produce a conflict between landmark color and landmark shape and would indicate which feature is more important. Finally, to determine

how accurately the pigeons would search when color was the only cue, we presented novel landmark shapes; to determine how accurately they could search when shape was the only cue, we presented novel landmark colors.

Method

Subjects

The subjects were 2 of the birds from Experiment 1 (Birds B488 and C207) and 2 additional subjects that were trained as described in Experiment 1. One of these birds (242) had no prior experience with touch-screen tasks; the other bird (243) had previously served in a touch-screen search task with a stationary target area (Spetch et al., 1992). Prior to this experiment, all 4 birds had been exposed to a number of nonreinforced tests (not reported here) in which single or multiple landmarks were manipulated. Birds were housed and maintained as in Experiment 1.

Apparatus, Search Space, and Stimuli

The same chambers and stimuli used in Experiment 1 were used for this experiment. Birds C207, 242, and 243 were tested in the modified BRS/LVE chamber, and Bird B488 was tested in the custom-built chamber described in Experiment 1. The search space was identical to that described in Experiment 1 except that on all test and control trials, additional units near the edges of the screen were excluded as target areas so that it was always possible to peck a target distance away on all sides of each landmark. For all birds, the graphic stimuli serving as landmarks were the same as in Arrangement A of Experiment 1.

Procedure

Pairs training. During this training phase, reinforced trials with each of the six possible pairs of the four landmarks were interspersed among reinforced and nonreinforced baseline trials with all four landmarks. During the initial pairs training sessions, each block of 18 trials included 8 reinforced baseline trials, 4 nonreinforced baseline trials, and 1 reinforced trial with each of the six pairs of landmarks. The order of trials was randomly determined for each block. Five blocks of trials were scheduled during each session. All aspects of the procedure were the same as described for reinforced and nonreinforced baseline trials of Experiment 1. The response criterion for termination of a trial (and presentation of food on reinforced trials) was initially set to a single peck in the target area (FR1) and was then increased over sessions to FR2, FR3, and then FR4. Next, the consecutive peck requirement described for Experiment 1 was introduced and increased over sessions from two consecutive pecks to three consecutive pecks. For each bird, the response requirement was increased only after the bird successfully completed at least 80 of the scheduled trials in a session. In the final stage of pairs training, the number of reinforced baseline trials was reduced so that each block of 14 trials included 4 reinforced baseline trials, 4 nonreinforced baseline trials, and 1 reinforced trial with each pair of landmarks. Seven blocks of trials were scheduled for each session. All birds began testing once they had received a minimum of 5 sessions with this last phase of training and had completed at least 80 trials on each of the last 2 sessions. Pairs training was completed in 11, 11, 12, and 15 sessions for Birds B488, C207, 243, and 242, respectively.

Pairs shift tests. Each session during this test phase included two reinforced and two nonreinforced baseline trials (with all four

landmarks), one reinforced trial with each of the six pairs of landmarks, one control trial with a given pair of landmarks, and three shift-test trials with that same pair of landmarks. The order of trials was randomly determined for each block. On the shift-test trials, one member of the pair of landmarks was shifted by 2 units horizontally, vertically, or diagonally (i.e., 2 units in both dimensions). It should be noted that 2-unit shifts resulted in nonoverlapping target areas for the two landmarks present. Although several combinations of shifts were possible for each pair of landmarks, only three shift tests were included for each pair so as to keep the density of test trials in each session reasonably low. Landmarks were always shifted away from each other so that they never covered the target area. For example, horizontal shifts involved leftward shifts of LM1 or LM3 but rightward shifts of LM2 and LM4. The specific shifts tested depended on the pair. For the left (LM1 and LM3) and right (LM2 and LM4) pairs each landmark was shifted once horizontally, and the bottom landmark was shifted once vertically (because there is no fixed target location, a downward shift of the bottom landmark is visually equivalent to an upward shift of the top landmark). For the top (LM1 and LM2) and bottom (LM3 and LM4) pairs each landmark was shifted once vertically, and the left landmark was shifted once horizontally. For diagonal pairs (LM1 and LM4; LM2 and LM3) the bottom landmark was shifted once vertically, once horizontally, and once diagonally. On both control and test trials, the trial terminated without reinforcement 8 s after the bird had made two pecks anywhere on the screen. Seven control trials and seven test trials of each type were scheduled for each test session. One test session with each pair of landmarks was included within each block of six test sessions. Four blocks of test sessions were conducted in total. One training session, identical to the last phase of pairs training, was presented between each block of tests.

Single-landmark feature tests. Initiation of this test phase was preceded by several training sessions that were identical to the last phase of pairs training. This test phase included tests with single landmarks in their normal color and orientation, tests with single landmarks in rotated orientation, and tests with single landmarks in the color of the diagonally opposite landmark (i.e., a color vs. shape test). Each trial block included eight reinforced and four nonreinforced baseline trials with all four landmarks, one control trial with all four landmarks, one test trial with one of the landmarks presented alone, one test trial with that landmark presented alone but rotated clockwise from its normal orientation by 90° (Landmarks 1, 2, and 3) or 45° (Landmark 4), and one test trial with that landmark presented alone but in the color of the diagonally opposite landmark. On both control and test trials, the trial terminated without reinforcement 8 s after the bird had made two pecks anywhere on the screen. One test session with each of the four landmarks was presented in each block of four test sessions. Four blocks of test sessions were conducted in total. One training session, identical to the last phase of pairs training, was presented between each block of tests.

Color/shape tests. These tests provided a further assessment of control by the color or shape of landmarks. Control by color alone was assessed by presenting landmarks in a novel shape (see Figure 9) designed to be distinct from each of the four landmark shapes. Control by shape alone was assessed by presenting landmarks in a novel color (white). Each block of trials in each test session included eight reinforced and four nonreinforced baseline trials with all four landmarks, one control trial with all four landmarks, and three test trials. On both control and test trials, the trial terminated without reinforcement 8 s after the bird had made two pecks anywhere on the screen. Two types of test sessions were conducted. During array color/shape tests, all four landmarks were presented on each test trial. Within each block of test trials, the landmarks were presented once in the appropriate shapes but each in white (novel color), once

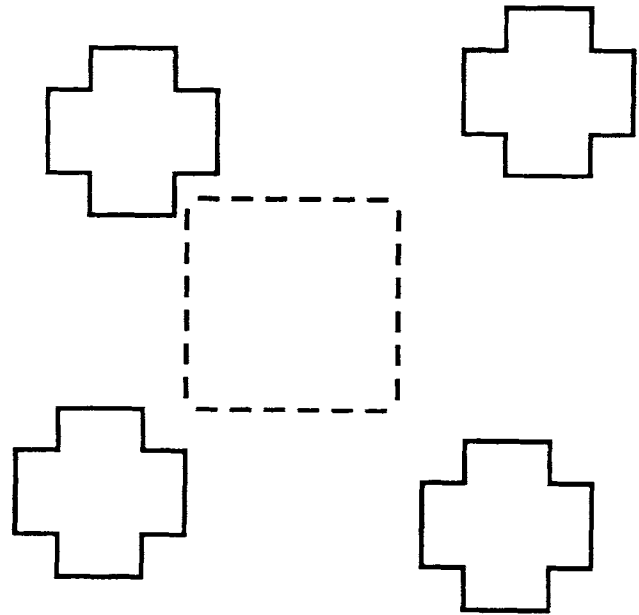


Figure 9. Diagram of the novel landmark shape used for the color/shape tests of Experiment 2.

in the appropriate colors but in the novel shapes (novel shape), and once in the novel shapes in white (novel color and shape). The novel color and shape test provided neither the appropriate color nor the appropriate shape but did provide an approximation to the frame generated by the arrangement of the four landmarks. During single landmark color/shape test sessions only one landmark was presented on test trials. Within each block of trials, the single landmark was presented once in its baseline color and shape, once in the novel color and once in the novel shape. For single-landmark tests we presented only the landmark that had generated the highest accuracy when presented alone during the preceding test phase. Consequently, Birds C207, 242, and B488 were tested with LM4, and Bird 243 was tested with LM3. One test session of each type was presented in each two-session block. Four blocks of test sessions were conducted in total. One training session, identical to the last phase of pairs training, was presented between each block of tests.

Data Recording and Analysis

Procedures for recording and analysis of data were identical to those described in Experiment 1.

Results

Pairs Shift Tests

Accuracy was significantly above the .11 chance level on control trials with all six pairs of landmarks for Birds B488, C207, and 243. Accuracy for Bird 242 was significantly above chance level on control trials with all except the top pair of landmarks. These accuracy scores on control trials are shown in Table 3 with summary results of the shift tests with each pair. For each pair, accuracy is shown for each member of the pair, averaged over the three shift tests. Figure 10

Table 3
Proportion of Pecks in Target Area for Pairs Shift Tests of Experiment 2

Pair	Trial	Target	Bird			
			242	B488	243	C207
LM1 & LM3	Control	Both	.30*	.32*	.51*	.57*
	Shift	LM1/LM3	.21*/.20*	.18*/.24*	.09/.43*	.40*/.20*
LM2 & LM3	Control	Both	.34*	.39*	.53*	.44*
	Shift	LM2/LM3	.13/.23*	.21*/.21*	.07/.47*	.22*/.28*
LM1 & LM2	Control	Both	.06	.28*	.30*	.50*
	Shift	LM1/LM2	.19*/.18*	.16*/.17*	.20*/.21*	.41*/.14*
LM1 & LM4	Control	Both	.30*	.46*	.44*	.68*
	Shift	LM1/LM4	.19*/.23*	.12/.32*	.17*/.35*	.34*/.31*
LM3 & LM4	Control	Both	.38*	.58*	.51*	.28*
	Shift	LM3/LM4	.27*/.31*	.15*/.45*	.39*/.24*	.28*/.27*
LM2 & LM4	Control	Both	.33*	.53*	.40*	.42*
	Shift	LM2/LM4	.21*/.22*	.18*/.35*	.22*/.27*	.10/.36*

Note. LM = landmark. Numbers marked with an asterisk are significantly above chance according to Z test; see text for details.

shows, for each bird and each landmark, the average accuracy based on all control trials in which that landmark was present and shows the average accuracy based on all shift-test trials in which that landmark was present.

These results indicated that the four landmarks were differentially weighted by the birds and indicated that the weighting was reasonably consistent within birds. For all birds, the two landmarks associated with the highest accuracy based on the average of the shift-test trials were also the ones that were associated with the highest accuracy

based on the average of the control trials. Moreover, the results of the individual shift tests were highly consistent with those provided by the overall average accuracy. Bird C207 weighted LM1 and LM4 most heavily, and the remaining 3 birds weighted LM3 and LM4 most heavily.

Single-Landmark Feature Tests

Table 4 shows accuracy on control trials, single-landmark trials, and trials in which the single landmark was rotated. Also shown are the tests in which a single landmark was presented in the color of the landmark diagonally opposite to it. Accuracy on these tests is shown both for the landmark that is associated with the color presented but is in the wrong shape.

Accuracy on control trials was well above chance for all birds and was very high for 3 of the birds (C207, 242, and 243). All birds also displayed accuracy levels that were well above chance for at least one of the single landmarks. Only 1 bird (C207) searched accurately with all four of the single landmarks. For all birds, the two landmarks that generated the highest accuracy when presented alone were those that had shown the greatest control on the pairs shift tests.

To determine the effects of rotating or changing the color of a single landmark, we examined the results for the landmark that generated the highest accuracy when presented alone (LM3 for Bird 243 and LM4 for the remaining 3 birds). Figure 11 shows accuracy on the trials with the landmark in its baseline color and shape, the landmark rotated, the landmark in the wrong color, and the landmark in the wrong shape. As can be seen, rotation of the landmark had little effect on accuracy. Paired *t* tests failed to reveal a significant difference between accuracy on trials with a single landmark in its baseline color and shape ($M = .384$) and accuracy on trials with a rotated landmark ($M = .380$), $t(3) = 0.17$.

When a single landmark was presented in the color of the landmark opposite to it, the pigeons were more likely to peck in the location that was appropriate to the color than in the location that was appropriate to the shape of the landmark. For the landmark associated with the highest accuracy for

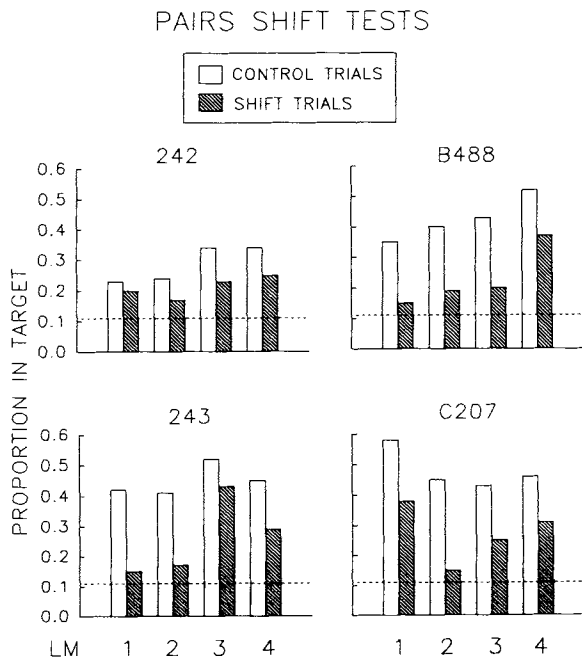


Figure 10. Proportion of pecks in the target area for each of the four landmarks (LMs) during the pairs shift tests of Experiment 2. (Open bars show accuracy for each landmark averaged over pair control trials in which that landmark was present. Hatched bars show the proportion of pecks in the target area for each landmark, averaged over all shift-test trials involving that landmark.)

Table 4
Proportion of Pecks in Target Area for Single Landmark Feature Tests in Experiment 2

Landmark present	Trial type	Bird			
		242	B488	243	C207
Tests with LM1					
All	C	.74*	.35*	.54*	.76*
LM1	R	.17*	.09	.09	.40*
LM1/LM4	WC/WS	.01/.42*	.00/.44*	.03/.16	.02/.26*
LM1	SB	.05	.11	.10	.38*
Tests with LM2					
All	C	.69*	.48*	.61*	.80*
LM2	R	.24*	.17*	.14	.20*
LM2/LM3	WC/WS	.02/.13	.00/.27*	.02/.26*	.01/.27*
LM2	SB	.08	.23*	.12	.19*
Tests with LM3					
All	C	.68*	.48*	.62*	.81*
LM3	R	.12	.27*	.37*	.31*
LM3/LM2	WC/WS	.04/.18*	.02/.11	.03/.01	.02/.10
LM3	SB	.10	.24*	.39*	.26*
Tests with LM4					
All	C	.62*	.36*	.61*	.73*
LM4	R	.43*	.31*	.03	.41*
LM4/LM1	WC/WS	.02/.03	.03/.14	.03/.01	.06/.05
LM4	SB	.37*	.33*	.15	.45*

Note. C = control, R = rotated, WC = wrong color, WS = wrong shape, SB = single landmark in baseline color and shape, LM = landmark. Numbers marked with an asterisk are significantly above chance according to Z test; see text for details.

each bird, *t* tests indicated that accuracy was significantly higher when that landmark was presented in the shape of the landmark opposite to it ($M = .345$) than when that landmark was presented in the color of the landmark opposite to it ($M = .034$), $t(3) = 5.63$.

Color/Shape Tests

All birds responded in a similar fashion to the color/shape tests. Specifically, accuracy was not disrupted by changes in landmark shape but was severely disrupted by changes in landmark color. Mean accuracy scores on control and test trials are shown in Figure 12 for single-landmark tests and in Figure 13 for array tests. For the single-landmark tests, an ANOVA revealed that accuracy differed significantly across trial types, $F(3, 9) = 13.67$. Newman-Keuls multiple comparisons revealed that accuracy on control trials was significantly higher than on any of the test trials. Accuracy on single baseline trials did not differ from accuracy on novel shape trials. Accuracy on novel color trials was significantly lower than on the single baseline or novel shape trials. An ANOVA also revealed significant differences for the array tests, $F(3, 9) = 70.43$. Newman-Keuls comparisons revealed that accuracy on control trials and novel shape trials was higher than on novel color or novel shape and color trials. Accuracy on novel shape trials was not significantly different from accuracy on control trials, and accuracy on novel color trials was not significantly different from accuracy on novel shape and color trials.

Discussion

Performance on the shift tests and the single-landmark tests indicated some sharing of control by the four landmarks following training with pairs of landmarks. However, each bird weighted some landmarks more heavily than others. According to both the shift- and single-landmark tests, the two highest ranked landmarks were LM3 and LM4 for 3 of the birds and LM4 and LM1 for 1 bird.

Rotation of single landmarks had no apparent effect on performance. In particular, for those birds displaying some control by LM3 (the pie), rotation did not lower accuracy (see Table 4), indicating that directional information was not derived from the asymmetry of that landmark. Tests with the landmarks presented in the wrong color, which pitted color against shape, indicated that pigeons responded to the color rather than the shape of the landmark. Control by landmark color and not by landmark shape was also evident in the subsequent color/shape tests. When landmarks were presented in a novel shape so that color was the only cue available, pigeons responded as accurately as when the landmark or landmarks were presented in their normal shapes. Accurate search was not displayed when the landmarks were presented in a novel color so that shape was the only cue. It appears that the pigeons relied exclusively on the color of the landmarks and disregarded the shape. It is, therefore, not surprising that rotating the orientation of the landmarks had no effect on search location.

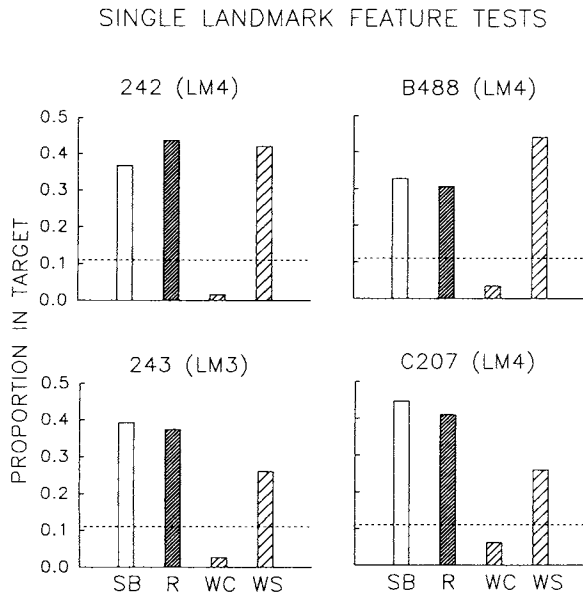


Figure 11. Proportion of pecks in the target area for a single landmark (LM) in baseline color and shape (SB), for that landmark rotated (R), presented in the wrong color (WC), or presented in the wrong shape (WS) during single-landmark feature tests of Experiment 2.

General Discussion

A recurrent theme throughout these experiments was that pigeons encoded some but not all of the available information about the graphic landmarks in this spatial search task. In Experiment 1, several of the birds showed extremely selective encoding of the four landmarks. Two birds in particular appeared to encode the target location exclusively in terms of one of the four landmarks and failed to show any control by the other three landmarks. Furthermore, the selective encoding of the landmarks was idiosyncratic. The birds differed in the number of landmarks that exerted significant control and in which particular landmark exerted the greatest control. The only apparent consistency in the selection of landmarks was that the farthest landmark from the target was not the dominant landmark for any bird. At first glance, these individual differences seem to suggest a lack of order in the data. However, a detailed examination of the results for individual birds indicated that each bird showed a very reliable pattern of control by the landmarks. In particular, for individual birds the relative control by each landmark revealed by the effects of landmark removal was highly consistent with the extent to which the bird followed each landmark when it was shifted. Thus, the birds varied in the extent to which each landmark controlled behavior but not in how search behavior was controlled by the landmarks.

Idiosyncratic differences in the relative control by the four landmarks were also seen to some extent in Experiment 2 after training that precluded reliance on any one landmark for accurate search. In this experiment, the shift tests and single-landmark tests indicated that 1 bird (243) showed strongest control by LM3, 2 birds (242 and B488) showed strongest

control by LM4, and 1 bird showed good control by both LM1 and LM4. As in Experiment 1, none of the birds showed strongest control by LM2, the landmark farthest from the target. Experiment 2 also revealed extreme selectivity in the distinguishing features of the encoded landmarks. Specifically, although all four landmarks differed in both color and shape, all 4 pigeons appeared to have attended exclusively to color.

The extreme selectivity of encoding displayed by some of the pigeons seems at odds with results of open-field spatial tasks, in which encoding of several redundant sources of information is more typical (e.g., Cheng, 1988; Spetch & Edwards, 1988). In addition, the configuration of multiple landmarks is often important in real-space search tasks (e.g., Spetch & Honig, 1988; Suzuki et al., 1980), whereas birds in our task did not show evidence of attending to the configuration of the four graphic landmarks. Although there are many differences between search in open space and our two-dimensional search task, one interesting difference is that in open space landmarks are often approached from several perspectives, whereas our search task provided a single, top-view perspective on the landmarks. Whether this single top-view perspective was responsible for the selective encoding of single landmarks remains to be determined in future research.

Despite individual differences in which particular landmark or landmarks exerted the best control, a number of consistencies emerged. First, none of the 8 birds tested in the present two experiments showed strongest control by the farthest landmark (LM2), and most of the birds showed very little control by LM2. Although more research is needed to conclusively demonstrate the importance of distance to the target area, this finding is consistent with evidence that nearer

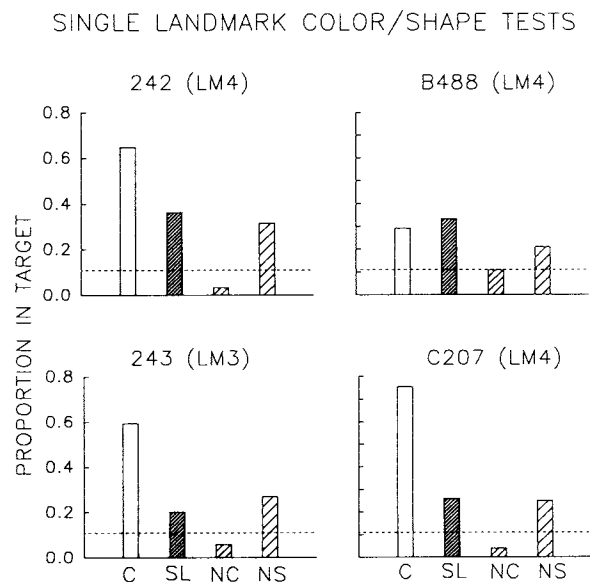


Figure 12. Proportion of pecks in the target area for each bird on control (C) and test trials of the single-landmark color/shape tests of Experiment 2. (SL = single landmark in baseline color and shape; NC = landmark presented in a novel color; NS = the landmark presented in a novel shape; LM = landmark.)

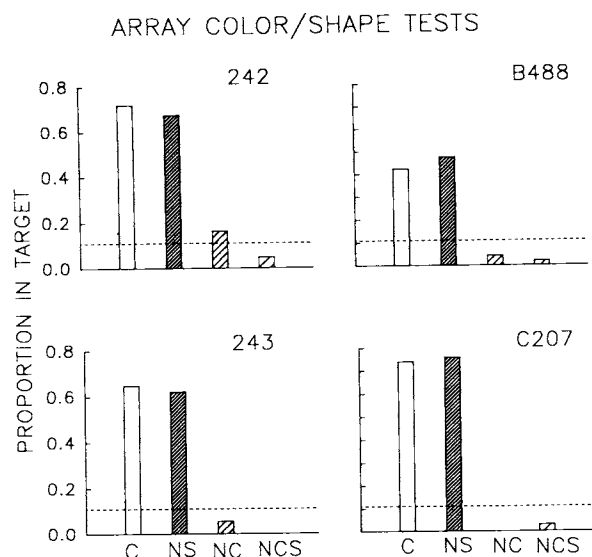


Figure 13. Proportion of pecks in the target area for each bird during the control (C) and test trials of the array color/shape tests of Experiment 2. (NS = all four landmarks presented in novel shapes; NC = all four landmarks presented in novel colors; NCS = all four landmarks presented in novel shapes and colors; LM = landmark.)

landmarks are weighted more heavily than distant ones in open-field search tasks (e.g., Cheng, 1989), presumably because nearer landmarks allow more precise localization. Second, Experiment 2 revealed a striking uniformity in which feature of the dominant landmark controlled behavior. Specifically, all birds showed strong control by landmark color and no evidence of control by landmark shape. When landmark color was pitted against landmark shape, all four birds pecked more in the target location appropriate to the color of the landmark. Moreover, rotation of a dominant single landmark had no significant effect on search location. Finally, all birds searched as accurately with novel landmark shapes as they did with the training shapes, whereas they all failed to search accurately with novel landmark colors.

The complete lack of control by landmark shape was surprising because to a human observer, differences among the four landmark shapes seem very salient. Indeed, human subjects trained with these same landmarks showed more control by landmark shape than by landmark color (unpublished data by Spetch, 1992). To determine whether pigeons' lack of control by shape might reflect a perceptual limitation on their ability to discriminate the shapes of the graphic stimuli, we trained Bird C207 on a simple go-no-go discrimination task with LM1 in white as S⁺ and LM4 in white as an S⁻. The S⁺ was associated with a fixed interval 8-s schedule of food presentation, and the S⁻ was associated with a fixed time 8-s extinction period. Discrimination ratios (response rate during S⁺/response rate during S⁺ plus response rate during S⁻) for successive blocks of two sessions were .55, .67, .73, .80, and .83. Clearly, this bird could discriminate the landmark shapes, even though it had shown no control by landmark shape in the search task. Whether the failure to process shape information in the search task reflected overshadowing by

color or reflected difficulty associating the shape of a stimulus with spatial behavior remains to be determined.

It is interesting to speculate on why some aspects of control by the landmarks showed consistency among the birds, whereas other aspects showed variation. The tendency to show more control by nearer landmarks is consistent with results of open-field search and would be adaptive to the extent that nearer landmarks allow more precise localization (Cheng, 1989). It is not clear whether the consistent tendency to encode landmark color but not landmark shape is specific to the stimuli used in the present task because comparable studies have not been conducted in open-field search tasks with pigeons. Thus, an interesting question for future research is whether selective encoding of color reflects a general predisposition of pigeons' landmark use and, if so, what the reason is for greater attention to color than to shape. The idiosyncratic selection among the three nearest landmarks may reflect the fact that all were equally satisfactory landmarks in terms of proximity to target, distinctiveness, and reliability, and hence there may have been no selective advantage of attending to one over another. Moreover, in nature the stimuli that can serve as useful landmarks are likely not restricted to any particular colors. Thus, pigeons may be predisposed to encode a target area in terms of nearby, visually distinct stimuli that bear a stable spatial relationship to the target, and it is possible that they are predisposed to encode these stimuli primarily on the basis of color. However, there may be no predisposition to use landmarks of any particular color, and this may result in idiosyncratic preferences.

As demonstrated in the present research, the flexibility of the touch-screen system and videographic capabilities provide enormous potential for investigating the processes governing spatial behavior. Although the present research used simple two-dimensional graphic stimuli, more complex pictorial stimuli can also be used with touch-screens to address issues such as the importance of variation in perspective. The touch-screen system provides sufficient resolution that models of spatial behavior might be evaluated, for example, the vector-sum model (e.g., Cheng, 1988, 1989, 1990; Spetch et al., 1992). However, the present data indicate that in addition to investigating how landmarks guide spatial behavior, we must also address the more fundamental question of what factors determine whether a particular stimulus will be encoded and used as a landmark. The selectivity of encoding revealed in the present study suggests that two of these factors may be the presence of other equally informative landmarks and distance to the target area. The present findings also suggest that color is a more important feature of graphic landmarks than shape. The generality of these findings to different stimuli and training conditions is an interesting issue for future research.

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