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VISUALLY GUIDED CATCHING AND TRACKING SKILLS IN PIGEONS: A PRELIMINARY ANALYSIS

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Research on reaching, tracking, and catching in the pigeon has been hampered by limitations of technology. A new system was developed in which the target was a small rectangle presented on a video display terminal and the pecking response was detected with touch technology. The target moved up and down vertically with sinusoidal velocity. A coincidence between the location of the pigeon's beak and the cursor produced reinforcement. The pigeon pecked ahead and behind the target, but most pecks occurred behind the target so the dominant tracking strategy was lagging. The pigeon was adept at "catching" the target at many locations throughout the trajectory. Transfer of motor learning was tested on probe trials during which the trajectory changed from vertical to horizontal. On transfer trials the pigeons' dominant pattern of pecking immediately shifted from vertical to horizontal. The motor skill displayed by the pigeons was flexible and adaptive, suggesting that the pigeons had learned to track the cursor.

Key words: tracking, catching, reaching, stimulus control by movement, transfer of training, motor behavior, peck, pigeons

Catching and tracking are two paradigms used in the experimental analysis of motor skill in humans. Experiments with pigeons of the type reported here provide an opportunity to test the validity and generality of theories of motor skill.

In research on human motor behavior, catching is often investigated in ball-catching tasks. The difficulty with this naturalistic task is that experimental control of the trajectory of movement is restricted by the mechanism for throwing the ball. The inspiration for the catching component of this research was a series of experiments by von Hofsten (1983, 1987) on catching skills in infancy. Rather than throwing a ball, von Hofsten used an object attached to a metal rod. Von Hofsten divided the possible catching strategies into two classes: simple timing and sophisticated catching. A simple timing strategy was one in which the target was always caught at the same time and place, whereas a sophisticated catching strategy permitted catches at all locations. Von Hofsten found that children employed a sophisticated predictive strategy, reaching ahead so the hand was aimed at the object's future location.

In this experiment, the ball was simulated by a cursor moving around a video display terminal. Infrared touch technology detected the location of the pigeon's beak. The pigeon's task was to "catch" a cursor by pecking within the touch target surrounding the location of the cursor.

The tracking component of the procedure used here was inspired by Flanders' (1985) work on visually guided head movement in the African chameleon, in which the target was a cricket held by a clip and mounted in space on a wire. The target moved horizontally along a linear trajectory following sinusoidal motion. In sinusoidal motion, velocity varies continuously as a function of time with zero velocity at the maxima and minima, respectively. The species-specific catching strategy of the chameleon is to shoot its tongue at prey insects. Flanders found that the strategy employed by the chameleon is pursuit; that is, it tracks the target with head movement that lags the prey. Flanders found that one chameleon eventually learned, after a year of training, to catch the bait at peak displacement or zero velocity, an optimal strategy.

Sporadic efforts to study tracking in the pigeon have established that it has some capacity to track moving objects (Jenkins & Sainsbury, 1970; Pisacreta, 1982; Skinner, 1965; Wilkie, 1986). However, Wilkie (1986) points out that

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the strategy used by pigeons in tracking remains unknown.

The purpose of this experiment was to develop a technique with the potential for determining the strategy used by pigeons in this catching task. The two primary dependent variables were the distribution of catches along the trajectory of movement and the phase or time relationship between the peck and the cursor. First consider the possible tracking strategies. The two types of misses were pecks that either led or lagged the stimulus. When the bird pecks ahead of the cursor, the lead is the time required for the cursor to catch up with the peck. When the bird pecks behind the cursor, the lag is the time required for the peck to catch up with the cursor. The question was whether the basic tracking strategy of the pigeons was leading or lagging the target.

Consider the possible catching strategies of the pigeon. The pigeon could catch the target with a simple timing strategy. The correlation between the location of the target and time from trial onset is perfect because the movement of the target always starts at the same location. Therefore, the pigeon could always catch the target at the earliest possible moment by timing the proper interval and pecking the corresponding location to coincide with the arrival of the target. Alternatively, the velocity of movement is zero at the top of the trajectory. By timing the interval for the target to move from the bottom to the top, the pigeon could catch the target at the peak of the sine wave. What simple timing strategies have in common is the prediction that the target is always caught at the same place. Because each strategy predicts a different distribution of catches, the dependent variable of primary interest on catch trials was the distribution of catches along the trajectory.

Two birds were trained to track a velocity of 0.073 Hz or one cycle every 13.729 seconds. The target moved up and down a linear trajectory with sinusoidal velocity. For each trial the locations of the cursor during the trajectory and the locations of the pecks were recorded. A coincidence between the location of the peck and the location of the target produced reinforcement. The birds were trained to a criterion of two sessions in which pecks produced reinforcement for 80% of the 30 trials within each session. Gallistel (1980) identifies extraordinary flexibility as the hallmark of an action system. As a test of such flexibility, birds were first trained to track with vertical sinusoidal movement and then tested with horizontal sinusoidal movement. The question was whether tracking performance transfers from one sinusoidal trajectory to another.

METHOD

Subjects

Two White Carneau pigeons served as subjects. These birds participated in a preliminary test of the system (Neiworth & Rilling, in press) in which food reinforcers followed each peck that fell within a black circle whose diameter was the same as the traditional pigeon key. The location of the key occurred randomly at one of the four locations near each corner of the screen. The pigeons were maintained at 80% ± 20 g of their free-feeding weights and were housed individually in a temperature-controlled, constantly illuminated colony room where water and grit were always available.

Apparatus

The apparatus used here is described in detail by Neiworth and Rilling (in press). It represents a new technology for comparative cognition in which touch technology is integrated with a sophisticated system of computer graphics. The heart of the experimental chamber was a 30-cm black and white Electrohome® monitor, obtained from Micrographic Images in Canoga Park, California. The graphics for the monitor were controlled by a Macintosh Plus® computer. The display on the monitor has the same number of pixels as the smaller Macintosh screen, so objects on the secondary monitor appeared slightly larger than objects on the Macintosh screen. A 30-cm Carrol Touch Smart Frame® was mounted on front of the monitor replacing the original plastic bezel of the Electrohome monitor.

An invisible lattice of infrared light beams in front of the monitor scanned each point 20 times each second. The matrix size of our Smart Frame was 44 by 30. By means of software interpolation, the coordinate reporting range was enhanced from 0 to 86 in the horizontal axis and 0 to 58 in the vertical axis. The minimum stylus size for this frame is 8.4 mm, well within the range of the base of the pigeon's beak. Neiworth and Rilling (in press) demonstrated that the pigeon's beak is a reliable stylus for activating the smart frame.

A conventional pigeon hopper was mounted on either side of the monitor. For this experiment, only the left hopper was operational. The hopper was operated by a BenchTop® Instrument, an interface designed to operate through the serial port of the Macintosh. (The BenchTop was obtained from Metaresearch in Portland, Oregon.) The BenchTop interface was connected to the printer port, and the touch screen was connected to the modem port.

A tradition in the study of continuous manual control in humans that dates from Fitts' (1954) time movement paradigm is the requirement of a response at a start location before a tracking response at a target at another location is made. Because pigeons may engage in behavior that is irrelevant to the tracking task during the intertrial interval (e.g., wing flapping and other "emotional" behaviors), each trial began with a requirement of an observing response on a key located at the upper left quadrant of the screen. After completion of the observing response requirement of variable ratio (VR) 7, the target was presented. The response key was located at Macintosh pixel coordinate (x = 87, y = 30) and at coordinates with respect to the monitor (3.4 cm from the left edge and 1.4 cm from the top). The diameter of the response key was 1.8 cm.

Procedure

The target was designed to be as small as possible and to approximate with a rectangle the size of grain upon which pigeons normally feed. For vertical movement, the target started moving at a location near the bottom of the screen. The start location was identical for all trials. In terms of pixels, the start location was (180, 165) and the peak location at the top of the trajectory was (180, 65). The length of the trajectory was 100 pixels, approximately 4.5 cm. The target was a rectangle 6 pixels high by 2 pixels wide and whose screen size was 0.27 cm high and 0.09 cm wide. The velocity of vertical movement during training was 13.729 s for a complete cycle. In one cycle of 13.729 s the stimulus moved from bottom to top and then from top to bottom. This equals a frequency of one cycle per 0.073 s. Because the stimulus terminated after 15 s if a peck failed to produce reinforcement, the cursor went through slightly more than one cycle at this speed.

For horizontal movement the trajectory was right, left, right with pixel coordinates at the start location of (185, 165), turning leftward at (230, 165), turning rightward at (130, 165), and terminating after 15 s at (225, 165). For horizontal movement the target was 10 pixels wide and 2 pixels high and was 0.45 cm wide and 0.09 cm high on the screen.

The touch target was defined by an invisible rectangle surrounding the cursor; this was the catch target. Pecks within the touch area had the potential for producing food reinforcement, whereas pecks outside the touch area were not reinforced. The touch target was designed to be larger than the cursor, so that slight errors in pecking the target would count as catches. The touch target was small relative to the total size of the screen, so as to present the pigeon with a challenging task. The touch target was 10 pixels wide by 10 pixels high. A peck within the touch target was defined as a catch, and a peck outside the target was defined as a miss.

Acquisition training. Originally, the program was conceived such that each peck within the target area would produce reinforcement, but unfortunately not all the pecks emitted by the pigeon were received by the computer. Pecks were effectively reinforced on a small VR schedule.

The birds were trained to an acquisition criterion of two sessions in which pecks produced reinforcement for 80% of the 30 trials within each session. Distributions of catch locations along the trajectory of vertical movement were then obtained during three sessions.

Transfer. As a measure of transfer, two sessions of probe testing were carried out within sessions of 25 trials of vertical movement. Five trials per session were probe trials with horizontal movement. Now, pecks within the touch target area along the vertical trajectory produced reinforcement. Here the question was whether tracking performance would survive a change in the trajectory of movement.

Extended training. After 73 sessions for Bird D374 and 75 sessions for Bird D398, the birds were given three additional sessions to determine the effects of extended training on performance in this task. The alignment between the touch screen and the graphics screen of the

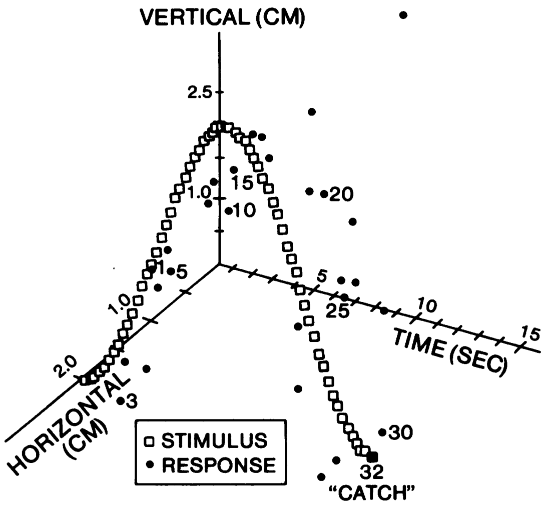

Fig. 1. A three-dimensional comparison of target and peck locations as a function of time and horizontal and vertical positions. Data are for one trial when the movement of the target was sinusoidally vertical. The numbers for selected pecks indicate sequence number and show that the bird chased the stimulus up and down the screen until Peck 32 produced reinforcement.

computer was improved during this training. The buffer between the touch screen and the computer was also improved so that most of the pecks emitted by the pigeon were detected by the system. During the preceding sessions of training the birds were exposed to a variety of conditions including reinforcement on a Fixed Ratio (FR) 5 schedule within the 15-s trial duration. The ratio schedule sustained behavior when five catches were required to produce reinforcement. Finally each catch was reinforced to provide a comparison between performance on early and extended training.

RESULTS

The birds were trained to track the vertically moving cursor until a catch was obtained on 80% of the trials in two successive sessions. The number of sessions for acquisition to criterion was six for Bird D398 and four for Bird D374.

Within a trial, the typical pattern of performance for each bird was pecking at the target as soon as it appeared at the bottom of the screen. Each bird chased the target up and down the screen until a peck produced food or the trial terminated without reinforcement. Figure 1 shows the sequence of pecks from a trial in which a "catch" or reinforced peck occurred for Peck 32 at 13.64 s. This trial is selected to show the pattern of errors when a large number of nonreinforced pecks occurred prior to the catch. This trial is not typical because catches occurred at all points along the trajectory. This figure is a three-dimensional graph in which the *x* axis corresponds to time in seconds, the *y* axis corresponds to the movement of the cursor up and down the screen, and the *z* axis displays the horizontal displacement by which the pecks missed the target. The target moved sinusoidally up and down the vertical axis. Horizontal displacement of the stimulus is 0.0. Selected pecks are numbered. The first peck was about 1.5 cm above the target. Peck 3 was closer to the target and directed toward the bottom of the trajectory of movement. By Peck 15, pecks were directed toward the top of the trajectory. Pecks 15–30 followed the target back down the screen. Peck 32, occurring at 13.64 s, was a catch that produced reinforcement, a coincidence between the location of the target and the location of the peck. The modal strategy of the pigeon on this trial was lagging, pecking below the ascending stimulus and pecking above the descending stimulus. For the 32 pecks in this figure 13 were leading, 18 were lagging, and 1 was a catch. Three of the responses shown in Figure 1 are overlapping.

Errors will occur when the bird's peck leads or lags the stimulus. The lead is the amount of time required for the cursor to catch up to the location of the peck. The lag is the amount of time required for the peck to catch up to the position of the cursor. If the bird followed a pure pursuit strategy, all of the pecks would lag the target. Alternatively, if the bird followed a pure anticipatory strategy, all of the pecks would lead the target. To determine the tracking strategy of the birds, the time relationships between pecks and the target were computed for each bird during an entire session after the birds met criterion. The first measure was an absolute score calculating whether the phase relationship was negative (lagging), zero (catches), or positive (leading). Of 164 pecks by Bird D374, 70% were negative, 22% were catches, and only 8% were positive. Of 328 pecks by Bird D398, 62% were negative, 12% were catches, and only 26% were positive. The second measure was phase lag, which is the mean time difference between the peck and the cursor. For Bird D374 the average phase lag was −316 ms, and for Bird D398 the average phase lag was −214.35 ms. These data clearly demonstrate that, on average, each bird followed a strategy of pursuit, lagging the stimulus.

Another measure of error is the respective vertical and horizontal displacement between the location of the peck and the location of the target. When the target was moving vertically the mean vertical displacement for Bird D374 was 6.16 mm, and the horizontal displacement was 8.19 mm. For Bird D398 the vertical displacement was 6.16 mm, and the horizontal displacement was 4.44 mm. The error was not systematically related to the direction of movement. These means include all pecks, including those with large displacement errors. For each displacement, the mean size of the error was a relatively small distance.

The distributions of catches along the trajectory of movement are relevant to the catching strategies described in the introduction. These distributions were compiled within 5-mm class intervals and are presented in Figures 2 and 3 for Birds D398 and D374, respectively. Catches that occurred at the beginning of the trial are presented in the bottom panel at Stimulus Position 0, and subsequent ascending catches are presented from left to right terminating at the top, Position 50. Descending catches are presented in the top panel from right, Position 59, to left, Position 0, so that catches at the same location are aligned vertically. Excluded from the analysis were the few catches that occurred toward the end of the trial on the second ascent just before the end of the 15-s trial. The distributions clearly reveal that the birds caught the cursor at all of the catch locations throughout the trajectory. Because pecks occurred throughout the stimulus trajectory, the evidence does not support strategies that predict a fixed catch location.

The trajectory of movement and the contingencies of reinforcement sustained substantial pecking toward the target notwithstanding a relatively low rate of reinforcement. For Bird D398, the percentage of pecks that produced reinforcement was 6.02, and for Bird D374 the percentage was 7.18. Thus, for each bird, tracking was sustained even though over 90% of the pecks failed to produce reinforcement.

Transfer from a vertical to a horizontal trajectory was used as a measure of the flexibility

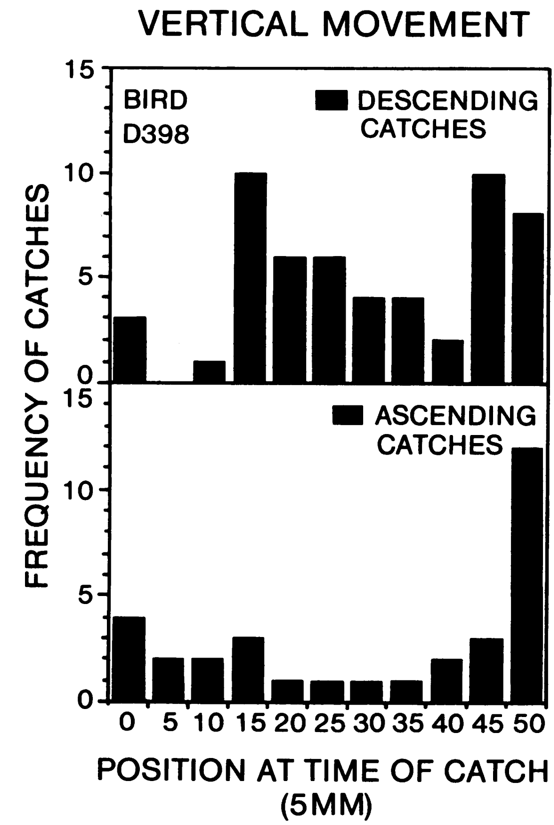

Fig. 2. Frequency of catches as a function of position along the vertical trajectory for Bird D398 for the three sessions after reaching criterion.

of the tracking process in pigeons. From the first trial of probe testing, each bird chased the target along the novel horizontal trajectory. Catch attempts occurred at virtually all positions along the new trajectory. Figure 4 shows the sequence of pecks for Bird D374 from one of the horizontal movement trials on which a catch occurred for Peck 26. The bird adjusted to the novel horizontal trajectory by placing most of its pecks along the horizontal pathway. The numbers beside selected pecks clearly show that the bird chased the target as it moved back and forth along the horizontal trajectory. A comparison of Figure 1, horizontal movement, with Figure 4, vertical movement, shows that pecks are predominantly clustered along the horizontal plane in Figure 1 and the vertical plane in Figure 4. In each case, the pecks cluster along the plane corresponding to the trajectory of the target. The basic strategy of the pigeon on transfer trials remained lagging.

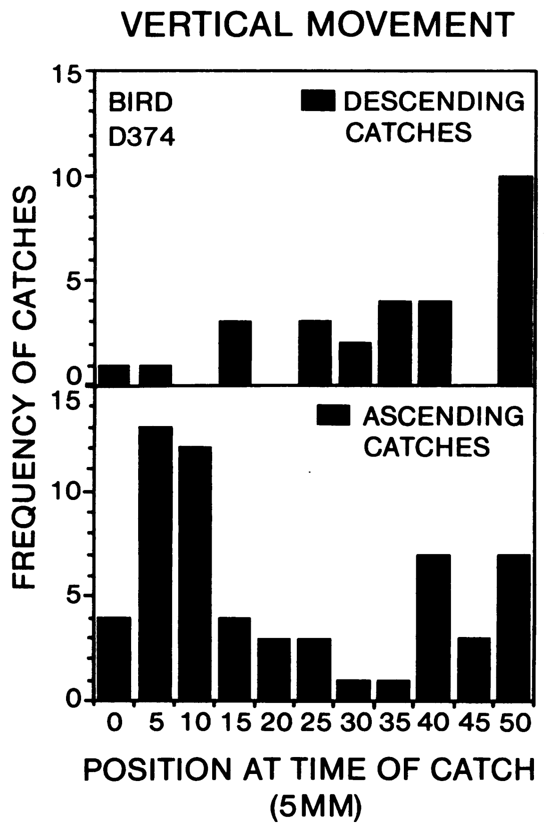

Fig. 3. Frequency of catches as a function of position along the vertical trajectory for Bird D374 for the three sessions after reaching criterion.

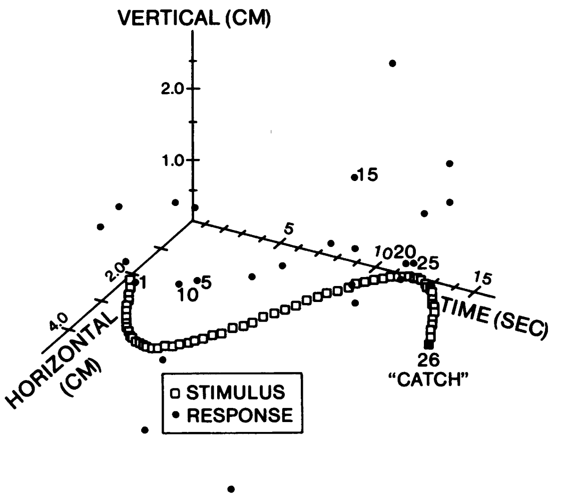

Fig. 4. A three-dimensional comparison of target and peck locations as a function of time and horizontal and vertical positions. Data are for one probe trial for transfer of training when the movement of the target was sinusoidally horizontal. The numbers for selected pecks indicate sequence number and show that the bird now chased the stimulus horizontally across the screen until Peck 26 produced reinforcement.

For the 26 pecks in Figure 4, 11 were leading, 14 were lagging, and 1 was a catch.

The major finding of the transfer condition was that the birds continued to chase the cursor along the new trajectory without substantial disruption of pecking behavior. This flexibility of tracking the new trajectory is demonstrated in Figure 5, which shows catches for both birds. Catches occurred at several locations as the stimulus moved right and left. Once again, strategies that predict all catch attempts at a single location do not appear to account for the data. Bird D374 caught the target on 5 out of 10 of the horizontal probe trials, and Bird D398 caught the target on 7 out of 10 of the horizontal probe trials. The percentage of reinforced pecks was 3% for Bird D374 and 11% for Bird D398. As with vertical movement, tracking was sustained for horizontal movement notwithstanding the low rate of reinforcement.

After extended training the percentage of pecks that produced reinforcement for the three sessions was 22% for Bird D398 and 19% for Bird D374; the birds ultimately became quite proficient at catching the target in this task.

DISCUSSION

The present experiment considered pigeons' pecking as a motor skill and introduced a new technique for investigating tracking. Based on a system of computer graphics and touch technology, the target moved sinusoidally up and down along a vertical trajectory. Acquisition required only a few sessions of training. In baseline training most pecks fell within the trajectory of vertical movement and were not scattered randomly across the touch screen. The average miss fell within 6 mm of the moving target, so the pecks were clearly aimed at the target. Tracking performance was fairly stable across 75 sessions of training. For the rate of movement selected (4.5 cm traversed in approximately 13.7 s), about 20% of the pecks fell within the touch target and produced reinforcement after extended training. Therefore, in confirmation of observations by Neiworth and Rilling (1987) and Pisacreta and

Witt (1985), the data suggest that the movement of the stimulus acquired stimulus control of pecking.

This experiment was designed to determine the strategy followed by pigeons in a tracking task. Following a suggestion by Wilkie (1986), the target was presented on a video display terminal, and pecks were detected by a relatively dense matrix of light-emitting diodes that accurately detected the location of the pigeon's beak. When a target moved sinusoidally up and down along a vertical trajectory, the pigeon pecked ahead and behind the target. More pecks occurred behind the target, so the basic strategy was lagging. Catches did not pile up at a single location as predicted by a single timing strategy, but were scattered throughout the entire trajectory. This strategy was sophisticated and flexible, enabling the pigeon to catch the target and produce food at many locations throughout the trajectory.

Theoretically the most interesting question is, what has the pigeon learned in mastering this task? Has the bird learned to track or has the bird simply learned to peck at the target? The best description of our observations is to say that they have learned to chase the target. When the target moves up and down the screen the bird follows it up and down. When the target moves from right to left, the bird follows it from right to left.

Normally, pigeons do not catch seeds "on the fly." Therefore, from a strictly ecological viewpoint one could predict that pigeons would experience difficulty performing well in a tracking task. On the contrary, however, our experiment with pigeons provides an excellent vehicle for studying motor control by movement with an organism whose behavior in the laboratory is well understood. An ecological framework predicts that species of birds that feed on moving prey should perform better in a tracking task than does a seed-eating species like the pigeon. One advantage of the system developed here is that it could be adapted for comparative work on reaching, tracking, and catching with different species.

The concepts of action systems and motor programs refer to the representation of goal-directed movements (Frese & Sabini, 1985; Gallistel, 1980; Heuer & Sanders, 1987; Jeannerod, 1988; Reed, 1982). The weakness of these concepts is their ambiguity. Nevertheless, the motor program concept predicts positive transfer to different trajectories of movement. When the trajectory of movement was displaced from vertical to horizontal on probe trials, the direction of pecking followed the direction of movement from the first probe trial. Each bird was successful in catching the target at a variety of points throughout the horizontal trajectory. The flexibility displayed by the pigeons suggests that the motor program concept might be useful in guiding future research. The data from the transfer task provide the strongest evidence to date for tracking in pigeons.

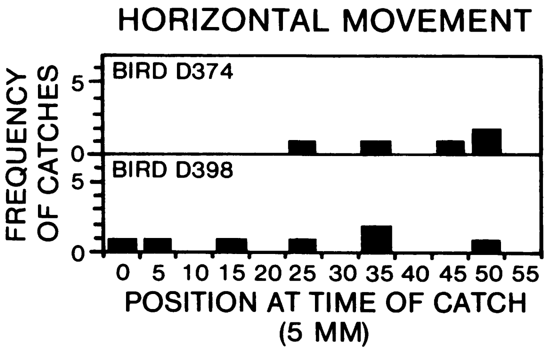

Fig. 5. Distribution of catches along the horizontal trajectory for the 10 probe trials for each of the 2 birds.

This experiment was conceived as a preliminary investigation designed to introduce a new technique, so the data must be interpreted with caution. The velocity of movement remained constant throughout the experiment. Velocity is a key variable in research on tracking with humans (Wickens, 1986). McVean and Davieson (1989) varied velocity in a tracking task with pigeons by dropping grain onto a conveyor belt and varying the speed of the belt. They found that the number of successful pecks declined as the belt speed increased, which suggests control of pecking by target velocity.

The transfer data showed that the direction of transfer is positive. However, these data do not provide a quantitative measure of the amount of transfer or indicate whether performance showed a decrement on probe trials. The complexity of the pattern of movement is readily manipulated with the system employed here. Because transfer of learning is a topic in which interest has been renewed (Cormier & Hagman, 1987), this technique provides a tool for determining the limits of transfer of motor skill in pigeons.

One difficulty in comparing these data with those of the children in von Hofsten's (1987) experiments is that he measured reaching with a system that recorded hand movements in three dimensions. In our task only the termination of reaching was recorded. Thus we were unable to determine whether the pigeon aims its beak directly at the current location of the target or whether the bird anticipates the future target location by aiming its beak ahead of the current target position. In his recent work, von Hofsten (von Hofsten & Rönnqvist, 1988) measured hand movements with light-emitting diodes attached to the fingers of the infant. By attaching light-emitting diodes to the pigeon's beak or photographing the movements of pecking in three dimensions, it should be possible to determine where the pigeon's beak is aimed at the initiation of the peck. Measuring the pigeon's eye movements during tracking with the techniques developed by Bloch, Lemeignan, and Martinoya (1987) would also provide valuable supplementary information.

The rationale for studying tracking in different species is to determine how a species' feeding behavior adapts to the tracking task. Fortunately, the organization of the pigeon's feeding behavior has been investigated extensively by neuroethologists. Goodale (1983) employed a 2-mm black dot as the target in a feature- positive discrimination in which pecks at the dot on positive trials were reinforced with food and pecks on negative trials when the dot was absent were extinguished. Goodale filmed the sequences of head movements made by the pigeons as they pecked the target. Pecks toward the key were interrupted twice by head fixations, first at approximately 81 mm from the target and then at approximately 54 mm from the target. During these fixations, the bird scanned the target with head and eye movements. The function of the first fixation appears to be selection of the general feeding area, and the function of the second appears to be selection of the specific target. Even during normal foraging, pigeons do not always catch grain on the first peck (Zweers, 1982). Zeigler, Levitt, and Levine (1980) observed that the pigeon's eating response consists of a series of bouts during which the bird's head is very close to the substrate. We observed patterns of behavior similar to those of Goodale and Zeigler et al. Our birds fixated once relatively close to the screen. Fixations were followed by a series of pecks that appeared to be directed at the target. After a series of misses, the pigeon moved its head back from the screen, fixated again at the target, and resumed the pattern of pecking. Thus the pattern observed in this task closely resembles the pigeon's normal feeding behavior.

Although stimulus control has been a topic of extensive experimental analysis (Honig & Urcuioli, 1981), specifications of the motor behavior controlled by the stimuli have been relatively neglected. Tracking and catching paradigms of the type used here provide a tool for bringing the study of motor processes in pigeons into the laboratory for experimental analysis.

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