

Pigeons' Use of Landmarks Presented in Digitized Images

MARCIA L. SPETCH

University of Alberta, Edmonton, Canada

AND

DONALD M. WILKIE

University of British Columbia, Vancouver, Canada

Pigeons received food for pecking a hidden goal location in digitized images of an outdoor scene, presented on a monitor/touchscreen system. Three landmarks (tree, flowers, log) were located near the goal on a field of grass. For some birds the goal was closest to the tree, whereas for other birds the goal was closer to the flower and log. After training, the landmarks were removed, shifted, or altered using imaging software. Landmark control was highly selective and depended on proximity to the goal. There was no evidence that search was controlled by the configuration of the three landmarks. Instead, search behavior appeared to be jointly controlled by a single local landmark and global cues associated with the area of the screen that contained goal locations during training. These findings extend results of a previous study that used simple graphic forms as landmarks in a touch-screen task, and they demonstrate the use of video imaging technology for studies of spatial landmark learning. © 1994 Academic Press, Inc.

Many animals use visual information provided by features of the terrain or objects in the environment to remember and navigate to important locations. Experimental tests in which potential landmarks are removed, altered, or displaced have provided convincing demonstrations of land-

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mark use in a number of species, and progress is being made toward understanding the mechanisms by which various organisms derive spatial information from landmarks (see Cheng, 1992; Collett, 1992; Gallistel, 1990).

Laboratory experiments have provided clear evidence that pigeons and other birds can use visual landmarks when searching for hidden food (Cheng, 1988, 1989, 1990; Cheng & Sherry, 1992; Spetch & Edwards, 1988; Sherry, 1992; Vander Wall, 1982). Evidence that pigeons use visual cues on homing flights has been less forthcoming (Keeton, 1974). Pigeons do not appear to rely upon visual cues for successful orientation from distant sites, but they may use visual landmarks during the final stage of homing flights to locate their loft (Wallraff, Neumann, & Sinsch, 1989). Visual cues may also play a role in pigeons' recognition and orientation from familiar distant release sites (Braithwaite & Guilford, 1991; Streng & Wallraff, 1992). That pigeons' spatial search in natural settings is at least sometimes guided by visual stimuli would be expected in light of evidence that they have excellent memories for visual detail (e.g., Vaughan & Greene, 1984).

Most real world locations provide a rich assortment of visual stimuli that could be encoded as landmarks. Little is known about how much of the available visual information pigeons encode, what visual features attract their attention, and what factors determine whether a particular stimulus will be relied upon as a landmark. Field studies often do not allow the control or manipulation of visual stimuli necessary to address these questions, and most laboratory studies have focused more on how landmarks guide search behavior than on factors that determine which objects or visual features will be encoded as landmarks. Cheng's (1988, 1989) laboratory studies of pigeons' landmark-based search have, however, suggested that pigeons typically encode the location of hidden food in relation to more than one landmark and have identified relative distance to the goal as an important determinant of the weight given to specific landmarks (Cheng, 1989). Proximity to the goal has also been shown to be an important determinant of landmark control in insects (e.g., Cheng, Collett, Pickard, & Wehner, 1987; Tinbergen, 1972).

Spetch, Cheng, and Mondloch (1992) recently introduced a touch-screen task for studies of pigeons' landmark-based search. In this task, pigeons search for an unmarked goal area on the surface of a touch-screen-equipped color monitor. In Spetch *et al.*'s study, the goal area was in a fixed location near either the top edge of the screen or the left edge of the screen. A simple graphic form near the goal served as the landmark. They found that control by the graphic landmark was similar in several ways to control by object landmarks in open-field spatial search tasks. For example, as in open-field studies (Cheng & Sherry, 1992), shifts of the landmark in directions parallel to the nearest edge produced larger

and more consistent shifts in search location than did shifts perpendicular to the edge. In addition, pigeons typically shifted only part way toward the shifted landmark, suggesting that search was controlled by more than one cue.

Spetch and Mondloch (1993) used a variant of this task to investigate control of pigeons' spatial search by multiple landmarks. In their study, pigeons searched for a hidden goal that was not in a fixed screen location but instead moved about on the screen from trial to trial. Four nearby visually distinct graphic stimuli, each bearing a consistent spatial relationship to the goal area, were presented on all training trials as potential landmarks. During subsequent nonreinforced test trials, control by each landmark was assessed by removing it or shifting its location relative to the other landmarks. These tests revealed surprising selectivity of control: most birds showed good control by one or at most two of the four landmarks, and some birds showed exclusive control by a single landmark. Moreover, although the control exerted by each landmark was highly consistent across tests for a given bird, the preferred landmark varied between birds. Proximity may have influenced control since none of the birds preferred the landmark farthest from the goal. There was no indication that birds relied upon the configuration of the four landmarks presented in training, even though the goal area was roughly in the center of the array of four landmarks. In subsequent tests, the color and shape of the graphic stimuli were manipulated to determine which of these two landmark features was more important. All birds displayed strong control by landmark color and little or no control by landmark shape.

The present research was designed to extend these previous studies of landmark use in touch screen tasks (Spetch *et al.*, 1992; Spetch & Mondloch, 1993) in three ways. First, we sought to provide direct evidence that proximity to the goal area is an important determinant of control by landmarks in touch-screen tasks. Although both previous studies provided indirect evidence suggesting the importance of proximity, direct evidence of its importance in touch-screen tasks has yet to be provided. Because proximity has been shown to be an important determinant of landmark control in open-field tasks with pigeons (Cheng, 1989) and insects (Cheng *et al.*, 1987; Tinbergen, 1972), a clear demonstration that it is similarly important within touch-screen tasks would further indicate the generality of principles of visual landmark use across very different types of landmarks and spatial arenas (cf. Spetch *et al.*, 1992).

Second, the present research included tests to assess whether control by individual landmarks was modulated by either the spatial conformation of the multiple landmarks presented during training, or the more global cues associated with the general area on the screen in which the goal area occurred. In nature, animals often need to distinguish between the encoded landmark (e.g., a particular tree) and other similar landmarks in

other locations. Although this might be achieved by close attention to detailed features of the landmark, a more likely possibility is that this differentiation is accomplished by learning its relationship to other local landmarks and/or global features of the environment (cf. Poucet, 1993). One intriguing aspect of Spetch and Mondloch's (1993) results was that pigeons showed no evidence of learning about the configuration of landmarks; that is, the conformation formed by the four landmarks appeared neither necessary nor sufficient for accurate search. Tests included in the present research assessed not only the necessity or sufficiency of conformational information, but also asked whether landmark conformation might serve in a disambiguating role, that is, to distinguish between the correct landmark and a visually identical one in a different location. The contribution of global screen location cues was also assessed. In the present research, the goal location varied on the screen across trials, but because the landmarks were reasonably large and spread out, some areas of the screen never contained the goal. We included tests to examine the contribution of global cues associated with screen location to the control exerted by the visual landmarks.

Finally, the present research asked whether the results obtained by Spetch and Mondloch (1993) would generalize to richer more complex stimuli. The simple visual stimuli used in their study—solid two-dimensional graphic landmarks presented on a uniform background—offered excellent control, but were clearly visually impoverished in comparison to the far richer and more complex stimuli that would be available in most natural settings. In studies with digger wasps, Tinbergen (1972) found that complex objects (such as pine cones, or patterned blocks) exerted considerably more landmark control than simple unpatterned colored disks or objects. It is possible that stimulus complexity is a factor not only in the extent of landmark control, but also in the way in which search is controlled by multiple landmarks. Accordingly, we sought to determine whether results similar to those obtained by Spetch and Mondloch would be obtained with richer and more naturalistic visual stimuli. To this end, the monitors used in the present research were programmed to display digitized images of a videotaped outdoor scene containing three natural objects that could serve as potential landmarks (a small tree, a planter containing flowers, and a log, all positioned on a grassy field).

Recently available technology for digitizing videotaped images offers an excellent opportunity to present and manipulate the rich and complex visual stimuli found in natural spatial locations. This technology was used in a recent study that complements the present investigation of landmark use by pigeons. In that experiment (Wilkie, Mak, & Saksida, 1994) an image similar to the one used in the present research served as the S+ in a successive discrimination procedure. The S- was the same image, edited to remove the tree, flowers, and log, leaving just the grassy field.

In this respect, the procedure was a variant of the "feature positive" paradigm first studied by Jenkins and Sainsbury (1969) and extended to complex, naturalistic stimuli by Edwards and Honig (1987). Images were presented on a touchscreen-equipped monitor. Capitalizing on pigeons' tendency to peck at the distinguishing feature in feature-positive discriminations, Wilkie *et al.* found that pigeons concentrated their pecking at a particular landmark (e.g., tree) and shifted the location of pecking when that landmark was shifted.

The use of complex, naturalistic stimuli in the study of animal behavior is becoming a fruitful trend (Honig & Fetterman, 1992). The successful use of imaging technology by Wilkie *et al.* suggested that it would be an ideal way to present visually richer and naturalistic stimuli in touchscreen studies of pigeons' landmark-based search.

EXPERIMENT 1

This experiment provided a replication of Experiment 1 of Spetch and Mondloch (1993) using more complex, naturalistic stimuli and using a design that allowed a more direct test of the importance of proximity to the goal in landmark control. Specifically, two groups of pigeons were trained with an identical set of three natural landmarks presented in an outdoor scene, but the location of the goal with respect to these landmarks differed for the two groups. Control by individual landmarks was assessed by removing or shifting the landmarks on subsequent test trials. If proximity is an important factor, the landmark that exerted the greatest control should differ between the two groups.

Method

Subjects

The subjects were six Silver King pigeons, five of which had previously served in a touch-screen search task using graphic landmarks. The sixth bird had previously served in a memory experiment conducted in a standard operant chamber. All birds were housed in large individual cages under a 12-h light/dark cycle (lights on at 6:00 AM). 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

One bird was trained and tested in a modified BRS/LVE chamber and the remaining birds were trained and tested in one of two custom-built chambers. All chambers were equipped with a color monitor (Zenith 1492) and an infrared touch frame (Carroll Touch, 1492 Smart Frame). In the modified chamber, the 28 by 20-cm monitor opening was cut into the

back wall, 9 cm above the floor. The chamber contained two BRS/LVE grain hoppers, one on each of the side walls, 8 cm from the back wall and 9 cm from the floor. The custom-built chambers were 44 cm high, 32 cm deep, and 74 cm wide (inside dimensions), with a 28 by 20-cm monitor opening centered in the back wall, 9 or 10 cm from the floor. Each custom chamber contained two Gerbrands pigeon feeders on the back wall, one 8 cm to the left and one 8 cm to the right of the monitor opening. In one chamber the feeders were 7 cm from the floor and in the other chamber they were 17 cm from the floor. One bird was tested in the modified BRS/LVE chamber and the remaining birds were tested in one of the two custom chambers.

In all 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. Microcomputers located in an adjacent room controlled experimental contingencies, presented images, operated feeders, 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 would be recorded).

Image Preparation

Images of an outdoor scene were digitized and constructed using procedures similar to those described in Wilkie *et al.* (1994). In brief, four objects—a yellow plastic container, a small potted tree, a planter with flowers, and a log—were laid out on a grassy field and videotaped. The tape was later played back into a frame grabber hardware/software system (Super VideoWindows, New Media Graphics Corp.) that was used to select a still frame as a “parent” image, which was then saved in a GIF format (Compuserve, Inc). This image was subsequently edited with Photofinish software (Zsoft) to make the numerous images used in the present experiment.

Search Space and Stimuli

The search space consisted of a rectangular area, approximately 26 × 20 cm on the surface of the color monitors. Two arrangements of the goal area (the plastic box) and three landmarks (tree, flower, and log) were constructed as shown in Fig. 1. Three birds were trained with the arrangement shown on the left (Group A); three were trained with the arrangement shown on the right (Group B). For both arrangements, the parent image was edited to create seven “views” which placed the goal area and corresponding array of landmarks in different portions of the image (i.e., sometimes they were in the left portion of the image, some-



FIG. 1. Images used during initial training for birds in Group A (left image) and Group B (right image). The tree, log, and flowers were landmarks. The plastic box served as an initial goal marker; the box is slightly larger than the 2-cm² goal area. The image was edited to remove the box during an early stage of training.

times in the right portion). This was accomplished by shifting the portion of the image that contained the landmarks and goal area, and then filling in the rest of the image with grass (by copying patches of grass using a “clone” tool). These seven different views were presented during training so that no fixed location on the screen served as the goal area. Five of these views were selected and manipulated to create the various images presented during testing.

General Procedures

Sessions were conducted 5, 6, or 7 days per week at approximately the same time each day. Sessions started from 2 to 9 h after onset of the light cycle. Sessions lasted until all scheduled trials were completed or for a maximum of 1 h. All reinforcement deliveries consisted of presentation of one of the two hoppers, selected at random on each trial. The use of two feeders was designed to minimize bias toward a particular part of the screen. The hopper remained available for 2 s following entry of the head into the hopper as detected by photocells. 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 peck at a yellow graphic rectangle presented in various screen locations against several background colors. Then the initial training image was introduced using an autoshaping procedure: At 60-s intervals, an image of the scene containing the tree, flowers, and log landmarks and the yellow plastic box marking the 2-cm² goal area was presented for 8 s and followed by food. Any pecks at the yellow box during this 8-s period caused food to be presented immediately. Once the bird began to peck at the goal, the intertrial interval (ITI) was

decreased to 5 s and a response requirement was added in which the image remained on until the bird made one peck at the goal.

During a second phase of training, the goal marker was gradually eliminated by editing the image to cover the yellow box with patches of grass (using the "clone" tool). This was accomplished in four steps with images that had increasingly more grass covering the goal. By the final session of this phase, the goal area was completely covered with grass and to the human eye could not be distinguished from the surrounding areas. To ensure that the goal area could not be identified on the basis of a small local detail such as a particular patch of grass, each training image (i.e., each of the seven views) was edited separately so that the patches of grass covering the goal area were not identical. For each image, grass in other parts of the scene was also rearranged slightly using the clone tool, to further ensure that the edited goal area was indistinguishable from other portions of the grassy field. Each step remained in effect until the pigeon was able to complete (by successfully locating the goal area) at least 80 trials in a session.

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 1 to 3. 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 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 goal 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 5 sessions and advanced to the test phase only after it successfully completed at least 80 trials on each of the last two sessions.

Testing Procedures

During all test sessions, the birds received occasional control and test trials interspersed among the reinforced and nonreinforced baseline trials. Each test session contained between 90 and 100 scheduled trials in total. Control trials were visually similar to baseline trials with all landmarks present in their normal positions, except that the images were edited with the clone tool to "rearrange" portions of the grassy field, both in the vicinity of the goal area and in other portions of the image. This ensured that accurate search on control trials could not be based on small local

details such as particular clumps of grass. On test trials, some aspect of the scene was manipulated. On both control and test trials, the trial terminated without reinforcement 8 s after the second peck recorded anywhere on the screen. Reinforced and nonreinforced baseline trials continued to provide seven views of the scene (i.e., views with the goal area in a different screen location), but only one view per session was used for the control and test trials. However, the view selected for control and test trials differed across repeated test sessions of a given type.

Each bird was exposed to four types of test sessions. During Single Landmark tests, the scene contained only one of the three landmarks on test trials. During One-Absent tests, one of the three landmarks was absent from the picture on test trials. During Shift Tests, all three landmarks were present on each test trial, but one of them was shifted by approximately 2.3 cm horizontally in the direction away from the goal area (i.e., the tree was shifted left and the flower and log were shifted right). During a fourth type of test (No Landmark/No Color tests), an image of the grassy field without any landmarks was presented on some test trials, and a black and white image of the training scene was presented on other test trials. The Single Landmark tests, One-Absent tests, and Shift tests were each presented for a total of five sessions and the No Landmark/No Color tests were presented for a total of three sessions. These tests were presented in random order with the constraint that tests of the same type and tests using the same view for test and control trials were not presented on consecutive sessions. One baseline training session occurred after every fifth test session.

Removal of landmarks was accomplished by copying (with a "clone" tool) patches of the grassy field over top of the landmark. Shifts were accomplished by moving the selected portion of the image that contained the landmark or landmarks and then filling in the original location with patches of the grassy field. Figure 2 shows a sample of the images used during testing.

Data Recording and Analysis

Data from all test sessions of a given type were combined so that all response distributions were based on data from between 18 and 30 trials. Peck coordinates were recorded in units of approximately 1 cm², which resulted in an 18 × 25 unit matrix. These data were then collapsed and summarized using the procedures described by Spetch and Mondloch (1993). In brief, because the goal location on the screen varied across the views used for testing, units were defined relative to the center of the goal area and thus did not correspond to fixed absolute screen locations. To adjust for the differential availability of these relative response units (e.g., units to the far left of the goal would not be available in views which placed the goal in the left portion of the image), all data were

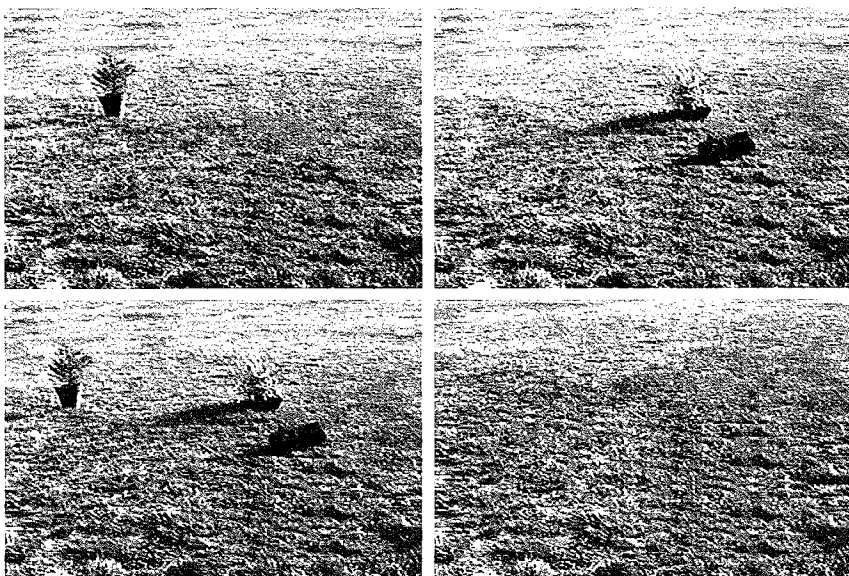


FIG. 2. A sample of the images used during Single Landmark tests (top left: tree alone), One-Absent tests (top right, tree absent), Shift tests (bottom left: tree shifted) and No Landmarks/No Color tests (bottom right: no landmarks).

weighted by dividing the number of responses in each unit by the number of times that unit was available. The data were then collapsed into 8 units on either side of the goal center by treating any pecks that fell further than 8 units from the goal as having fallen in the 8th unit. Thus, all data presented are relative to the goal, and weighted according to availability. All response distributions are shown as the proportion of total weighted pecks that fell in each unit.

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 anywhere on the screen, the range of goal areas used during training and testing spanned approximately 9 horizontal units and 6 vertical units. Thus, if the birds learned to peck in this general region of the screen, chance level accuracy would be 4 out of 54 units, or .07.

For Landmark Shift tests, we also computed the horizontal peak place of searching using the iterated median procedure described in Cheng (1989) and Spetch *et al.* (1992). For all tests of statistical significance, α was set to .05.

Results

Training required a total of between 30 and 60 sessions for the different birds. Accuracy on control trials of the test sessions was well above chance

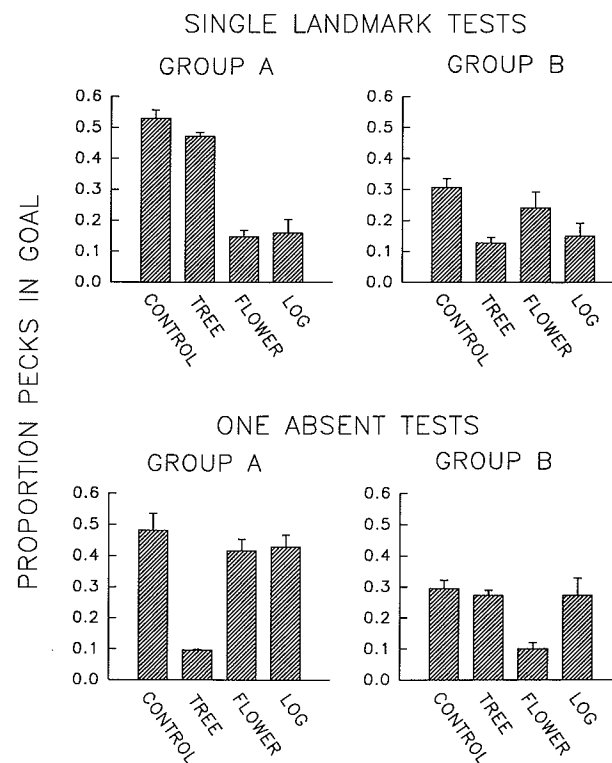


FIG. 3. Mean (SEM) proportion of pecks that fell in the goal area during control and test trials of the Single Landmark tests and One-Absent tests of Experiment 1. For Single Landmark tests, the landmark indicated below the bars is the one present in the image; for One-Absent tests, the landmark indicated is the one removed from the image.

for all birds during all test series. For each of the test series, one-sample t-tests confirmed that the mean accuracy scores of the six birds on control trials were significantly above the chance level value of 0.07 (Single Landmark tests, mean = .418, $t(5) = 6.58$; One-Absent test, mean = .389, $t(5) = 6.45$; Shift tests, mean = .359, $t(5) = 8.18$; No Landmark/No Color tests, mean = .412, $t(5) = 7.78$).

Single Landmark Tests

The top graphs in Fig. 3 show mean accuracy for birds in each group during control trials and test trials with the tree presented alone, the flower presented alone, and the log presented alone. Birds in Group A (goal area beneath the tree) showed far better control by the tree alone than by either the flower or the log alone. Moreover, they responded almost as accurately when the tree was the only landmark in the picture

as they did on control trials with all three landmarks. Birds in Group B (with the goal closer to the flower and log) responded more accurately with the flower alone.

A two-way ANOVA on the accuracy scores with Group and Condition (control and three types of tests) as factors revealed a significant interaction between Group and Condition, $F(3, 12) = 19.76$. Subsequent one-way ANOVAs revealed a significant effect of test condition for Group A, $F(3, 6) = 92.42$, but not for Group B, $F(3, 6) = 4.36$. Tukey's post-hoc comparisons on the data from Group A revealed the following pattern: control = tree only > log only = flower only.

One Absent Tests

The bottom graphs of Fig. 3 show mean accuracy on control trials and tests with the tree absent, the flower absent, and the log absent for each group. Group A showed a substantial drop in accuracy when the tree was removed from the picture and little or no change in accuracy when either the log or flower were removed. In contrast, Group B was more disrupted by removal of the flower than by removal of the tree.

A two-way ANOVA revealed a significant interaction between Group and Condition, $F(3, 12) = 23.38$. Subsequent one-way ANOVAs revealed a significant effect of condition for both groups (Group A, $F(3, 6) = 50.27$; Group B, $F(3, 6) = 6.42$). For Group A, Tukey's post-hoc comparisons revealed the following pattern: control = log absent = flower absent > tree absent. For Group B, the Tukey's test revealed higher accuracy on control trials than on flower absent trials, but no other significant differences.

Shift Tests

The top graphs in Fig. 4 show mean accuracy scores during control trials and test trials with shifts of the tree, the flower, and the log for each group. These accuracy scores are defined in terms of the unshifted cues. Therefore a decrease in accuracy should be seen if the pigeon follows the shifted landmark. Birds in Group A showed a substantial disruption in accuracy when the tree was displaced but not when either the flower or log were displaced. In contrast, birds in Group B showed little reduction in accuracy when the tree was displaced but they showed some disruption of accuracy when the flower was displaced.

A two-way ANOVA revealed a significant interaction between Group and Condition, $F(3, 12) = 37.88$. Subsequent one-way ANOVAs revealed a significant effect of condition for both groups (Group A, $F(3, 6) = 46.60$; Group B, $F(3, 6) = 6.20$). For Group A, Tukey's post-hoc comparisons revealed the following pattern: control = log shifted = flower shifted > tree shifted. For Group B, the Tukey's test revealed higher

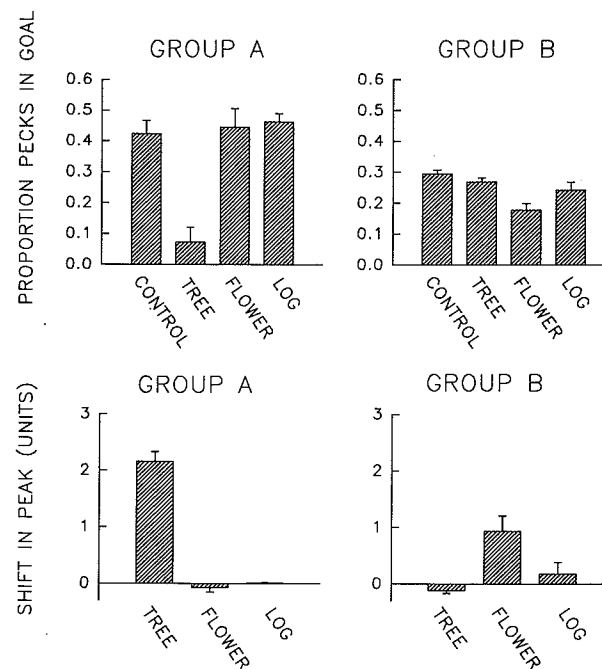


FIG. 4. Shift tests. Top graphs: Mean (SEM) proportion of pecks that fell in the goal area on control trials and on test trials in which one of the three landmarks was shifted horizontally away from the goal area for both groups in Experiment 1. Bottom graphs: Mean (SEM) shift in peak place of searching in response to shifts of the tree, the flower or the log for both groups of Experiment 1. Positive values indicate that searching shifted in the same direction as the landmark shift; negative values indicate that searching shifted in the opposite direction to the landmark shift. No landmarks, no color tests.

accuracy on control trials than on flower shift trials, but no other significant differences.

A comparison of the calculated peak place of searching on control and shift test trials provides a second and more direct indication of whether searching followed a displaced landmark. The bottom graphs in Fig. 4 show, for each group, the mean shift (in 1-cm units) in the horizontal peak place of searching on shift test trials from that on control trials. Positive values indicate a shift in the direction in which the landmark was shifted, and negative values indicate that the peak shifted in the opposite direction to the landmark shift. When the tree was shifted, Group A birds shifted the full extent, or almost the full extent, of the landmark shift, whereas Group B birds did not shift with the tree. Group A birds did not shift their peak responding in the direction of the shifted flower or log, whereas Group B birds shifted their responding with the flower, with their peak shifting part way toward the shifted flower. These scores then,

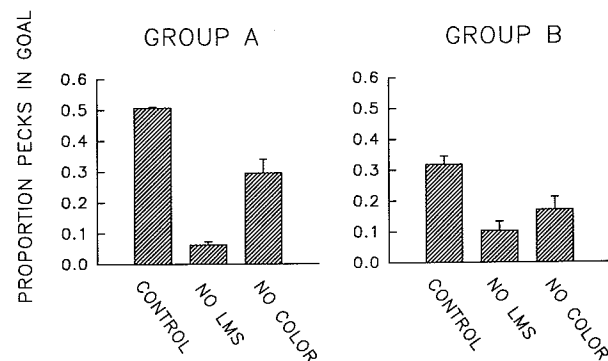


FIG. 5. No landmarks, no color tests. Mean (SEM) proportion of total pecks that fell in the goal area on control trials and on test trials in which no landmarks were present (no LMs), or in which the image was presented in black and white (no color) for both groups of Experiment 1.

are consistent with the accuracy scores in suggesting that Birds in Group A followed the tree, but not the flower and the log, whereas birds in Group B followed only the flower.

No Landmark, No Color Tests

Figure 5 shows mean accuracy scores on control trials and on test trials in which no landmarks were presented or in which the scene with all landmarks was presented in black and white (no color). As expected, accuracy was low in the absence of any landmarks. On tests in which the scene was presented in black and white, there was some disruption of accuracy relative to control trials.

A two-way ANOVA revealed a significant main effect of Condition, $F(2, 8) = 53.47$, and Group, $F(1, 4) = 19.13$, as well as a significant Group \times Condition interaction, $F(2, 8) = 6.84$. Subsequent one-sample t tests on the data from all six birds indicated that mean accuracy was significantly above chance (.07) when the scene was presented in black and white ($M = .233$, $t(5) = 4.19$) but not when all three landmarks were removed from the scene ($M = .082$, $t(5) = .74$).

Response Distributions

On control trials, response distributions were characterized by a single peak centered in the goal region. Shifts of a dominant landmark tended to produce strongly peaked distributions with the peak displaced toward the shifted landmark, whereas removal of a dominant landmark tended to produce flat and scattered distributions. As a sample, Fig. 6 shows the response distributions of one of the birds from each of the four types of tests. 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 .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, units in which there is 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 the goal center, which is indicated by the intersection of the two zero lines.

Discussion

Several features of these data are noteworthy. First, birds readily learned to find the hidden goal in the scene on the basis of the landmarks. That the landmarks allowed them to find the goal is indicated by their failure to respond accurately when all landmarks were removed from the picture. Second, birds that were trained with the goal area closest to the tree (Group A) appeared to rely exclusively upon the tree to find the goal. This was indicated by the high accuracy displayed when the tree was the only landmark in the picture, by the disruption in accuracy when the tree was removed, and by the shift in peak place of searching when the tree was shifted. Third, the results for birds in Group B indicated that the almost exclusive control by the tree displayed by birds in Group A was not due solely to greater inherent salience of the tree. Birds in Group B were trained and tested with the identical set of landmarks but the goal area was closer to the flower and log than to the tree. These birds did not show superior control by the tree. Instead, the overall profiles of these birds across the shift and landmark removal tests indicated that the flowers exerted the strongest control. This direct evidence for the role of proximity to the goal supports the indirect evidence provided by previous touch-screen studies of pigeons' landmark use (Spetch *et al.*, 1992; Spetch & Mondloch, 1993) and is consistent with open-field studies showing that proximity to the goal is an important determinant of landmark control (Cheng, 1989; Cheng *et al.*, 1987).

The partial reduction in accuracy seen when the image was presented in black and white may indicate that color is an important, but not an essential, component of the pigeons' representation of the scene and/or landmarks. However, it is not clear whether accuracy was lower because the birds had difficulty recognizing the landmarks, or because the change in the image was so salient that it produced a general performance decrement.

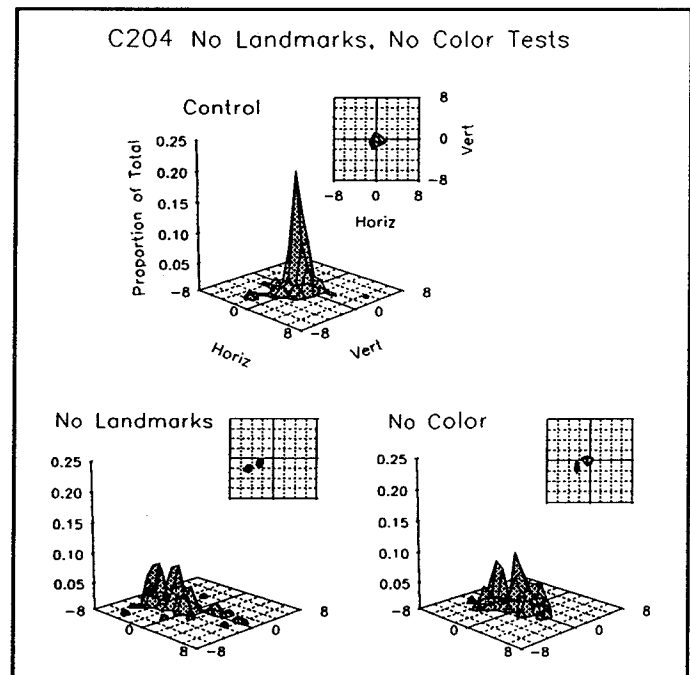
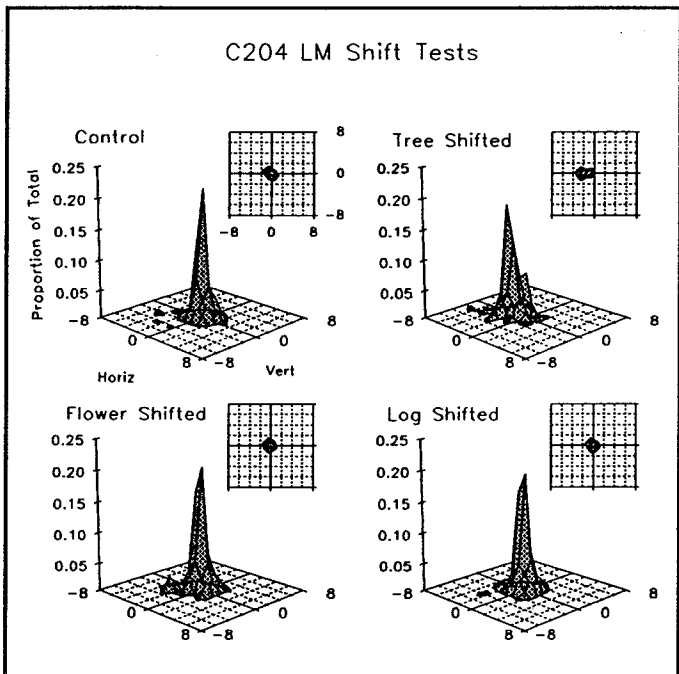
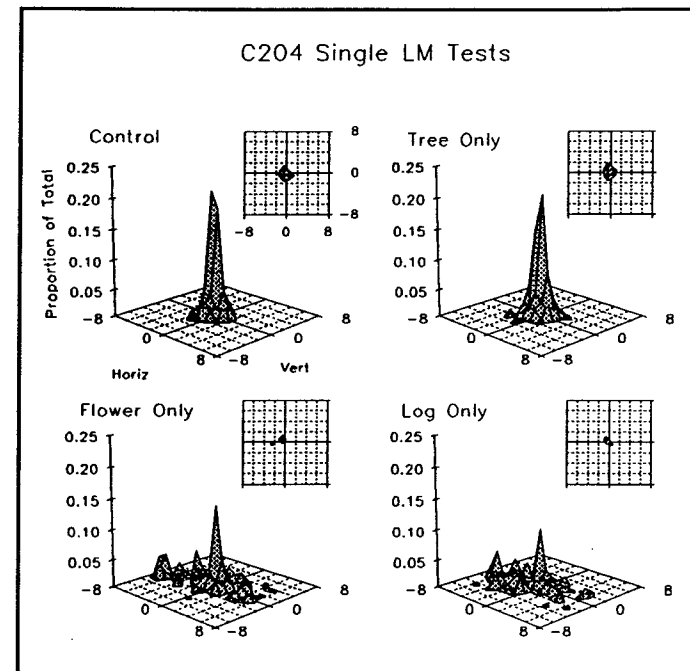
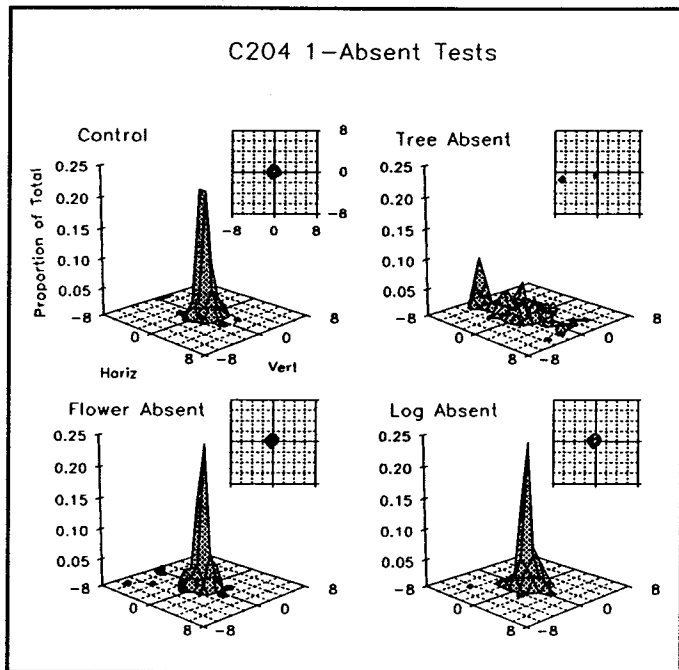


FIG. 6. Response distributions of bird C204 (Group A) on control and test trials of the four test series presented in Experiment 1. The goal is a 2-unit² area centered at the intersection of the 0 lines. See text for details.

FIG. 6—Continued

EXPERIMENT 2

The three pigeons in Experiment 1 that were trained with the goal area beneath the tree showed almost exclusive control of searching by the tree. The present experiment was designed to examine the features of the tree that controlled their search behavior. Accordingly, we tested the pigeons with images in which certain visual properties of the tree were altered.

Method

Subjects and Apparatus

The three birds from Group A served in this experiment. The apparatus was the same as in Experiment 1.

Procedure

The birds participated in this experiment several weeks after completion of the Experiment 1 tests. Prior to the present test series, each bird received a minimum of five 50% reinforcement baseline training sessions and was moved to tests only after two successive sessions in which at least 80 of the scheduled trials were successfully completed. General testing procedures were the same as in Experiment 1.

To isolate the important controlling features of the tree, images used during test trials were edited to alter the tree in one of five ways: (a) removing the top of the tree, leaving only the pot; (b) removing the pot, leaving only the tree top; (c) turning the pot sideways; (d) changing the color of the pot to white; or (e) presenting the entire tree as a black and white object. A sixth type of test trial provided a comparison condition for the tests with a black and white tree and was designed to assess whether a performance deficit would also occur when the nonpreferred landmarks were changed to black and white. Accordingly, the images used for the sixth type of test were edited to present both the flower and the log as black and white objects. Three types of test trials were presented in each test session. Twelve test sessions were given in total so that each type of test was presented for six test sessions.

Results

Figure 7 shows mean accuracy scores on control trials and on each of the six types of test trials. Accuracy scores on control trials were well above the .07 level expected by chance (Mean = .36, $t(2) = 18.97$). Accuracy scores on the test trials are shown in three pairs, corresponding to a-priori comparisons of interest. First, the birds showed significantly lower accuracy when the tree pot was removed than when the top of the tree was removed ($t(2) = 6.83$). Second, the birds were significantly less accurate when the color of the pot was changed to white than when the pot was turned sideways ($t(2) = 5.31$). Finally, birds showed lower ac-

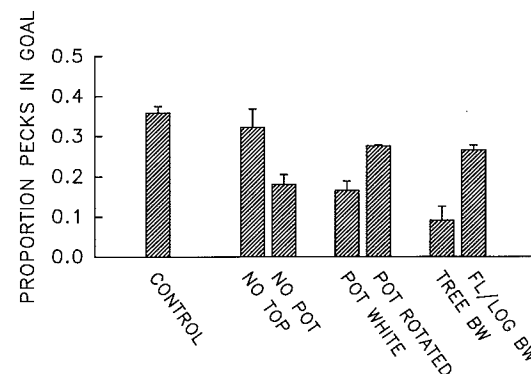


FIG. 7. Mean (SEM) proportion of pecks that fell in the goal area on control trials and on test trials during the Tree Feature Tests of Experiment 2. No Top, top of the tree is absent; No Pot, tree pot is absent; Pot White, tree pot changed to white; Pot Rotated, tree pot turned on its side; Tree BW, entire tree changed to black and white; F1/Log BW, both the flower and log changed to black and white.

curacy when the tree was changed to black and white than when both non-preferred landmarks were changed to black and white, a difference that was significant according to a one-tailed test ($t(2) = 3.73$).

Discussion

The results of the feature tests revealed several interesting characteristics of control by the tree. First, the feature of the tree that exerted the greatest control was not the tree itself, but instead the pot in which the tree was planted. This finding may reflect the greater proximity of the pot than of the tree top to the goal area, or the greater salience of the color of the tree pot (red) than of the color of the tree top (dark green) against the green grass background. Second, changing the pot to white was more disruptive than turning it sideways. This may indicate greater control by landmark color than by landmark shape. Third, changing the entire tree to a black and white object produced more disruption than changing the non-preferred landmarks to black and white.

EXPERIMENT 3

The selectivity of control by single landmarks observed in Experiment 1, particularly by birds in Group A, suggested that they did not rely upon the configuration of the landmarks to locate the goal area. This experiment included tests designed to assess whether any information was derived from the spatial arrangement of the three landmarks. In particular, we examined the possibility that the configuration or conformation of the landmarks might serve a disambiguating role. In nature, many objects that could potentially be used as landmarks (e.g., trees, rocks) would

need to be distinguishable from similar objects in other locations. Configurational information provided by a stable arrangement of landmarks could serve this function.

Attention to global features of the environment could also allow the encoded landmark to be distinguished from similar landmarks in other locations. In the present research, the goal location and array of landmarks varied on the screen across views, but only certain portions of the screen could serve as goal areas and still leave room for all the landmarks. For birds trained in Condition A (see Fig. 1), the goal was never in the right portion of the screen, and for birds in Condition B, the goal never extended to the far left of the screen. We therefore included tests to determine whether the birds, in addition to learning about the relationship between the goal location and a dominant landmark, had also learned about the general area on the screen that included the goal.

We approached these questions in two ways. First, we conducted tests in which the flower and the log were replaced with duplicates of the tree (the preferred landmark for Group A birds), and tests in which the tree and log were replaced with duplicates of the flower (the preferred landmark for Group B birds). In each case the landmark positions were unchanged so that the three identical objects were placed in the same conformation as that formed by the training array. If information about the conformation of the landmarks had been encoded and was sufficient to locate the goal area, then accurate search might occur with these test images, whether the three identical objects were the preferred or the non-preferred landmarks. If conformational information is not sufficient, however, then accurate search should not occur with images containing three non-preferred landmarks, but may or may not occur with images containing the preferred landmarks. In the latter case, accurate search would be possible if either (a) the conformational information served in a disambiguating role to distinguish the correct landmark from the two duplicates or (b) global screen location cues were used to distinguish between the correct landmark and the two duplicates. To differentiate between these possibilities we also included tests in which the duplicates of the tree or flower were moved to different screen locations so that the conformational information was eliminated. For some of these, the duplicates were moved to locations that fell within the range of training locations for that landmark, and in other tests the duplicates were moved to locations that were outside of the training range.

In a second series, birds were tested with images that contained two of the preferred landmark as well as both non-preferred landmarks; one of the preferred landmarks was in the correct location with respect to the non-preferred landmarks and the other one was not. In comparison tests, the two non-preferred landmarks were removed. An ability to distinguish between the correct landmark and its duplicate when the two non-pre-

ferred landmarks were present but not when they were absent would indicate a disambiguating role of configurational information.

Finally, we tested whether control by the dominant landmark was limited to the range of goal locations used in training. For these tests, the preferred landmark was presented alone in a location not used during training. The new location was either within the range employed during training or outside of that range. In open-field landmark tests, Cheng (1988) found that larger shifts of a landmark sometimes resulted in smaller shifts in behavior, suggesting that the landmark ceased to exert as much control if it was moved too far from its training location within the spatial arena. Thus, we expected that our pigeons might search according to the landmark when it is located in a new location within the range of training locations, but that they may not follow the landmark if it is presented outside of that range.

Method

Subjects and Apparatus

All birds from Group A, and two of the birds from Group B participated in this experiment several weeks following completion of Experiment 1 (Group B) or Experiment 2 (Group A). The apparatus was the same as used in the previous experiments.

Procedure

The general procedures used during testing were the same as in the previous experiments. All birds received three test series, in the order presented below. Completion of each test series was followed by two baseline training sessions. As in previous experiments, the nonreinforced control and test trials were interspersed among reinforced and nonreinforced baseline trials.

Identical landmark tests. The images presented during test trials of this series all contained three identical copies of either the tree or the flower; the remaining two landmarks were removed from the image. Duplication of the landmark was accomplished by cloning the correct landmark onto two other locations in the image. For some test images, the duplicates were placed in the locations of the two removed landmarks, so that they retained the same conformation as the objects in the training images. For other test images, the duplicates were placed in varied locations with respect to the correct one, with the constraint that the duplicate never covered the goal location and was never placed so that it would be physically impossible to peck in a location appropriate to it (i.e., too close to one of the edges). For two of these latter images, both duplicates were placed outside of the training range; for two others at least one of the duplicates was inside the training range.

Each bird received four test sessions, each using a different set of images for the control and test trials (constructed from different training views).

Duplicate landmark tests. These tests were designed to assess the possible disambiguating role of configural information in a situation where global spatial cues could not serve this role. The test images contained one duplicate of either the tree or the flower. These images were generated by selecting a pair of training views, and for each one, duplicating the landmark at the coordinates that contained that landmark in the other view. Thus, both the correct goal location and the goal location as defined by the duplicate landmark were at screen locations that served as goal areas on baseline trials and each served as the correct location in one test image and as the incorrect location in the complementary test image. For one pair of images, the other landmarks were left in place, and thus could provide configural information to differentiate the correct landmark from its duplicate. For the other pair, the other landmarks were removed from the scene, thereby eliminating any configural information.

These tests were conducted using only the preferred landmark for each bird. Thus, birds in Group A were tested with duplicates of the tree, and birds in Group B were tested with duplicates of the flower. Each bird was given two test sessions.

Single landmark/global location tests. This series included two types of test trials in which the preferred landmark (tree for Group A, flower for Group B) was presented alone. On one type of test the landmark was presented in a new location within the range of locations used in training and on the other it was presented outside of the range used in training (the tree was presented further to the right and the flower was presented further to the left). Each bird received two test sessions.

Results

For all test series, the data for birds in the two groups were combined by presenting performance in terms of the preferred landmark.

Identical Landmark Tests

Figure 8 shows mean accuracy on control trials and on test trials in which three of the preferred or three of the nonpreferred landmarks were presented in the training conformation or in a new conformation. When the conformation was the same as in training, accuracy was high with three identical preferred landmarks but not with three identical nonpreferred landmarks. Accuracy with the three preferred landmarks was lower when they were presented in a new conformation than when they were positioned in the training conformation.

An ANOVA showed that accuracy differed significantly across the five conditions (control and four test types), $F(4, 16) = 38.40$. Subsequent Tukey's multiple comparisons revealed that accuracy on tests with three

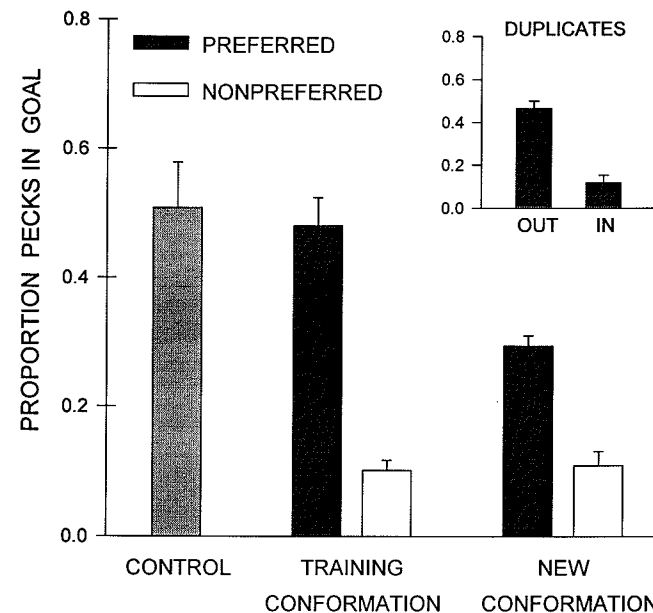


Fig. 8. Mean (SEM) proportion of pecks that fell in the goal area on control (first bar) and test trials of the identical landmark tests of Experiment 3. On test trials, three of the preferred landmarks (tree for Group A, flower for Group B) or three non-preferred landmarks (flower for Group A, tree for Group B) were presented in the training conformation or in a new conformation. The insert shows results from test trials in which three preferred landmarks are presented in a new conformation, plotted in terms of whether both duplicates of the landmark were out of the baseline range of screen locations or whether one was in that range. See text for details.

preferred landmarks in the training conformation did not differ from control trials and was significantly higher than on any of the other test types. Accuracy with three preferred landmarks in a new conformation was higher than on either of the tests involving nonpreferred landmarks. The two test types with nonpreferred landmarks did not differ from each other.

The insert in Fig. 8 shows accuracy on tests with three preferred landmarks presented in a new conformation, subdivided according to whether both duplicates were outside of the training range or whether one or both was inside the training range. Accuracy was higher when both duplicates were out of range than when one or two of the duplicates were within the training range, $t(4) = 5.61$.

Duplicate Landmark Tests

Figure 9 shows mean accuracy on control trials, and on tests in which a duplicate of the preferred landmark was placed at another training

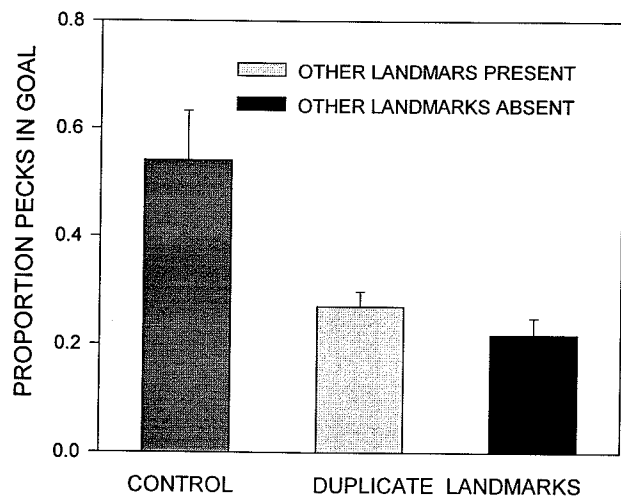


FIG. 9. Mean (SEM) proportion of pecks that fell in the goal area on control and test trials of the duplicate landmark tests of Experiment 3. See text for details.

location and nonpreferred landmarks either present or absent. Accuracy on both of these tests was lower than on control trials. Presence of the nonpreferred landmarks had little effect on accuracy. In both cases, individual birds tended to prefer one landmark location whether it was correct or incorrect according to the other landmarks. Hence the moderate level of accuracy reflects the averaging of trials in which the preferred location was correct and trials in which it was incorrect.

An ANOVA revealed a significant effect of condition, $F(2, 8) = 17.58$, and subsequent Tukey's multiple comparisons revealed that accuracy on both tests with duplicate landmarks was lower than on control trials. Accuracy on duplicate landmark tests with the non-preferred landmarks present did not differ from accuracy on duplicate landmark tests with the nonpreferred landmarks absent.

Single Landmark/Global Location Tests

Figure 10 shows accuracy on test trials in which the preferred landmark was presented in a new location in the training range, or in a new location outside of the training range. Accuracy was significantly higher when the single landmark was in the training range than when it was outside of the training range, $t(4) = 4.45$.

Discussion

Taken together, the results of the three test series suggest that configural information about the three landmarks did not help the pigeons to locate the goal or to distinguish between a correct landmark and its duplicate,

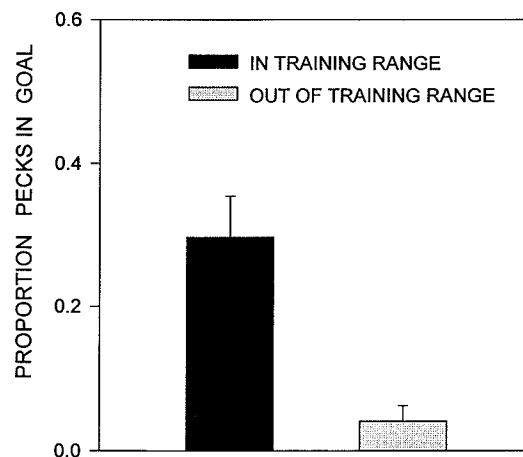


FIG. 10. Mean (SEM) proportion of pecks that fell in the goal area on test trials in which a single landmark was presented in a new location within the training range or in a new location outside the training range during the single landmark/global location tests of Experiment 3.

but that global location cues did modulate control by the preferred landmark. The pigeons searched accurately in all cases in which the preferred landmark could be distinguished from its duplicates on the basis of global screen location, but they failed to search accurately whenever a duplicate of the preferred landmarks was presented within the training range. In particular, they failed to use configural information provided by the non-preferred landmark to distinguish between the preferred landmark and a duplicate that was presented in one of the locations used during training. The finding that pigeons searched accurately when a single preferred landmark was shifted to a new location in the training range but not when it was shifted outside of the training range suggests that global cues pertaining to general goal location can override control by the local landmark, even though the latter is necessary to pinpoint the goal location. Similar limitations on the extent to which a pigeon will follow a shifted landmark have been observed in open-field search tasks (e.g., Cheng, 1988).

GENERAL DISCUSSION

The present research extends previous investigations of pigeons' landmark use in touch-screen search tasks (Spetch *et al.*, 1992; Spetch and Mondloch, 1993) in several ways. First, the present research showed that many of the effects found with simple graphic forms as landmarks can be replicated using the richer more complex visual stimuli afforded through video imaging technology. For example, as in Spetch and Mondloch's (1993) study with graphic landmarks, pigeons in the present research

readily learned to locate an unmarked goal on the basis of visual landmarks even though the location on the screen of the landmark array and corresponding goal area varied across trials. This finding is interesting because recent research with rats (Biegler & Morris, 1993) suggested that stability of landmarks within a geometric frame may be a prerequisite to spatial learning. They trained rats to find food in a square arena that contained two distinct landmarks and that was surrounded by a set of one white and three black curtains. The white curtain was rotated across trials to manipulate directional polarization of the arena. For some rats (group fixed), the location of both landmarks relative to the curtain was constant on every trial. For other rats (group varied), the location of the landmarks varied randomly across trials. For both groups, the food was always near one of the landmarks, and the direction of the food from that landmark (relative to the white curtain) was held constant. Rats in the fixed group learned not only which landmark was near the food but also the location of the food with respect to that landmark. In contrast, rats in the varied group learned which landmark was near the food but they failed to learn the direction of the food from that landmark. Biegler and Morris suggested that spatial learning follows the rule of thumb "if it moves, don't use it as a landmark" (p. 633). Our results indicate that this rule does not always apply, as does evidence that insects can use landmarks that do not occupy a fixed location within a spatial arena (e.g., Cartwright & Collett, 1983).

The apparent discrepancy between our results and those of Biegler and Morris may be related to the different roles that landmarks can play in guiding search behavior. In our task, directional polarity of the search space was not manipulated and many stimuli (including proprioceptive cues) provided stable directional information. Thus, it is unlikely that our pigeons used the landmarks to orient themselves in the search space. Experiment 3 indicated that our pigeons also did not rely on the local landmarks to define the general region of the screen in which to search. Instead, they appeared to use the landmarks primarily or exclusively to pinpoint the goal within a search region that was oriented and defined on the basis of other cues. In contrast, the landmarks used in Biegler and Morris's study may have served several roles. Biegler and Morris attempted to manipulate directional polarization of their arena by rotating a white curtain. However, rats typically rely on geometric shape of the environment and not distinctive features of one surface to get compass bearings (Cheng, 1986; Margules & Gallistel, 1988), and Biegler and Morris did not provide specific evidence that the white curtain effectively controlled the rats' sense of direction. A stable orientation in a search space is necessary before directional information provided by a landmark can be meaningfully extracted. If rats in their study were not consistently oriented, or were oriented according to cues that did not rotate with the curtain, then the direction of the food from the nearest landmark would

be indeterminate or would seem to vary across trials. It is possible that rats in their fixed group, but not in their varied group, were able to solve this task by using the landmark configuration to get directional bearings. Landmark stability may be crucial if the landmarks are used to get oriented within a search space but may not be necessary when a landmark is used primarily to pinpoint a goal, provided that the spatial relationship between the landmark and goal remains constant according to the subject's sense of direction.

Our results were similar to those of Spetch and Mondloch (1993) in revealing highly selective control by the landmarks: Tests with landmarks removed or displaced suggested that pigeons depended on only one or, at most, two of the landmarks presented during training. The consistency of the present results with those found with simple graphic landmarks suggests that this selectivity is not restricted to situations involving highly artificial and visually impoverished graphic stimuli. Interestingly, selectivity of control was also reported in Wilkie *et al.*'s (1994) feature-positive study using the same landmarks as used in the present study. In research currently underway, we are using the technology presented here to explore whether control by landmarks is more selective when an array of landmarks is always viewed from a single perspective (as in the images used for the present study) than when the images used during training allow the animal to view the array from varying vantage points (as in many open-field tasks).

Our results also corroborated Spetch and Mondloch's (1993) finding that, for a given bird, there was a strong correspondence between the accuracy exerted by a landmark when it was presented alone and the extent to which searching followed the landmark when it was shifted. Thus, landmark removal tests and landmark shift tests appear to provide congruent indications of the control exerted by a particular landmark.

The present results further extend those of previous touch-screen studies by providing clear evidence that a major determinant of selectivity is proximity to the goal area. Specifically, two groups of pigeons trained with the same landmarks but with different goal locations showed very different profiles of landmark control. Pigeons trained with the goal area closest to the tree showed exclusive control by the tree, whereas pigeons trained with the goal area closer to the flower and log showed more control by the flower than by the tree. This evidence for the importance of proximity to the goal in touch screen tasks is consistent with results from open-field studies of landmark use by pigeons (Cheng, 1989) and insects (Cheng *et al.*, 1987; Tinbergen, 1972).

Although less definitive, the present results are also consistent with Spetch and Mondloch's (1993) finding that control by a particular landmark was based on its color rather than its shape. Specifically, in Experiment 2, accuracy was substantially disrupted by a change in the color

of the tree but was not disrupted by removal of the tree top, which dramatically altered its shape. In addition, accuracy was disrupted more by a change in color of the tree pot than by a change in orientation of the tree pot. Accuracy was not, however, controlled exclusively by color because changing the entire image to black and white disrupted but did not completely eliminate accurate search.

Finally, the results of Experiment 3 indicated that control by a dominant landmark was modulated by the global screen location but not by the configuration of landmarks. The lack of control by the configuration of the landmarks is consistent with Spetch and Mondloch's (1993) findings with graphic landmarks. At first blush, the selective control by a single landmark and the lack of control by landmark configuration seems inconsistent with findings from open-field or maze studies, which have suggested that spatial behavior is typically controlled by multiple landmarks and that their configuration exerts strong control (e.g., see Poucet, 1993). However, much of the evidence for the importance of configuration has come from the manipulation of landmarks more distal than the present ones and/or from tasks that involve aspects of spatial behavior (e.g., exploration, spatial working memory) that may differ from that investigated here (e.g., Poucet, Chapuis, Durup, & Thinus-Blanc, 1986; Spetch & Honig, 1988; Suzuki, Augerinos, & Black, 1980). While there is substantial evidence to suggest that configurational information is often important for spatial behavior, it is not clear that the configuration of local landmarks near a goal is always encoded, particularly if directional frames of reference are provided by other cues and the landmarks are used only to guide search to the exact location of a single goal. Moreover, although Cheng's research on landmark-based search in pigeons has suggested that pigeons do not rely upon a single landmark, it is interesting that most of the evidence for this comes from tests showing that pigeons do not shift the full extent of shifts of a single landmark. This has indicated that other cues are controlling their behavior, but these other cues are not necessarily local landmarks (e.g., Cheng & Sherry, 1992). In the present research, pigeons displayed selective control by only one of the local landmarks, but the results of Experiment 3 revealed that their behavior was nevertheless determined by more than one source of spatial information, just as it is in open-field tasks.

One interesting question raised by our use of images of natural visual stimuli is whether the pigeons process the images as representations of three dimensional space. Although the present research does not address this issue, evidence from other studies (reviewed in Wilkie, Willson, & MacDonald, 1992) suggests that the answer to this question is probably yes. For example, pigeons that have been induced to display aggressive behavior by interruptions in feeding have been found to attack and peck color photographs of other pigeons and their pecks are directed at the

head area as might be expected if they viewed the photograph as a con-specific (Looney and Cohen, 1974). Watanabe (1993) found two-way transfer between real objects (food items) and photographs of these objects in pigeons trained to peck a clear key when an edible object appeared on a conveyor belt behind the key. Cabe (1976) found transfer between geometric objects and pictures of the objects in pigeons. Cole and Honig (1994) found that pigeons trained to discriminate between colored slides of two locations in a room successfully transferred the discrimination when tested in the room. Wilkie, Willson & Kardal (1989) found some evidence that experience in an outdoor location facilitated discrimination of photographic slides of that location, a result that suggests that the pigeons perceived a correspondence between the slides and the actual location. The evidence from these studies and studies with other species of birds (e.g., Roberts & Weigl, 1984), suggests that correspondence between pictorial stimuli and the three dimensional objects or locations is possible in avians. Direct evidence that pigeons perceived the digitized images we presented as three dimensional scenes must, however, await further research. One exciting advantage of the present methodology is that it will allow a direct comparison of control by landmarks in an open-field setting with control by the same landmarks as presented in digitized images of the open-field setting. Research along these lines is currently underway.

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