STIMULUS CONTROL IN THE USE OF LANDMARKS BY PIGEONS IN A TOUCH-SCREEN TASK

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Pigeons were tested in a search task on the surface of a monitor on which their responses were registered by a touch-sensitive device. A graphic landmark array was presented consisting of a square outline (the frame) and a colored "landmark." The unmarked goal, pecks at which produced reward, was located near the center of one edge of the frame, and the landmark was near it. The entire array was displaced without rotation on the monitor from trial to trial. On occasional no-reward tests, the following manipulations were made to the landmark array: (a) either the frame or the landmark was removed; (2) either one edge of the frame or the landmark was shifted; and (3) two landmarks were presented with or without the frame present. On these two-landmark tests, the frame, when present, defined which was the "correct" landmark. When the frame was absent, the "correct" landmark was arbitrarily determined. Results showed that pecks of 2 pigeons were controlled almost solely by the landmark, pecks of 3 were controlled primarily by the landmark but the frame could distinguish the correct landmark, and 1 bird's behavior was controlled primarily by the frame. Stimulus control in this search task is thus selective and differs across individuals. Comparisons to other search tasks and to other stimulus control experiments are made.

Key words: stimulus control, search, landmarks, spatial learning, attention, peck, pigeon

Many animals use visual landmarks to find their way back to a desired spatial location (see Gallistel, 1990). Some aspects of the spatial relations between the goal and the surrounding landmarks play a role in guiding the way back. Convincing evidence that landmarks control behavior comes from studies in which the array of landmarks supposedly used by the organism is manipulated before the search for the hidden goal. Removal of the landmarks should cause disruption of the search, and displacements should lead to systematic displacements in search behavior. These strategies have been used to show that landmark-based search is found 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 & Räber, 1979).

Some recent research has addressed how the pigeon uses landmarks to find a place. Spetch and Edwards (1988) displaced an array of possible goal locations and found that pigeons were sensitive to both the position in the array and the absolute position within the room in locating the goal. Cheng (1988, 1989) tested pigeons in a search task in a square arena and concluded that the birds' behavior was influenced by both the arena itself and landmarks provided within the arena. He further proposed that pigeons use a weighted average of vectors from various landmarks to the goal in their search. This vector sum model was later rejected on the basis of further evidence from tests in square arenas (Cheng, 1990; Cheng & Sherry, 1992). It is now supposed that pigeons separately average the direction and distance components of vectors (Cheng, 1994). Spetch, Cheng, and Mondloch (1992) repeated on a touch-screen device some manipulations Cheng and Sherry (1992) performed on the floor of a laboratory room. In the touch-screen task, the search space is the vertical surface of a monitor, on which various graphic stimuli are presented as "landmarks." An infrared-sensitive touch screen records where and when the pigeons peck. Spetch et al. (1992) found that pigeons used both the graphic landmarks and the monitor itself in their search task, and the pattern of results was similar to that found by Cheng and Sherry (1992).

The studies reviewed above indicate that pigeons often use multiple landmarks in search. Functionally, this is advantageous because the information based on each landmark is unsystematically inaccurate to some extent. Averaging information from many landmarks can statistically reduce inaccuracies, much as taking a larger sample gives one a more accurate estimate of the mean. Similarly, sources of information that are more accurate should be given more weight. For instance, nearer landmarks should exert more effect than farther ones. This has been found for pigeons (Cheng, 1989) and honeybees (Cheng, Collett, Pickard, & Wehner, 1987). But pigeons do not always use multiple landmarks. Spetch and Mondloch (1993) tested pigeons on a search task on a touch-screen monitor on which the goal (location to be pecked) was found somewhere in the middle of an array of four landmarks. The entire array appeared in different locations on the screen from trial to trial, so that the screen itself was not a valid cue. Pigeons usually relied on a subset of the cues for the task, sometimes primarily one landmark, and different pigeons relied on different landmarks. Two convergent pieces of evidence show this. First, if the landmark relied on was removed, search was poor. Removal of other landmarks caused little disruption. Second, if the landmark relied on was moved, the pigeons shifted their search in the direction of the landmark shift. Shifting of other landmarks had little effect on search behavior. Selective control by only a subset of the available cues was also replicated in a touch-screen study using displays that consisted of digitized images of an outdoor scene (Spetch & Wilkie, 1994). Distances from each landmark to the goal varied to a greater extent than in the Spetch and Mondloch study, and all pigeons showed strongest or exclusive control by the nearest landmark.

In the present study, we tested the selective use of landmarks in the touch-screen search task in another arrangement based on the research in square arenas in laboratory rooms (e.g., Cheng & Sherry, 1992). A graphic frame (approximately 11 cm by 11 cm) provided an analogue of the arena. The goal was near the middle of one edge of the square frame, and another landmark was found near the goal. The entire "graphic arena" (i.e., frame, landmark, and goal) was moved from trial to trial on the monitor, so that the monitor itself was

not a valid cue. The goal stayed in the same place in the graphic arena from trial to trial. After the birds learned the task, we manipulated the cues to see whether the pigeons' behavior depended more on the frame or on the landmark. As in the study by Spetch and Mondloch (1993), two primary types of manipulations were conducted. On removal tests, either the frame or the landmark was removed. On shift tests, either the landmark was shifted or one edge of the frame was shifted. A final test phase was conducted to determine whether pigeons whose behavior showed little control by the frame might nevertheless be able to use the frame to distinguish a correctly placed landmark from an identical, incorrectly placed duplicate landmark.

METHOD

Subjects

The subjects were 6 adult pigeons, none of which had previously served in a touch-screen search task using graphic landmarks. All had previously served in experiments conducted in standard operant conditioning chambers. They were housed in large individual cages. Two of the pigeons (at the University of Alberta) were housed in a colony maintained on a 12:12 hr light/dark cycle (lights on at 6:00 a.m.). The 4 others (at the University of Toronto) were maintained on a 14:10 hr light/dark cycle (lights on at 6:00 a.m.). The birds were maintained at approximately 85% of their free-feeding weights by mixed grain obtained during and after experimental sessions. Water and grit were available ad libitum in the home cages.

Apparatus

Each bird was trained and tested in a custom-built chamber equipped with a color monitor (Zenith 1492) and an infrared touch frame (Carroll Touch, 1492 Smart Frame). The chambers used for 2 of the birds (41 and 3 at the University of Alberta) were 44 cm high, 32 cm deep, and 74 cm wide (inside dimensions), with a monitor opening (28 cm by 20 cm) in the center of the back wall, 9 or 10 cm from the floor. Two Gerbrands pigeon feeders were located on the back wall, one 8 cm to the left and one 8 cm to the right of the monitor opening. In the chamber used for Bird 3, the feeders were 7 cm from the floor; in the one

used for Bird 41, they were 17 cm from the floor. In both chambers, a thin sheet of Plexiglas covered the monitor screen, and spacers were used to recess the touch frame by approximately 3 cm from the monitor opening and to separate the frame from the monitor by approximately 1.5 cm. Lamps located within each feeder were used to illuminate feeder presentations. Photocells in each hopper measured head entries into the hopper. All food deliveries consisted of 2-s access to one of the two hoppers. The hopper that was presented was selected randomly on each trial so as to minimize bias toward a particular side of the screen.

For the 4 birds at the University of Toronto, the two chambers used each measured 35 cm long by 30 cm wide by 45 cm high (inside dimensions). The floor of the chamber (parallel bars) was raised 4 cm. An opening at the front of the chamber was large enough for the entire Zenith monitor surface. At the floor at the front, a stand (5 cm wide and 6 cm from the floor of the chamber) was constructed. On this stand was a hopper into which a Gerbrands feeder delivered pellets from the left side. A 7-W light above the hopper lit up during and for 1 s following food delivery. All food deliveries consisted of presentation of three 20-mg pellets. White noise played during experimentation.

Microcomputers located in an adjacent room controlled experimental contingencies and recorded peck coordinates. The touch frames were programmed to detect individual pecks (i.e., detection of a beam break, then a return to unbroken beams before another peck could be recorded).

Search Space and Stimuli

The search space consisted of a rectangular area, approximately 26 cm by 20 cm on the surface of the color monitors. Two arrangements of the goal, frame and landmark were constructed, as shown in Figure 1. In both arrangements, the goal area (2 cm by 2 cm, indicated in Figure 1 by the small outlined square) and a single graphic landmark (indicated by the filled square or triangle) always occurred in a fixed location within a square white graphic frame that constituted the arena (approximately 11 cm by 11 cm). However, the location of the arena on the screen varied from trial to trial so that the goal area was not
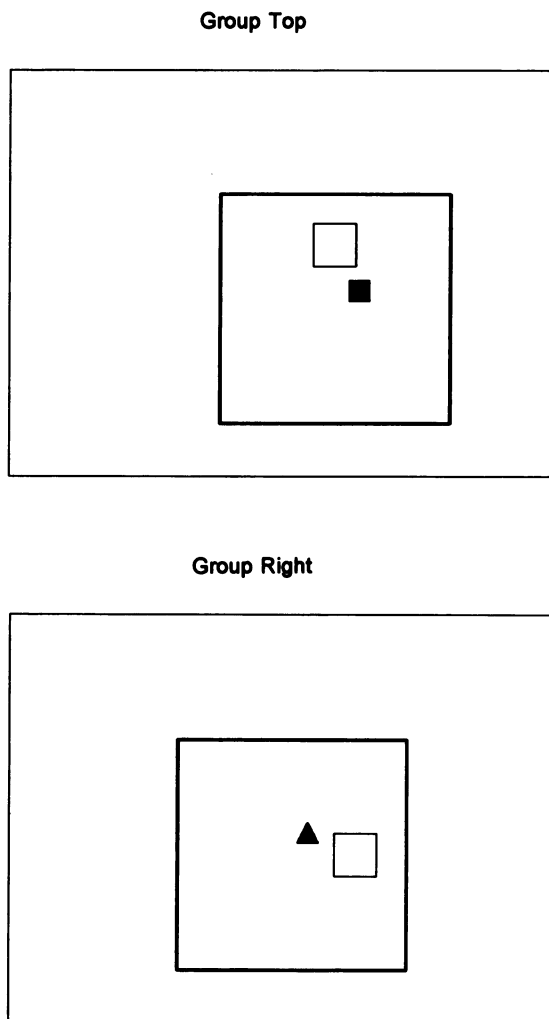
Group Top

Group Right

Fig. 1. Arrangement of goal, landmark, and graphic frame for birds in the top group (top diagram) and in the right group (bottom diagram). The outside rectangle represents the surface of the monitor screen (approximately 26 cm by 20 cm). The small outlined square is the goal area (2 cm by 2 cm), the solid symbol is the graphic landmark, and the intermediate-sized outlined square is the white graphic frame. Only the frame and the landmark were visible.

presented at a fixed location. The location of the center of the goal was randomly selected on each trial, with two constraints: (a) that it allowed the entire graphic frame to fit on the screen, and (b) that the center of the goal was midway between two infrared (touch-frame) beams in both dimensions. In one arrangement (the top group), the goal area was close to the top edge of the graphic frame and was centered in the frame horizontally; a square red graphic

landmark was below the goal and to the right of the goal center. In the other arrangement (the right group), the goal area was centered in the frame vertically and was close to the right edge of the frame; a triangular green graphic landmark was located to the left of the goal and above the goal center. Three pigeons were assigned to each group.

General Procedure

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 and was then given several sessions of autoshaping. Each autoshaping trial began with illumination of a goal marker (a 2 cm by 2 cm solid yellow square centered at the goal). The location of the goal varied across trials as described above. The goal marker remained illuminated for 8 s or until a peck in the goal area was recorded; then food was presented. Trials were separated by a 60-s intertrial interval (ITI), during which the monitor was illuminated with the dark gray background but no graphic stimuli were present.

Once a pigeon was pecking on at least 80% of the trials, the procedure was changed to require a response in the goal area to terminate the trial and produce food. Over subsequent sessions, the ITI was reduced to 5 s and the graphic landmark and graphic frame were introduced. Then, the goal marker was faded within and between sessions by gradually changing the graphic fill style according to the following sequence: solid fill, interleaving line fill, closely spaced dot fill, widely spaced dot fill, and empty fill (i.e., marker absent). The rate at which these changes were made depended on the bird's behavior. Each correct peck incremented a counter by 5, and each incorrect peck decremented the counter by 1. When the counter increased by 30, the next step in the sequence was implemented. But if the counter decreased by 30, the preceding step in the sequence was reinstated. This training phase continued until the bird completed at least 80 consecutive trials with the goal marker absent.

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

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 no-reinforcement 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 goal area several times each trial and to receiving food reinforcement only 50% of the time that they met the response criteria.

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

Each bird was initially exposed to three types of test sessions. In frame- and landmark-absent sessions, the frame was absent on some test trials and the landmark was absent on other test trials. In frame-shift test sessions, one side of the frame was shifted 2 cm from its normal position on test trials; the top of the frame was shifted up, the bottom was shifted down, the right side was shifted to the right, or the left side was shifted to the left. In each case the adjacent lines were stretched so that a complete frame was still presented. The arena thus appeared to be stretched either vertically or horizontally. In landmark-shift tests, the landmark was shifted by 2 cm on test trials either horizontally, vertically, or diagonally (2 cm in both dimensions) from its normal position relative to the goal and frame. The direction of these shifts was away from the goal area. Consequently, for birds in the right group, the vertical landmark shift was up, the hori-

zontal shift was to the left, and the diagonal shift was up and to the left. For birds in the top group, the vertical shift was down, the horizontal shift was right, and the diagonal shift was down and to the right. These three types of test sessions were each presented two or three times in a randomly determined order for each bird. In total, each bird completed at least 15 test trials of each type.

In a subsequent test series, each bird received four test sessions designed to determine whether the frame would allow the birds to distinguish between the correct landmark and an identical duplicate of the landmark. On test trials of these duplicate landmark tests, the duplicate landmark was located 3 cm left, right, above, or below the correct landmark. On half of these tests, the frame was present; on the other half, the frame was absent.

Data Recording and Analysis

Peck coordinates were recorded in units of approximately 1 square cm. For each trial this resulted in an 18 by 25 unit matrix. Because the goal location varied across trials, all units were defined relative to the goal. The variable goal location resulted in variation in the availability of some units. For example, a response unit far to the right of the goal was not available on trials in which the goal was near the right edge of the monitor. To adjust for the differential availability of the response units, all data were weighted in this way: First, the number of responses in each unit was divided by the number of tests on which the unit was available to obtain a weighted count. These weighted counts were then expressed as a proportion of the total weighted counts in the whole distribution. Because very few pecks occurred at a distance far from the goal area, and to simplify the data analysis and presentation, all pecks that fell farther than 8 units from the goal were treated as having fallen in the 8th unit. Thus, all data presented are shown in terms of location relative to a moving goal, and all are weighted according to opportunity to respond in each particular location.

For each bird, an accuracy score was computed by determining the proportion of total weighted pecks that fell in the four units comprising the goal location. Although it was physically possible for the birds to peck in each of the 450 units available on the screen, only 96 units served as possible goal areas during training (because only goal areas that allowed room for the frame were used). If the birds responded randomly in these 96 units, the proportion of pecks that should fall in the four goal units on the basis of chance is only .04.

For shift tests, we also computed the peak place of searching in both the vertical and horizontal dimensions, using the iterated median procedure as described in Cheng (1989) and Spetch et al. (1992). This procedure determines the middle of the highest region in the distribution. First, the median of the weighted response distribution was calculated. Then the median calculation was iterated by calculating it over the region in which the previous median was centered. For example, if the first calculation over the range of 1 to 16 units yielded a median of 3, the next calculation would be over the range of Units 1 to 5. This process was repeated until two consecutive iterated medians differed by less than 0.05 of a unit. The last calculated median was taken to be the peak of the distribution.

RESULTS

The training phase required between 17 and 32 sessions for the various birds.

Frame- and landmark-absent tests. Figures 2 and 3 show response distributions for the 3 birds in the top group and the right group, respectively, on control trials and on test trials in which the landmark was absent or the frame was absent. These response distributions are pooled across all trials of each 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; these plot only those units containing at least 5% of the total weighted pecks, or in other words, units in which there was a concentration of responding. The top views therefore provide an indication of the location of peak responding. Both views show 8 units (approximately 8 cm) on either side of center of the goal, which is indicated by the intersection of the two zero lines.

Inspection of the response distributions
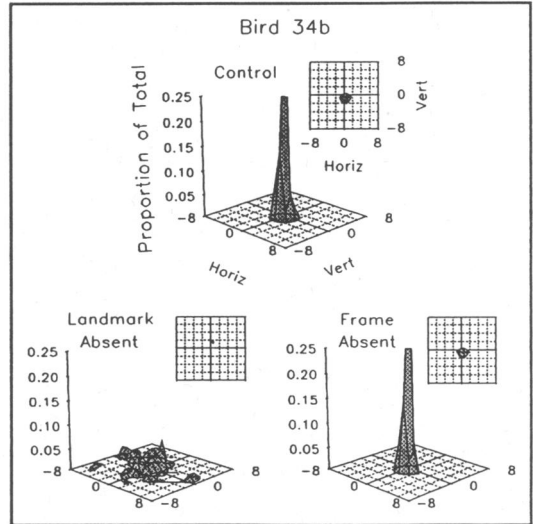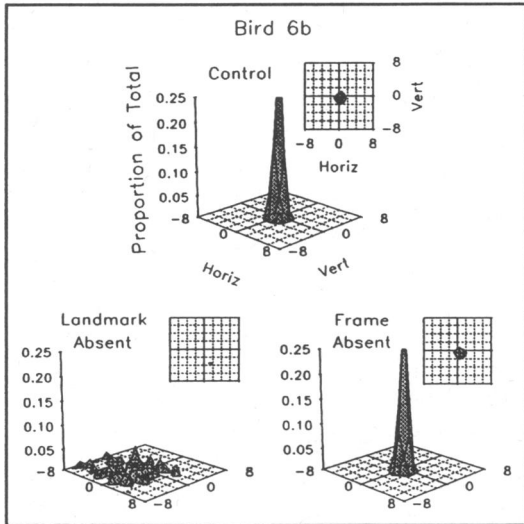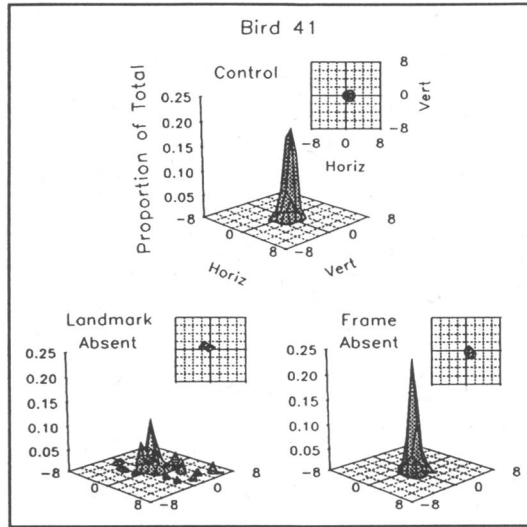
Group Top

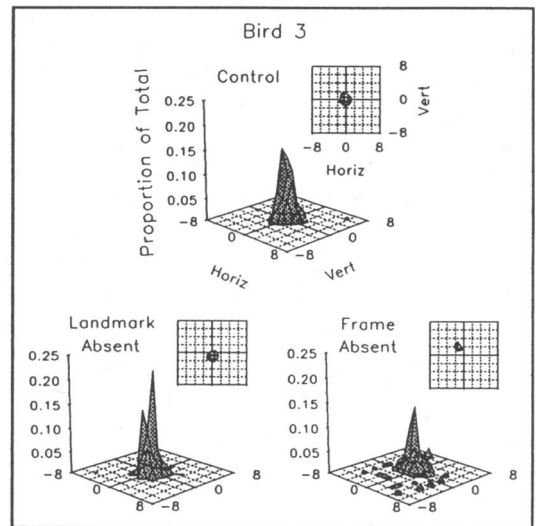
Fig. 2.   Response distributions of the 3 birds in the top group on control trials and on landmark-absent and frame-absent test trials. See text for details.

shows that on control trials all birds displayed localized responding that was centered at the target area. When the landmark was removed, all birds except Bird 3 (the right group) showed complete or partial disruption of localized responding. When the frame was removed, only

Bird 3 showed a substantial disruption of localized responding. Response distributions of the other 5 birds on trials with the frame absent appeared to be similar to their response distributions on control trials.

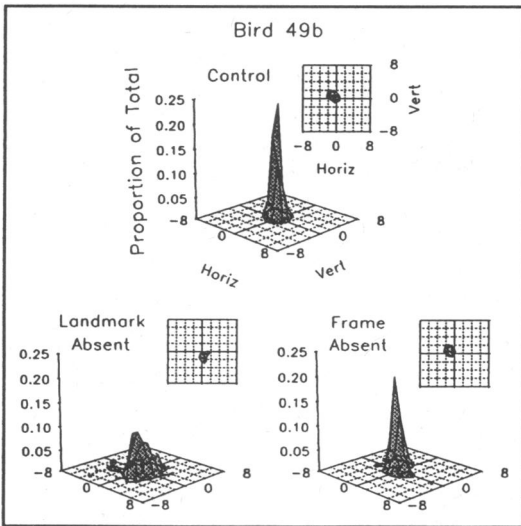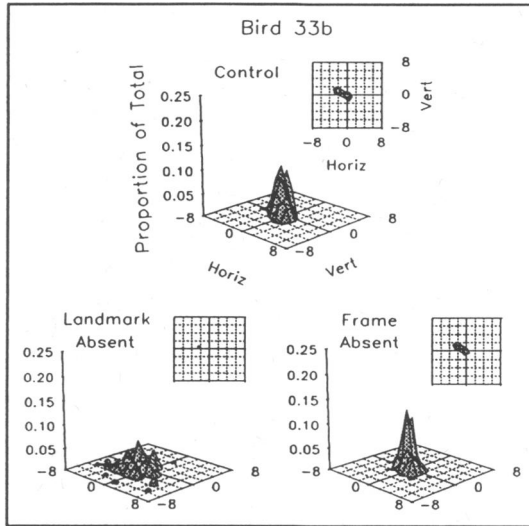These observations based on inspection of

Group Right

Fig. 3. Response distributions of the 3 birds in the right group on control trials and on landmark-absent and frame-absent test trials. See text for details.

the response distributions are consistent with the accuracy scores on control and landmark- or frame-absent test trials, shown at the top of Table 1. All birds except Bird 3 showed a greater disruption in accuracy when the landmark was removed than when the frame was

removed. In contrast, Bird 3 showed only a small disruption in accuracy when the landmark was removed, but showed a dramatic reduction in accuracy when the frame was removed. The results of these cue-removal tests therefore indicated that 5 of the birds showed

Table 1

Proportion of pecks in the goal area (with total number of pecks recorded in parentheses) on control and test trials in which the landmark (Lm) or frame (Fr) was absent or was shifted from its normal location with respect to the goal.

	Top group			Right group		
	41	6b	34b	33b	49b	3
Absent tests						
Control	.475 (271)	.697 (615)	.708 (435)	.303 (536)	.483 (346)	.501 (173)
Lm absent	.268 (72)	.039 (78)	.069 (230)	.104 (120)	.173 (174)	.405 (164)
Fr absent	.394 (252)	.521 (532)	.711 (444)	.276 (356)	.228 (221)	.081 (116)
Lm shift tests						
Control	.490 (235)	.621 (556)	.660 (384)	.289 (486)	.492 (250)	.525 (179)
Horizontal	.093 (198)	.008 (501)	.000 (386)	.152 (474)	.139 (267)	.441 (158)
Vertical	.161 (179)	.014 (495)	.000 (366)	.143 (387)	.345 (274)	.431 (175)
Diagonal	.056 (195)	.004 (490)	.000 (355)	.200 (395)	.191 (277)	.367 (169)
Fr shift tests						
Control	.481 (168)	.594 (475)	.702 (314)	.285 (493)	.486 (243)	.456 (128)
Top	.322 (153)	.656 (470)	.775 (315)	.303 (505)	.427 (218)	.479 (122)
Bottom	.502 (182)	.655 (433)	.810 (310)	.281 (478)	.483 (232)	.333 (138)
Left	.502 (199)	.650 (407)	.745 (314)	.32 (465)	.43 (249)	.515 (130)
Right	.602 (198)	.650 (420)	.803 (306)	.281 (459)	.389 (257)	.251 (136)

primary or exclusive control by the landmark, whereas 1 bird showed primary control by the frame.

Landmark-shift tests and frame-shift tests. Figures 4 and 5 show the calculated peak place of responding for birds in the top group and the right group, respectively, on control trials and on test trials in which the frame or landmark was shifted. In each figure, the solid cross marks the "hypothetical" goal area according to all unshifted cues (hypothetical because reinforcement was never available on control or test trials). The dotted cross indicates where the goal area would be according to a shifted cue. In either case, the hypothetical goal area encompasses four 1-cm response units. For the frame-shift tests, only the results of shifts of the top and right edges are plotted.

Of the birds in the top group, only Bird 41 showed any evidence of following the frame when it was shifted. Bird 41 responded to an upward shift of the top of the frame (the closest edge) by shifting its search approximately half-

way toward the shifted edge, but showed no shift in response to a rightward shift of the right edge. The remaining 2 birds showed no shift in response to shifts of either edge. All 3 birds in this group showed large shifts in peak place of searching when the landmark was shifted. Birds 6b and 34b showed complete shifts in search location. This can be best seen by noting that the peak place of searching fell in the bottom right quadrant of the hypothetical goal area on control trials, and that it shifted to the same quadrant of the hypothetical goal area according to the vertically (down), horizontally (right), or diagonally (down and right) shifted landmark. Bird 41 shifted about 75% of the way toward the shifted landmark in the horizontal dimension and about 60% of the way toward it in the vertical dimension.

Of the birds in the right group, only Bird 3 showed shifts in peak search location when the frame was shifted. When the right edge of the frame (i.e., the edge nearest the goal) was shifted to the right, Bird 3 shifted approxi-

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Fig. 4. Calculated peak place of searching by birds in the top group during control and test trials of the frame-shift tests (left) and landmark-shift tests (right). For frame-shift tests, peaks are shown for the tests in which the top edge was shifted up or the right edge was shifted to the right. For landmark-shift tests, peaks are shown for shifts of the landmark to the right, down, or diagonally right and down. In all graphs, the solid cross indicates the hypothetical goal area according to all cues on control trials and according to unshifted cues on test trials. The dotted crosses show where the goal would be according to the shifted cue on test trials.
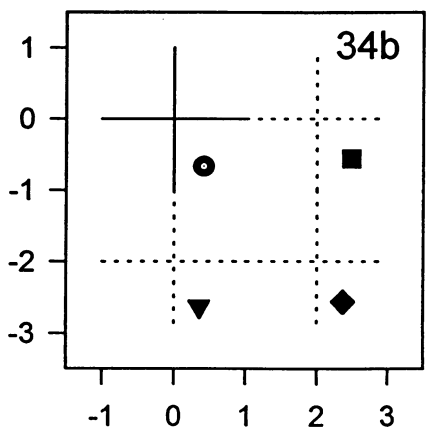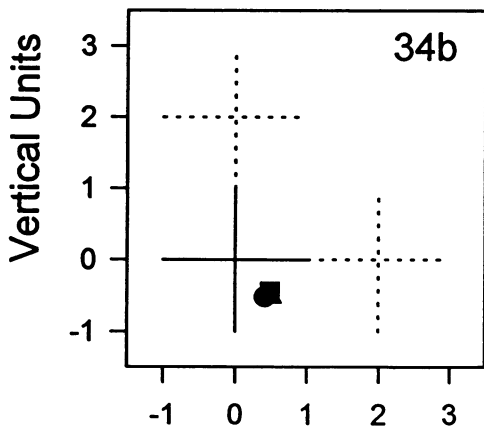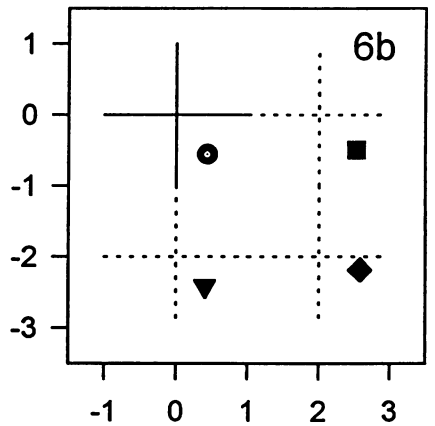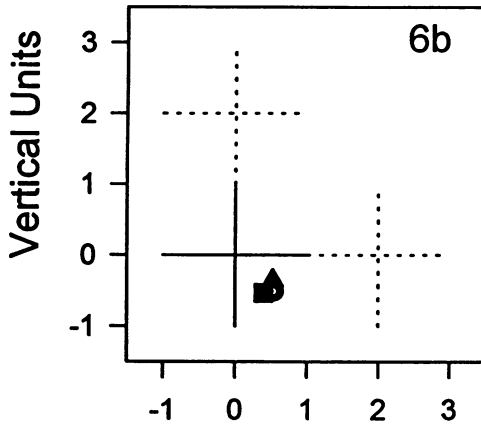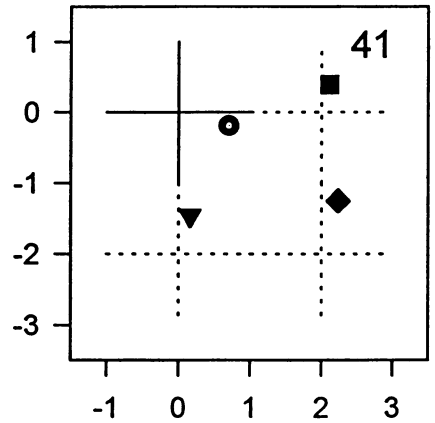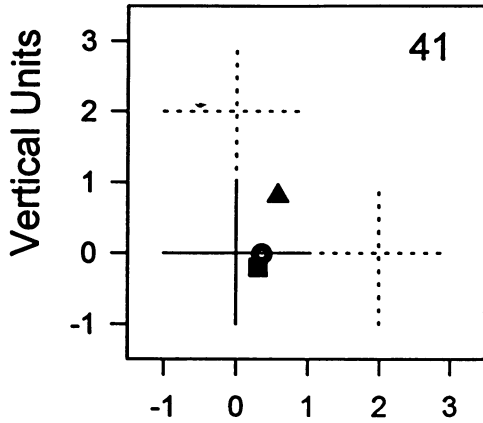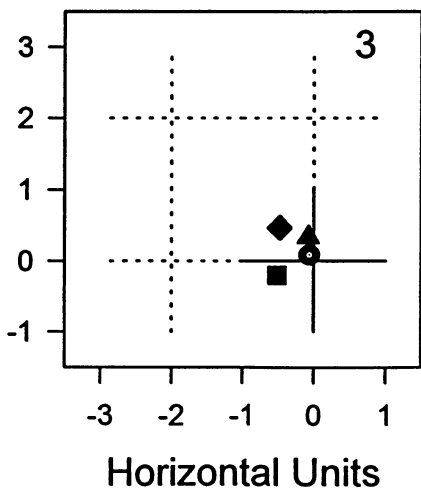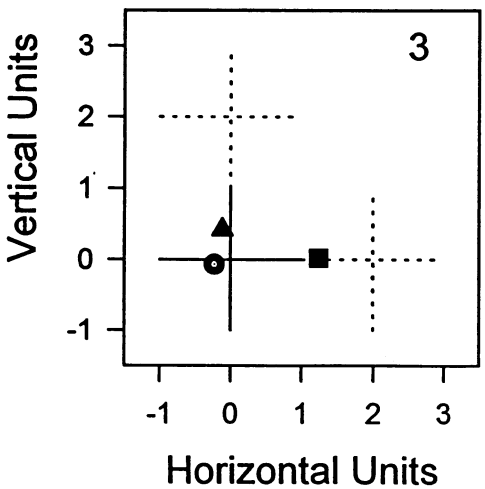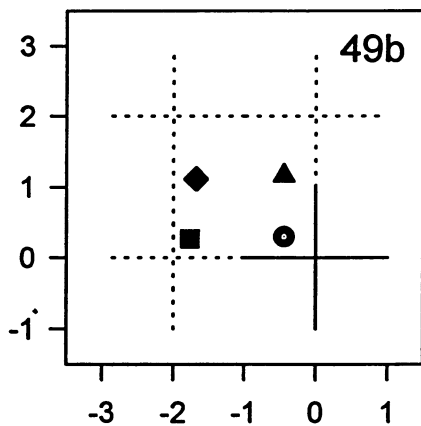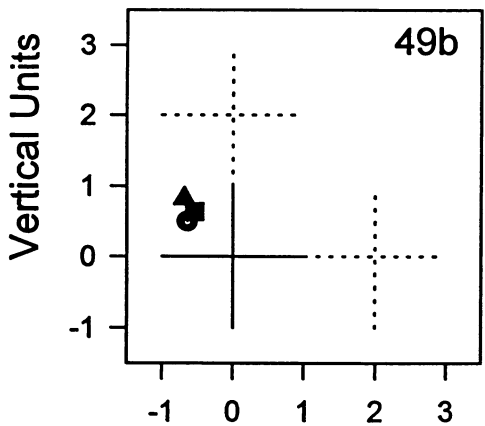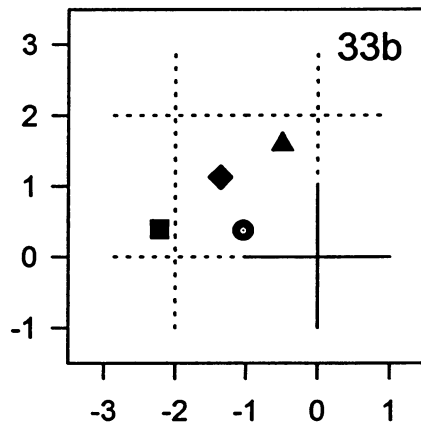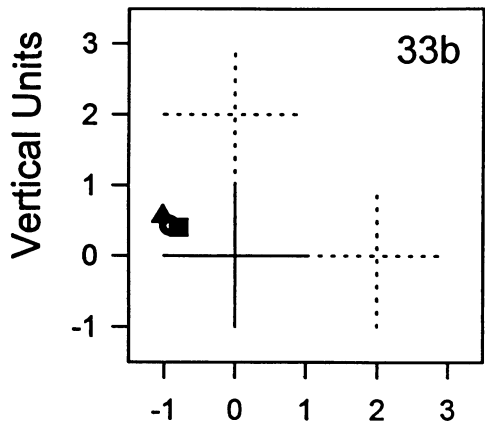
mately 75% of the way toward the shifted edge. When the top edge was shifted up, Bird 3 showed a small upward shift in peak place of searching. Neither of the other birds showed a shift in response to shifts of either edge. In response to landmark shifts, Birds 33b and 49b both showed peaks that suggested a compromise between the shifted landmark and the frame; these birds shifted approximately halfway toward the shifted landmark in both the horizontal and vertical dimensions. Bird 3 showed only very small shifts in peak place of searching when the landmark was shifted.

Accuracy scores on control and all shift test trials are shown in Table 1. In each case, accuracy is defined in terms of the goal according to unshifted cues. Therefore, low accuracy scores would be expected if a bird's searching followed the shifted landmark; high accuracy scores would be expected if the bird responded on the basis of the unshifted cue. The pattern of results indicated by the accuracy scores is consistent with that indicated by the calculated peak place. All birds except Bird 3 showed a substantial disruption in accuracy when the landmark was shifted and either no disruption or a smaller disruption in accuracy when the frame was shifted. Bird 3 showed only minor disruptions in accuracy in response to landmark shifts, but showed a substantial disruption in accuracy in response to a shift of the right edge of the frame. Bird 3 also showed some disruption in accuracy when the bottom edge of the frame was shifted. Thus, the results of the shift tests are consistent with those of the removal tests in suggesting that Bird 3's pecking was controlled primarily by the frame, whereas that of the other 5 birds was controlled primarily by the landmark.

Duplicate landmark tests. Figure 6 shows accuracy scores of all 6 birds on control trials and on test trials in which an extra identical landmark was present with or without the frame. Four of the birds (41, 33b, 49b, and 3) showed substantially higher accuracy on trials

with the frame present than on trials with the frame absent. On trials with the frame present, these birds responded primarily in the location appropriate to the correct landmark rather than in the location appropriate to the extra landmark; consequently, they achieved accuracy levels that were as high or almost as high as on control trials. On trials with the frame absent, these 4 birds displayed low levels of accuracy. Bird 34b, in contrast, showed no difference in accuracy between trials with the frame present and trials with the frame absent. In both cases, this bird responded about half of the time according to the correct one of the two landmarks and thereby achieved accuracy levels that were approximately half that of control levels. Thus, Bird 34b showed no ability to use the frame to distinguish between the correct landmark and the duplicate. Bird 6b showed an intermediate pattern. Accuracy was only slightly higher with the frame present than with the frame absent. With the frame absent, accuracy was about half of that on control trials, indicating that the bird responded according to the correct landmark rather than to the duplicate about half of the time. The somewhat higher accuracy on trials with the frame present suggested some ability to use the frame to identify the correct landmark.

DISCUSSION

Taken together, the results of the removal tests, shift tests, and duplicate landmark tests indicate three patterns of cue control. One pattern, that displayed by Birds 34b and 6b, is exclusive or nearly exclusive control by the landmark. These birds both showed complete disruption when the landmark was removed. When the landmark was shifted, their peak places of searching followed the landmark and shifted by the full extent of the landmark shift. These birds showed little or no disruption of accuracy when the frame was removed, and

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Fig. 5. Calculated peak place of searching by birds in the right group during control and test trials of the frame-shift tests (left) and landmark-shift tests (right). For frame-shift tests, peaks are shown for the tests in which the top edge was shifted up or the right edge was shifted to the right. For landmark-shift tests, peaks are shown for shifts of the landmark to the left, up, or diagonally left and up. In all graphs, the solid cross indicates the hypothetical goal area according to all cues on control trials and according to unshifted cues on test trials. The dotted cross shows where the goal would be according to the shifted cue on test trials.
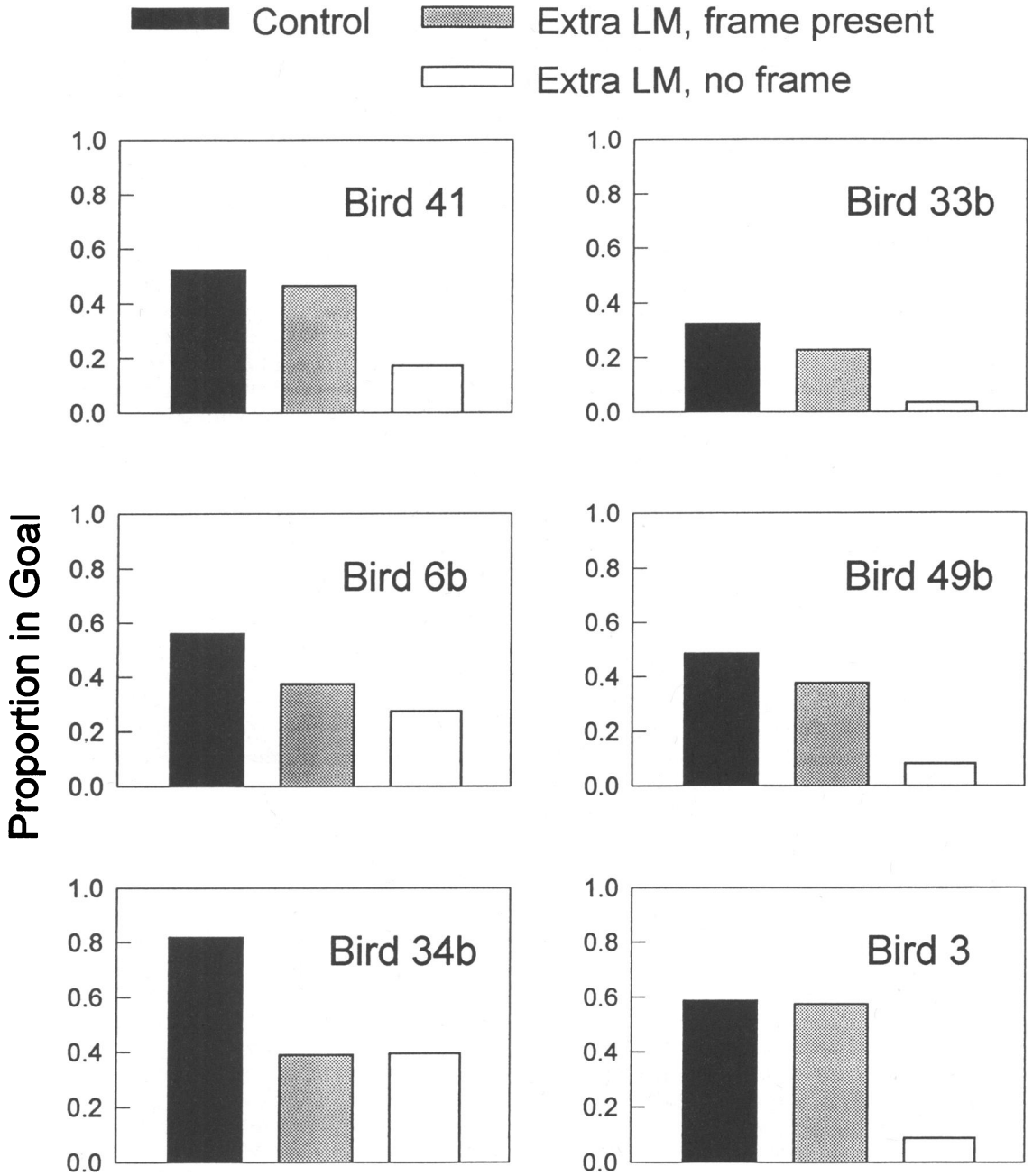
Fig. 6.   Proportion of pecks in the goal area on control and duplicate landmark tests for the 3 birds in the top group (left) and the 3 birds in the right group (right). See text for details.

they displayed no tendency to follow shifts of an edge of the frame. The frame also appeared to provide little (Bird 6b) or no (Bird 34b) help in distinguishing a correctly placed land-mark from an incorrectly placed duplicate.

The second pattern, that displayed by Birds 41, 33b, and 49b, is primary control by the landmark and secondary control by the frame. The performances of these birds were more disrupted by removal of the landmark than by

removal of the frame, and they showed a greater tendency to shift with the landmark than with the frame. However, the shifts of peck location in response to landmark shifts were not complete, suggesting some compromise between the shifted landmark and the unshifted frame. These 3 birds were also able to use the frame to distinguish the correctly placed landmark from the incorrectly placed duplicate.

The third pattern, that displayed by Bird 3, was primary control by the frame and little or no control by the landmark. Bird 3 showed far more disruption in accuracy in response to removal of the frame than to removal of the landmark. Bird 3 also showed a greater shift in response to a shift of the right edge of the frame than in response to shifts of the landmark. Weak control by the landmark was suggested by the small disruptions in accuracy that occurred when the landmark was removed or shifted and by the incomplete shifts that occurred in response to shifts of the frame edges.

Thus, in finding a location on a monitor based on graphic landmarks, different pigeons were controlled by different stimuli. Moreover, search behavior was often controlled primarily by only a part of the graphic display: either the landmark or the frame. Nevertheless, the absence of direct control by a stimulus does not necessarily mean that it plays no role in guiding search. On duplicate tests with two landmarks, some birds that showed little direct control by the frame nevertheless used it to distinguish the correct landmark from the incorrectly placed duplicate. Thus, the frame can be used to guide searching even though its direct control was masked or overshadowed by the landmark during the absent and shift tests. This finding suggests that a full assessment of stimulus control by elements in a compound requires several kinds of tests.

The pattern of selective control observed here resembles that found by Spetch and Mondloch (1993) in a similar search task on the touch screen. In Spetch and Mondloch's study, the goal was located in the middle of an array of four graphic landmarks. Tests in which landmarks were removed or shifted showed that the pigeons were each controlled by only a part of the landmark array, sometimes primarily by a single landmark. As in the present study, different pigeons used different aspects of the landmark array. Selectivity of landmark control was also found in a touch-screen task in

which the display was a digitized image of an outdoor scene (Spetch & Wilkie, 1994). The image contained three visual landmarks placed at various distances from a hidden goal. Pigeons showed primary or exclusive control by the landmark nearest the goal.

The present research extends the results of these previous studies by showing that selectivity of control by spatial landmarks is not restricted to situations in which the landmarks are all similar to one another (i.e., all small localized objects). In the present study, the two sources of landmark information were visually quite different: a small localized form and a graphic frame. Although most pigeons selectively used the localized form, 1 pigeon attended primarily to the frame, suggesting that selectivity did not reflect an inability of pigeons to use the frame for localization.

Selective control by one aspect of the stimulus situation has also been found in other experiments in which compound stimuli served as discriminative stimuli. For example, Reynolds (1961) investigated stimulus control by the elements of shape–color compounds. During training, 2 pigeons were presented successively with two compounds consisting of a white shape superimposed on a background color. One compound signaled a variable-interval (VI) schedule, and the other signaled extinction. After discrimination had been established, Reynolds tested the birds with each of the elements alone. It was found that 1 bird responded to the shape that was positive but not to the color that was positive, whereas the other bird responded to the color that was positive but not to the shape. Neither bird responded to the negative elements.

Control by only one element of a compound also may occur in classical conditioning, as indicated by the phenomenon of overshadowing (e.g., Kamin, 1969; Pavlov, 1927). When a compound stimulus is presented as the conditional stimulus, often only one element of the compound becomes associated with the unconditional stimulus. The other element may not be conditioned at all, even though it is capable of being conditioned if it is presented alone during pairing with the unconditional stimulus. Thus, learning about one element appears to detract from learning about the other element. Reciprocal overshadowing between intramaze and extramaze cues has also been demonstrated for rats' spatial memory in the

radial maze task (March, Chamizo, & Mackintosh, 1992). A fruitful area for future research may be to explore further the extent to which principles and accounts of selective associations in classical conditioning and instrumental discrimination learning are applicable to spatial landmark learning.

Although consistent with findings from other touch-screen studies and other stimulus control situations, the tendency to show primary or exclusive control by only part of the stimulus situation appears to contrast with results from other spatial search tasks. In general, results from many spatial tasks have suggested that multiple stimuli are typically used in determining where to search (see Cheng, 1992). In particular, joint control by multiple stimuli was found in search tasks using landmark arrangements after which the present research was modeled (Cheng & Sherry, 1992; Spetch et al., 1992). For example, Cheng and Sherry (1992) tested pigeons and black-capped chickadees in a square arena in a room. The goal was near the middle of one edge of the arena. Near the goal was a bottle serving as a landmark. Tests in which the bottle was shifted indicated that both species used both the edge of the arena and the bottle in determining where to search. Spetch et al. (1992) tested pigeons in a touch-screen search task similar to the one described in this paper, except that the entire monitor served as the search space and the goal was in a fixed location near one edge of the screen. A gray strip around the edges of the monitor provided a graphic border, and a graphic landmark was located near the goal. Tests in which the landmark was shifted revealed a pattern of results similar to that found by Cheng and Sherry (1992). Search was determined by both the landmark and some aspect of the edge. The controlling edge was not the graphic edge, however, because shifting the graphic edge had no discernible effect on search behavior. Thus, graphic edges may be less salient or effective than three-dimensional edges.

It should be noted that selective control by only one of the visual stimuli presented on the screen in this and other touch-screen studies does not mean that the pigeons' search was controlled solely by that one stimulus (see Spetch & Wilkie, 1994). At the least, when the landmark controlling search is symmetrical, some other cue must provide directional information. That is, learning that a goal is a

particular direction from a symmetrical landmark is meaningful only if there is a well-defined frame of reference to indicate which direction is which. In touch-screen tasks, many stable cues in the chamber can serve this function, as can proprioceptive cues.

A second factor to bear in mind is that in touch-screen tasks, the search space is very small. Pigeons likely would not rely on the graphic cues for orientation and approach to the general region of the goal; the screen itself may serve this function. The graphic stimuli may therefore serve only to pinpoint the goal in a search space that is defined and oriented on the basis of other cues, and it may be that only this aspect of searching was controlled by single rather than multiple stimuli. This distinction between orientation and approach to the general region and pinpointing the goal is based on intuition at the moment, but it is a topic that deserves further study. One empirical technique for tackling the issue is to use an environment with multiple touch screens—for instance, a rectangular operant conditioning chamber each of whose sides is equipped with a touch-screen monitor. This would force the birds to choose the correct monitor as well as the correct location on the monitor, and factors controlling the choice of each may be manipulated. In an attempt to instantiate a metric spatial representation on computer, Davis (1986) has found it necessary to create a hierarchical representation system, a system with different scales and degrees of accuracy at different levels of the hierarchy. It is likely that biological spatial representation systems would also contain a hierarchical structure.

The sufficiency of a single cue in supporting accurate search may also be a factor in the selectivity of control. In the present study, the goal was sufficiently close to both the landmark and an edge of the frame that accurate search should be possible on the basis of either cue alone. Only one of these cues may have gained control, because only one was needed to search accurately. In tasks for which such precision may not be possible on the basis of a single local landmark (e.g., with greater distances between the landmarks and goal), or in which local landmarks serve more than one role (i.e., to orient to and approach the general goal region as well as to pinpoint the goal), control by multiple landmarks may be more typical.

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