JOURNAL OF THE EXPERIMENTAL ANALYSIS OF BEHAVIOR 2002, **78,** 249–270 NUMBER 3 (NOVEMBER)

CATEGORIZING A MOVING TARGET IN TERMS OF ITS SPEED, DIRECTION, OR BOTH

WALTER T. HERBRANSON, THANE FREMOUW, AND CHARLES P. SHIMP

WHITMAN COLLEGE, UNIVERSITY OF WASHINGTON, AND
UNIVERSITY OF UTAH

Pigeons categorized a moving target in terms of its speed and direction in an adaptation of the randomization procedure used to study human categorization behavior (Ashby & Maddox, 1998). The target moved according to vectors that were sampled with equal probabilities from two slightly overlapping bivariate normal distributions with the dimensions of speed and direction. On the average, pigeons categorized optimally in that they attended to either speed or direction alone, or divided attention between them, as was required by different reinforcement contingencies. Decision bounds were estimated for individual pigeons for each attentional task. Average slopes and *y* intercepts of these individually estimated decision bounds closely approximated the corresponding values for optimal decision bounds. There is therefore at least one task in which pigeons, on the average, display flexibility and quantitative precision in allocating attention to speed and direction when they categorize moving targets.

Key words: categorization, moving targets, speed, direction

The discrimination of motion can be critical for survival. For many species, it is vital to know if a predator is approaching or a prey is escaping. Correspondingly, motion perception may have preceded the evolution of other visual processes, such as color perception or visual acuity (Husband & Shimizu, 2001; Sekuler, 1975; Walls, 1942). An evolutionary perspective led Walls to suggest that different aspects of vision, such as acuity, sensitivity, and color, might be of chief importance to different human activities, such as watchmaking, night flying, and painting, respectively. Walls wrote, however, ''to animals which invented the vertebrate eye, and hold patents on most of the features of the human model, the visual registration of movement was of the greatest importance'' (p. 342). Accordingly, one might expect that highly visual nonmammalian vertebrates, such as birds, would have evolved complex motion perception given their awe-inspiring flight characteristics that seem to require exquisitely precise abilities to process dynamic visual stimuli. This line of reasoning has led researchers to look for, and to find, neuroanatomical, electrophysiological, and behavioral structures and processes that underlie or are correlated with movement perception in several avian species (Frost, Wylie, & Wang, 1994; Husband & Shimizu, 2001; Lea & Dittrich, 2001; Martinoya, Rivaud, & Bloch, 1983; Potts, 1984; Watanabe, 1991).

Behavioral explorations of the pigeon's responses to motion included attempts to train pigeons to discriminate different stimulus velocities (Hodos, Smith, & Bonbright, 1975) and to train them to track moving targets visually (Skinner, 1960). More recently, Emmerton (1986) showed that pigeons integrated a moving dot pattern to form an integrated stimulus, Neiworth and Rilling (1987) showed that pigeons formed an internal representation of a moving stimulus and extrapolated its movement during a period when it was occluded (also see Rilling & LeClair, 1989; Rilling, LeClair, & Warner, 1993), McVean and Davieson (1989) showed that a pigeon intercepted targets moving on a conveyor belt, and Dittrich and Lea (1993) and Dittrich, Lea, Barrett, and Gurr (1998) showed that pigeons learned to form abstract concepts of naturalistic patterns of movement such as walking or flying. Even this incomplete list of behavioral research shows that pigeons do indeed have at least some of the

---

This research was supported by grants from the National Science Foundation and the National Institute for Mental Health. We thank David Wood for help in running the experiments and in conducting some of the initial data analyses. We also thank Sarah Creem, Alyson Froehlich, and David Strayer for helpful discussion and comments on an earlier draft. We are grateful to Greg Ashby and Todd Maddox for graciously sending us useful computer software for the randomization procedure.

Please address correspondence to Charles P. Shimp, Department of Psychology, 380 South 1530 East Room 502, University of Utah, Salt Lake City, Utah 84112-0251 (e-mail: charlie.shimp@psych.utah.edu).

specific abilities to perceive and respond to movement that one would expect of them based on their formidable natural flight characteristics.

What other abilities might pigeons have to process visual movement information? One might expect highly visual nonmammalian vertebrates, such as pigeons, to have evolved both to perceive motion and so that the specific motion of an object facilitates the recognition of *what* has moved. Specifically, we speculated that a pigeon might categorize moving targets purely on the basis of their movements, even when the targets provide no other basis for categorization, there are many different target movements, and some movements are highly ambiguous as to how they should be categorized. Consider that natural moving stimuli presumably often belong to multidimensional fuzzy categories without either necessary or sufficient combinations of component features (Huber, 2001; Rosch & Mervis, 1975; Shimp, 1973). An object blowing about in the wind, for example, can move in many ways, with continuously varying speeds and directions, and any local combination of speed and direction only probabilistically diagnoses its future movement. Also, the very same local combination of speed and direction sometimes might occur in the context of one overall pattern of movement, if, say, the object is a hummingbird, and sometimes in the context of a different overall pattern, if the object is a dragonfly. A pigeon presumably discriminates different categories of moving objects (e.g., pigeons, hawks, leaves, insects, and pieces of paper) in part by their dynamic properties, including their speeds and directions. Although any one brief estimate of a moving object's speed and direction might not unambiguously diagnose whether it is a pigeon or a hawk, or a hummingbird or a dragonfly, several such estimates might diagnose with at least better than chance levels which it is. In fact, it seems possible that if a flying object is sufficiently far away and in poor light, its dynamic flight characteristics could identify it better than its visual features like the size and shape of its wings. An especially interesting case therefore obtains if there are no visual identifying features at all between two objects except for their patterns of movement. In such a case, no visual scrutiny of the static object itself could specify its nature: Only its movement would identify it (Dittrich et al., 1998; Emmerton, 1990).

A method used in the literature on human categorization can be adapted to facilitate the understanding of attentional processing of the kinds of ambiguous stimuli just described, in which there are two dimensions like speed and direction, each variable varies continuously over a great many values, and any speed–direction pair might diagnose either one or the other of two categories of moving objects. The procedure with humans is called the *randomization procedure* and has been used extensively to study the role of attention and memory in categorization of multidimensional stimuli (Ashby & Maddox, 1998). We will present this procedure in terms of a version we previously developed for use with pigeons. In that research (Herbranson, Fremouw, & Shimp, 1999), pigeons viewed two-dimensional stimuli defined as rectangles varying in width and height. Stimuli were drawn from two categories that overlapped, in the sense that any rectangle could be sampled from either category. Most rectangles, however, were more likely to be sampled from one category than from the other: Rectangles were usually diagnostic of the category from which they were sampled. For example, in one condition, rectangles that were taller than they were wide were more likely to be sampled from one category, and rectangles wider than tall were more likely to be sampled from the other category, but any given rectangle could be sampled from either category. An on-line real-time demonstration of this task is available in Shimp, Herbranson, and Fremouw (2001).

Figure 1 is taken from Herbranson et al. (1999) and summarizes such a task. The left panel shows two ill-defined categories, A and B, in the form of two overlapping normal bivariate distributions. The space over which the distributions are defined is typically referred to as the stimulus space, in which each point represents a particular two-dimensional rectangle with width x and height y. The third coordinate, z, is the likelihood with which the rectangle will occur given a particular category. In Figure 1, as in the experiments described below, each variable in each distribution has the same variance, and the covariance between variables in each distri-

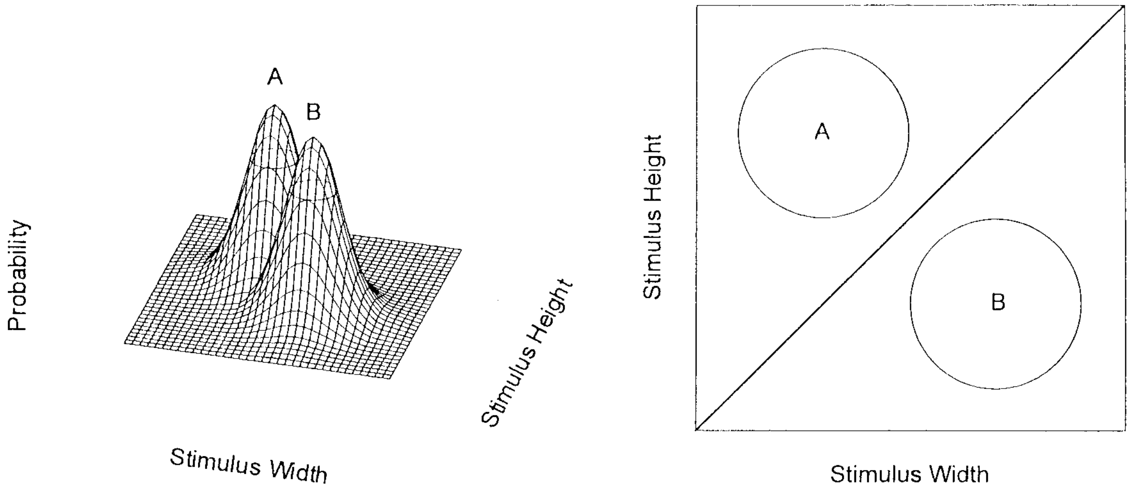

Fig. 1. Left: Bivariate normal distributions represent likelihoods with which rectangles in the experiment by Herbranson, Fremouw, and Shimp (1999) were sampled from either of two ill-defined (overlapping) categories, A and B. A rectangle is represented in the stimulus space as a point with coordinates equal to the corresponding width and height. A pigeon successively categorized individual two-dimensional stimuli, and a choice was reinforced if it corresponded to the category, either A (left key) or B (right key), from which a stimulus was sampled. One arbitrary contour of equal likelihood is shown for each category. Each contour consists of all points corresponding to rectangles equally likely to be sampled from a category (taken from Figure 1 in Herbranson et al., 1999, p. 114). Right: arbitrary contours of equal likelihood for each category and the corresponding linear optimal decision bound, $x = y$, according to which a rectangle should be categorized as an A or as a B, depending on whether the rectangle was taller than wide or wider than tall, respectively. A real-time interactive demonstration of this task is available at www.pigeon.psy.tufts.edu/avc/shimp.

bution is zero. The right panel in Figure 1 shows two equal-likelihood contours, each of which efficiently summarizes a bivariate normal distribution by showing points corresponding to stimuli that are equally likely to occur given a particular category. The right panel also shows the optimal decision bound, the line formed by the points corresponding to rectangles that are equally likely to occur given either category. In the task represented in Figure 1, as in all of the tasks described below, the optimal decision bound is a straight line, according to which stimuli are categorized optimally when a stimulus on one side is categorized as belonging to Category A and a stimulus on the other side is categorized as belonging to Category B (Ashby & Gott, 1988).

A pigeon categorizing stimuli over trials produces an empirical equivalent to the stimulus space shown in Figure 1. Each point in such a stimulus space shows how an individual pigeon categorized a particular stimulus. An empirical decision bound can be estimated from the data points to summarize a pigeon's categorizations, and that estimated bound can be compared to the optimal bound. See the Method section below for further details.

The present experiment adapted the randomization procedure to study how pigeons categorize a target moving in any of many possible directions at any of many possible speeds. We used a procedure virtually identical to that of Herbranson et al. (1999), except that we replaced the two dimensions of height and width of static rectangles with speed and direction of moving targets. One may assume that a pigeon can "selectively attend" to either or both dimensions, speed and direction, of an object's movement. We therefore asked whether a pigeon can categorize a target moving in any of various directions and at any of various speeds in terms of both its speed and direction combined, its direction alone, or its speed alone. The first task was arranged to determine the extent to which a pigeon could make nearly optimal categorizations of a moving target when optimality required divided attention to both speed and direction and suitable integration of information from both. Subsequent tasks determined the extent to which a pigeon could make nearly optimal categorzations when optimality required the pigeon to attend selectively to just one relevant dimension and ignore the other, irrelevant, dimension of a moving target.

METHOD

Subjects

Four experimentally naive male White Carneau pigeons (*Columba livia*) were obtained from the Palmetto Pigeon Plant (Sumter, SC). Each was maintained at approximately 80% of its free-feeding weight, with supplemental grain provided as needed in home cages after daily experimental sessions. Each pigeon was housed individually in a standard pigeon cage with free access to water and grit, in a colony room with a 14:10 hr light/dark cycle. All experimental sessions took place during the light cycle at approximately the same time 5 or 6 days per week. Pigeon 2 died during Condition 2.

Apparatus

The four experimental chambers had internal dimensions of 38 cm long by 34.5 cm wide by 50 cm high. Each had three clear plastic response keys (3.5 cm by 3.5 cm) mounted in a horizontal row within a clear Plexiglas viewing window (17 cm wide by 7 cm high). The viewing window itself was mounted in the front wall of the chamber, with its base 20 cm above the chamber floor. A computer monitor with a 15-in. screen was located 8 cm behind this front wall. Each chamber was interfaced via digital input-output cards to a 90- or 100-mHz personal computer that controlled all experimental contingencies, presented stimuli, and recorded data. A fan and white noise helped to mask extraneous sounds. A digital sound meter held at approximately the position of a pigeon's head gave a reading (C scale) that varied across chambers from approximately 88 to 93 dB, which was sufficient to mask most, if not all, sounds from outside the chamber.

Procedure

The general procedure involved displaying a small illuminated moving region (the "target") on a computer screen for a brief period and then requiring the pigeon to categorize the target's movement as belonging to one or the other of two bivariate normal distributions. (An interactive demonstration of all four categorization tasks described below is available in Malloy et al., 1991.)

Pretraining. Pigeons were pretrained in sessions consisting successively of habituation to the chamber, magazine training, and autoshaping to peck consistently on each key. Stimuli used for autoshaping were blocks of various colors (2.4 cm square; green, red, or blue) appearing one at a time behind the three response keys.

Stimuli. Stimuli consisted of a small white target, approximately circular (≈1 cm diameter), moving at a particular speed in a particular direction. The white target appeared against the background of an otherwise blank screen. At the beginning of a trial, the target was initially displayed at a random location within an area (3.8 cm by 3.8 cm square) behind the center response key. A single peck to the center key after the target was presented initiated movement in a straight line and at a constant speed. The direction and speed of movement varied across trials. Speed varied from a low of about 0.10 cm/s to a high of about 1.0 cm/s. Direction of movement varied approximately 89.5° from vertical in both directions. That is, targets could move almost directly to the left or to the right, or in any intermediate upwards direction. The range of each variable was made about as large as the apparatus would permit, and no effort was made to scale the two dimensions so that numerically equal variances were psychologically equal. Accordingly, any resulting consequences of one dimension's being "easier" than the other are unknown.

Both dimensions varied almost continuously: Possible speeds and directions in these experiments were limited chiefly by the pixels, the size of the monitors, processor speed, and the software used (Turbo Pascal 7.0). (Unlike the experiments in Herbranson et al., 1999, in which stimuli were presented in character mode, here we used graphics mode.) In addition, the position of the transparent response keys imposed limitations on possible or appropriate target locations, because it was not desirable for targets to overrun the response keys. Accordingly, the target size and vector properties described above were chosen so that targets could not be produced that would overrun response keys or travel off the edge of the screen.

On each trial, a stimulus was randomly chosen from one of the two equally likely categories. Each category had a corresponding two-dimensional bivariate normal distribution, with the two dimensions being speed and direction. The bivariate normal distributions were approximate, in the sense that speeds and directions were drawn from bounded stimulus spaces, as shown below in Figures 2 to 10. If a speed or direction was sampled that did not fall within the stimulus space, it was rejected, and sampling continued until an appropriate stimulus was sampled. Any possible speed or direction within a specified stimulus space could be selected from either category, so that the categories in this sense were ''ill defined'' and the task was a probabilistic discrimination (Shimp, 1973). Most speed–direction pairs, however, were more likely to be generated by one category than the other so that for most vectors, one response was more likely to be reinforced than the other.

Once a target's speed and direction were selected for a particular trial, an additional control procedure was implemented for the following reason. Speed is the ratio of distance to time, so categorization responses based on distance or time, rather than speed, could lead to better than chance accuracy: If the target were always presented for the same duration, given a selected speed, then the length of the line over which the target traveled could serve as a cue for better than chance accuracy. Alternatively, if the target were always presented for the same length of line, again given a particular selected speed, then time of presentation could serve similarly. Therefore, after the target's speed and direction were selected, the computer randomly chose to present the stimulus for either a specified duration or a specified distance. Finally, depending on whether this control procedure selected duration or length of line, the computer randomly chose either a time varying from 2 to 3 s or a length varying from 1.9 to 3.8 cm. In summary, this control procedure was designed to encourage categorization of stimuli based on speed and direction, rather than on either the distance the target moved or the duration it was visible (see McKee, 1981, for further discussion related to these control issues). It is important in the face of all these procedural details, however, not to lose sight of the fact that, regardless of whether control was by distance, speed, time, or some combination of these variables, all these possibilities are independent of the other dimension, direction.

Trial organization. Each of a session's 80 trials consisted sequentially of an orienting cue, presentation of the moving target, a categorization response, either reinforcement or a correction procedure, and an intertrial interval.

Each trial began with an orienting cue (a 2.4-cm green square) presented directly behind the center key. The first center-key peck to occur after 1 s turned off this orienting cue and turned on a white circular target (1 cm diameter) presented randomly within a circumscribed region (see above) behind the center key. The next peck to the center key started the target moving with a speed and direction chosen as described above. The target stopped moving after it either traveled a randomly chosen distance or had traveled for a randomly chosen length of time, as described above. Once the moving target reached its terminal distance or duration, it disappeared from the screen and colored squares (2.4 cm; red and blue on left and right, respectively) appeared directly behind the two side keys. A pigeon then categorized the moving target that had been presented as an exemplar of Category A or Category B. A left response was reinforced if the stimulus was generated by Category A, and a right response was reinforced if the stimulus was generated by Category B.

Reinforcement. If a choice corresponded to the category from which the stimulus had been sampled, mixed grain was presented in a hopper located directly beneath the window. Hopper presentation time varied across pigeons from 1.7 to 2.3 s to maintain individual deprivation levels accurately. Following reinforcement, there was a 5-s intertrial interval, during which the monitor was blank.

Correction procedure. If a choice did not correspond to the category from which a stimulus was sampled, a 10-s correction interval began. This interval was signaled by the houselight flashing on and off every 0.5 s. A trial was then repeated, with the same moving target. Any subsequent errors caused the correction procedure to continue to recycle, with the same stimulus, until the correct response occurred. Only the initial choice was recorded and included in data analysis.

Experimental Conditions

Conditions varied in terms of the stimulus dimensions upon which reinforcement depended: both speed and direction, speed alone while direction varied randomly, or direction alone while speed varied randomly. Conditions lasted 40 to 48 days and were ended mostly due to a combination of informal examination of the stability of overall accuracy of categorization and experimenter convenience. Best fitting decision bounds were estimated only after the completion of the entire experiment. In all five conditions, there was a 5% overlap between Categories A and B, so that optimal categorization would lead to reinforcement on an average of 95% of the trials.

Speed and direction were varied across conditions in terms of arbitrary units in the Turbo Pascal programming language, with a fraction of a degree corresponding to direction and repetitions of a fixed delay corresponding to speed. An experimenter estimated the actual speeds and directions, and thereby estimated how to translate Pascal parameters to actual speeds and directions, by repeatedly measuring the target's movement on a pigeon's monitor for a given speed and direction, then for a different speed–direction pair, and so on. These estimates were difficult to make, however, because the monitor surface was not completely flat, and the target was not a perfect point. A pigeon, of course, presumably experienced similar difficulties in estimating speed and direction.

For the sake of completeness, experimental conditions are described in terms of both the arbitrary software values and the corresponding estimated speeds and directions. Smaller software numbers for speeds and directions in the figures below refer to faster speeds and to movement to the right, respectively. An approximate correspondence between speed and arbitrary software units is provided by the following relation: Target speed (in centimeters per second) was estimated to equal $1.05 - 0.000685 \times s$, where s was the speed, in software units, drawn from a normal distribution. Direction varied in increments of 0.5692°, and target direction in degrees was equal to $-447.567 + 0.570149 \times 0.5692d$, where d was the direction, in software units, drawn from a normal distribution.

Condition 1: Divided attention across both speed and direction. In Condition 1, the speed of a Category A stimulus was drawn from a normal distribution with a mean of 1,050 (0.33 cm/s) and a standard deviation of 180 (0.12 cm/s). For Category B, speed was drawn from a normal distribution with a mean of 550 (0.67 cm/s) and standard deviation of 180 (0.12 cm/s). Direction for a Category A stimulus was drawn from a normal distribution having a mean of 733 (29.6° right of vertical) and a standard deviation of 60 (34.20°), and for a Category B stimulus from a normal distribution with a mean of 837 (−29.6° left of vertical) and standard deviation of 60 (34.20°). The top panel of Figure 2 shows the locations of the two prototypes (category means) in the stimulus space, equal-likelihood contours at one and two standard deviations, and the optimal decision bound. The optimal decision bound in Figure 2 represents the intersection of the two stimulus distributions, and indicates the optimal strategy for responding, which would result in 95% of choice responses being reinforced. Optimal performance on this task required a pigeon to attend to both speed and direction, and to integrate them in a specific way. Failure to attend to both dimensions or to combine the information from each correctly would result in suboptimal performance.

The bottom panel of Figure 2 shows the two prototypes corresponding to Categories A and B, with direction indicated by the direction of the arrows and speed indicated by the length of the arrows, with length directly proportional to speed. The bottom panel of Figure 2 shows that targets moving more slowly to the upper right were usually exemplars of Category A, and targets moving more quickly to the upper left were usually exemplars of Category B. Optimal behavior required a pigeon to categorize most targets moving to the right as belonging to Category A. Because Category A was associated with the left key, pigeons should have pecked the left key after viewing targets moving to the right.

Condition 2: Divided attention across both speed and direction. In Condition 2, the association

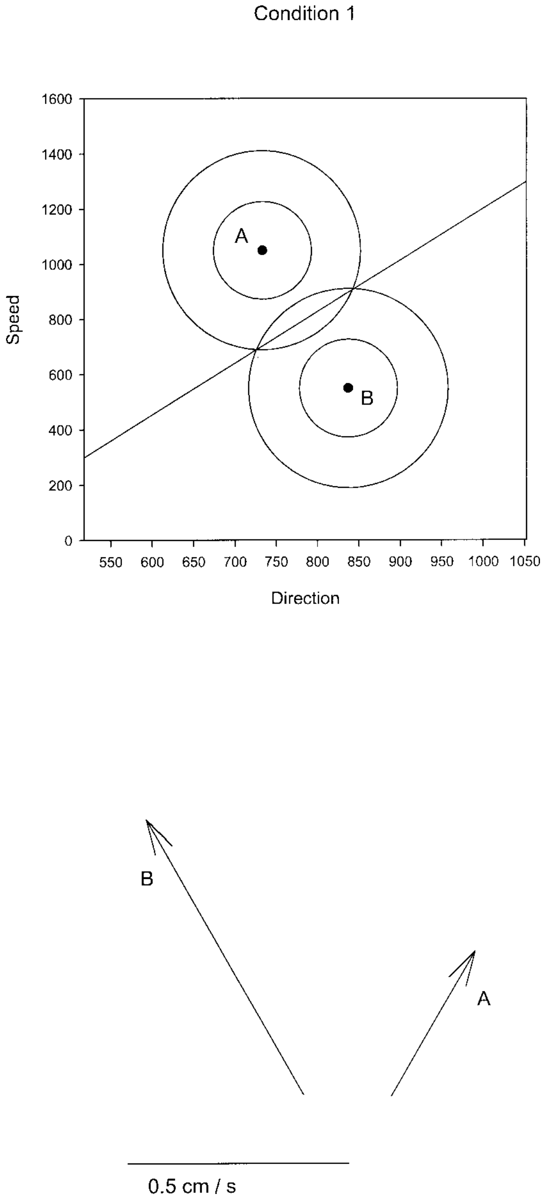

Fig. 2. Left: the stimulus space, two equal likelihood contours at one and two standard deviations from the average of each category, and the optimal bound for Condition 1. Optimal performance on the task required a pigeon to divide attention between both dimensions, speed and direction, and to integrate the information from both. Scale units are arbitrary Turbo Pascal software numbers according to which smaller numbers refer to faster speeds and to movement to the right (see text for details). Right: the prototypes corresponding to Categories A and B, in which direction of the target is represented by the direction of an arrow and speed is represented by the length of the line (faster targets correspond to longer lines).

between categories and vectors was changed, but integration of information from both dimensions was still required for optimal performance. The speed of a Category A stimulus was drawn from a normal distribution with a mean of 1,050 (0.33 cm/s) and a standard deviation of 180. For Category B, speed was drawn from a normal distribution with a mean of 550 (0.67 cm/s) and standard deviation of 180. Thus, the speed dimension of vectors for Categories A and B remained the same. Direction, however, was reversed. The direction of a Category A stimulus was drawn from a normal distribution having a mean of 837 (−29.6° left of vertical) and a standard deviation of 60, and the direction of a Category B stimulus was drawn from a normal distribution with a mean of 733 (29.6° right of vertical) and standard deviation of 60. Figure 3 corresponds to Figure 2. The top panel again shows the locations of the two prototypes in the stimulus space, two equal-likelihood contours at one and two standard deviations, and the optimal bound. The bottom panel again shows the two prototypes, with targets corresponding to Category A now usually moving more slowly to the upper left instead of to the upper right and targets corresponding to Category B usually moving more quickly to the upper right instead of to the upper left. The optimal decision bound in Figure 3 represents the intersection of the two stimulus distributions, and indicates the optimal strategy for responding. To perform optimally, a pigeon had to continue to attend to both speed and direction, but now had to combine the corresponding information differently. Integration alone, however, was not sufficient: Continuing to integrate speed and direction as in Condition 1 would have resulted in chance performance.

Condition 3: Selective attention to direction, with speed irrelevant. In Condition 3, the speed of both a Category A stimulus and a Category B stimulus was drawn from a normal distribution with a mean of 800 (0.50 cm/s) and a standard deviation of 180. Speed was therefore irrelevant. Direction was drawn from a normal distribution having a mean of 687 (55.9° right of vertical) and a standard deviation of 60 for Category A stimuli, and directions of Category B stimuli were drawn from a distribution with a mean of 883 (−55.9° left of vertical) and a standard deviation of 60.

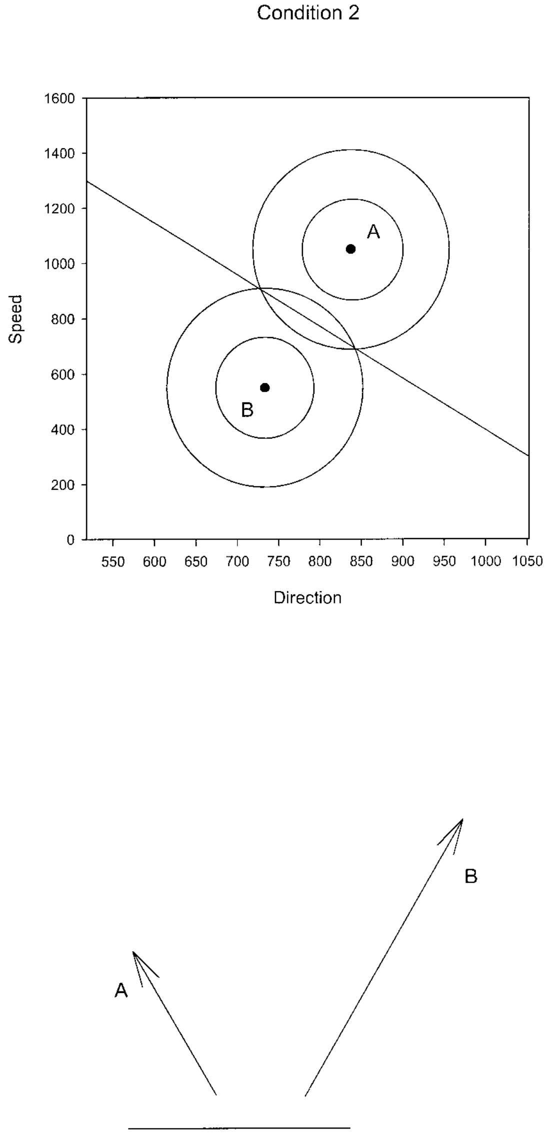

Fig. 3. Top: the stimulus space, two equal likelihood contours at one and two standard deviations from the average of each category, and the optimal bound for Condition 2. Optimal performance on the task required a pigeon to divide attention between both dimensions and to integrate the information from both. Scale units are arbitrary numbers according to which smaller numbers refer to faster speeds and to movement to the right (see text for details). Bottom: the prototypes corresponding to Categories A and B, in which direction of the target is represented by the direction of the arrow and speed is represented by the length of the line (faster targets correspond to longer lines).

Figure 4 parallels Figures 2 and 3 and shows the prototypes, stimulus space, and optimal decision bound. The optimal decision bound in Figure 4 indicates the optimal strategy for responding, which again would result in 95% of the choice responses being reinforced. The critical feature of Condition 3 was that speed was no longer diagnostic of category membership. To perform optimally on this task, a pigeon had to attend to direction alone.

Condition 4: Selective attention to speed, with direction irrelevant. In Condition 4, the speed of a Category A stimulus was drawn from a normal distribution with a mean of 1,094 (0.31 cm/s) and a standard deviation of 180. For Category B, speed was drawn from a normal distribution with a mean of 506 (0.70 cm/s) and a standard deviation of 180. Direction was drawn for both categories from a normal distribution having a mean of 785 (vertical) and a standard deviation of 60. Figure 5 illustrates the task in the same manner as did Figures 2 to 4 for Conditions 1 to 3. The critical feature of Condition 4 was that direction was no longer diagnostic of category membership. Thus, to perform optimally on this task, a pigeon had to attend to speed alone and to ignore direction.

Condition 5: Replication of integration task of Condition 1. Condition 5 replicated the task in Condition 1, so Figure 2 summarizes Condition 5 as well as Condition 1.

Method of estimating decision bounds. Best fitting estimated decision bounds were obtained in the following way. A decision bound was estimated for each individual pigeon. For each condition, each of a pigeon's categorizations over the last 10 days of that condition was compared successively to the predictions made by a series of possible linear decision bounds passing through the stimulus space. A comparison was made for each of these possible decision bounds. Specifically, for each possible bound, the number of trials on which the bound predicted the same categorization as was observed from an individual pigeon was calculated. The exhaustive search used a step size equal to 0.005 for slope and 0.4 for intercept. The best fitting bound was defined as that which accounted for more individual categorizations than any other bound. It was, that is, the bound that maximized the number of individual categoriza-

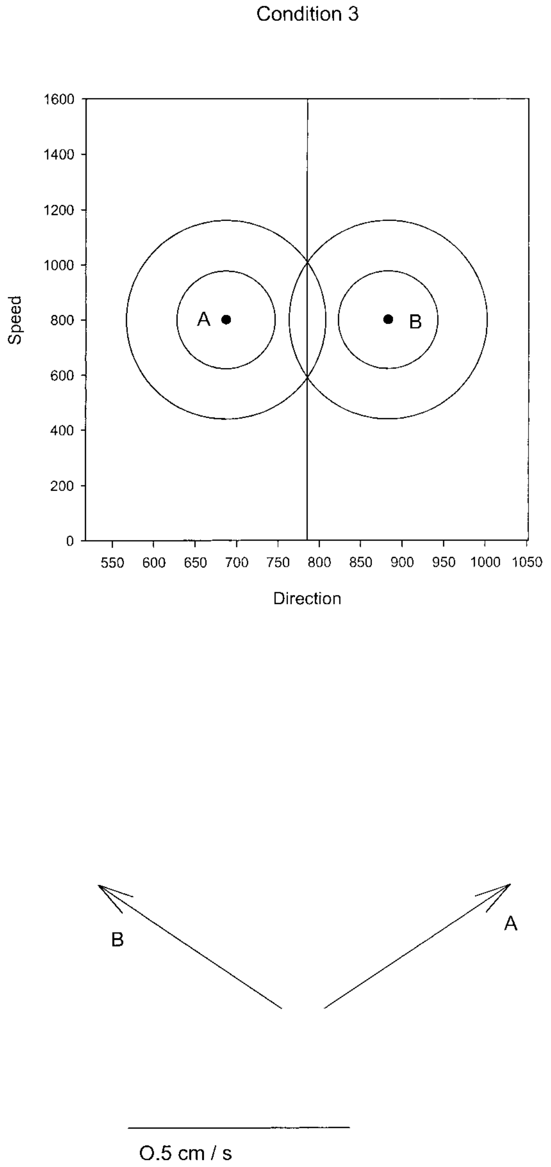

Fig. 4. Top: The stimulus space, two equal likelihood contours at one and two standard deviations from the average of each category, and the optimal bound for Condition 3. Optimal performance on the task required a pigeon to attend selectively to direction and to ignore speed. Scale units are arbitrary numbers according to which smaller numbers refer to faster speeds and to movement to the right (see text for details). Bottom: the prototypes corresponding to Categories A and B, in which direction is represented by the direction of the arrow and speed is represented by the length of the arrow.

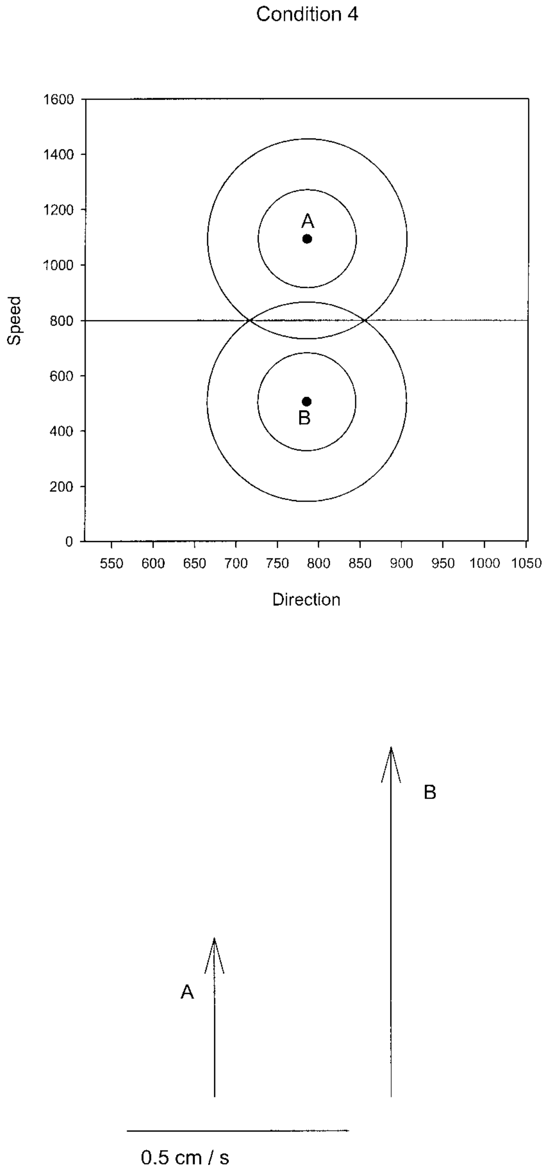

Fig. 5. Top: the stimulus space, two equal likelihood contours at one and two standard deviations from the average of each category, and the optimal bound for Condition 4. Optimal performance on the task required a pigeon to attend selectively to speed and to ignore direction. Scale units are arbitrary numbers according to which smaller numbers refer to faster speeds and to movement to the right (see text for details). Bottom: the prototypes corresponding to Categories A and B, in which direction is represented by the direction of the arrow and speed is represented by the length of the arrow.

tions of stimuli that were the same as a pigeon's categorizations of those same stimuli. Most searches produced more than one best fitting solution: The estimated decision bound was usually not unique. Table 1 shows the most extreme values of the slope and intercept for the estimates tied for the largest number of categorizations accounted for (see also Herbranson et al., 1999).

A decision bound estimated in this way, even if it approximates the optimal decision bound, does not necessarily either maximize the number of categorizations accounted for or accurately reflect all possible decision bounds. Consider the following hypothetical example of performance in an integration task in which optimal performance requires attention to, and appropriate integration of, information from both dimensions. A pigeon might, on a random trial-by-trial basis, selectively attend to either speed or direction, but not both simultaneously. The resulting estimated decision bound might approximate an optimal decision bound and thereby incorrectly imply integration of information from both dimensions. The estimated bound would not accurately reflect the actual decision processes, and in general, estimated bounds do not, by themselves, diagnose underlying decision processes. To diagnose actual processes more accurately, examination of other features of behavior, such as the overall response pattern in the stimulus space and overall accuracy, is essential. For example, in the case just described, the estimated decision bound would be flanked in the stimulus space by a different pattern of responses from that which corresponds to responding based on information integration, and overall accuracy could not consistently outperform a suboptimal selective attention strategy. In the following, all three forms of results—the estimated decision bound, the stimulus space, and accuracy—are therefore presented.

RESULTS

Condition 1: Divided Attention Across Both Speed and Direction

Table 1 gives the critical individual-pigeon and group-average numerical data averaged over the last 10 days of the condition. Pigeon 1's stimulus space is displayed in the left panel of Figure 6 because Pigeon 1, along with Pigeon 5, had an accuracy intermediate between the best (Pigeon 2) and the worst (Pigeon 4), and because Pigeon 5's results are presented below for other conditions. Figure 6 gives an estimate of Pigeon 1's decision bound: It shows the median of the five equally best fitting estimated bounds. (Table 1 gives the numerical values of the corresponding slope and *y* intercept.) Pigeon 1 categorized most moving targets generally in accord with the optimal decision bound. The right panel of Figure 6 shows each individual pigeon's median estimated decision bound and also shows the group average of those individual medians. Pigeon 1's behavior was not atypical: Estimated and optimal bounds were generally similar, especially so for the group average.

Averaged over pigeons, 81.1% of categorizations were to the optimal key (Table 1). The theoretical optimal decision bound, assuming appropriate integration of information from both speed and direction, accounted for a higher percentage of categorizations than did either optimal decision bound assuming selective attention purely to either speed or direction alone (Table 1). Pigeons therefore to some degree integrated information across dimensions, as required by the optimal decision bound for the task in Condition 1. The slopes of the best fitting estimated decision bounds ranged for individual pigeons from approximately 0.92 to 4.76, with an average of 2.07, which corresponded well to the optimal value of 1.87. The *y* intercepts ranged from −46.97 to −2,948.57, with an average of −908.08, which roughly approximated the optimal value of −669.52.

Table 1 also shows two additional estimated best fitting decision bounds, best fitting speed only and best fitting direction only. The best fitting speed-only bound was obtained by examining the fit of all possible bounds that were perpendicular to the speed axis and then selecting the bound that maximized the number of categorizations that were the same as a pigeon's. The best fitting direction-only bound was obtained in the corresponding manner. The best fitting integration bound, described previously, fit better for each pigeon than either of these selective attention bounds. This comparison provides additional support for the view that in Condition 1, the

Table 1

Accuracy and best fitting decision bounds.

Condition	Pigeon 1	Pigeon 2	Pigeon 4	Pigeon 5	Average
1: Optimal decision bound, $Y = 1.87X - 669.52$					
% of choices that were reinforced	79.3	82.8	77.1	80.3	79.9
% of choices that were optimal	80.0	84.3	77.6	82.3	81.1
% of choices accounted for by speed = 800	77.7	83.2	76.2	81.1	79.6
% of choices accounted for by direction = 785	73.8	73.9	71.5	73.8	73.3
% of choices accounted for by best fitting bound	81.6	86.3	81.0	83.1	83.0
best fitting speed only	78.4	84.4	80.3	81.9	81.3
best fitting direction only	74.6	74.6	73.1	74.0	74.1
Number of best fitting bounds	5	50	23	44	30.5
Slope of median best fitting bound	4.76	1.50	0.92	1.09	2.07
Intercept of median best fitting bound	−2,948.57	−543.76	−46.97	−93.04	−908.08
2: Optimal decision bound, $Y = -1.87X + 2269.52$					
% of choices that were reinforced	70.5		81.8	76.6	76.3
% of choices that were optimal	70.3		84.0	78.0	77.4
% of choices accounted for by speed = 800	71.6		81.4	77.7	76.9
% of choices accounted for by direction = 785	65.5		75.5	69.2	70.1
% of choices accounted for by best fitting bound	76.6		85.8	81.5	81.3
best fitting speed only	75.5		83.3	82.3	80.4
best fitting direction only	71.4		76.4	73.5	73.8
Number of best fitting bounds	6		7	21	11.3
Slope of median best fitting bound	−3.39		−1.18	−0.76	−1.78
Intercept of median best fitting bound	3,026.44		1,778.82	1,166.41	1,990.56
3: Optimal decision bound, $X = 785$					
% of choices that were reinforced	67.6		82.5	76.8	75.6
% of choices that were optimal	66.5		83.6	76.1	75.4
% of choices accounted for by speed = 800	50.8		52.4	54.2	52.5
% of choices accounted for by direction = 785	66.5		83.6	76.1	75.4
% of choices accounted for by best fitting bound	78.5		84.1	77.6	80.1
best fitting speed only	71.3		54.1	55.4	60.3
best fitting direction only	78.1		84.0	77.4	79.8
$X = AY + B$					
Number of best fitting bounds	2		7	1	3.3
Slope of median best fitting bound	−0.03		−0.06	−0.02	−0.04
Intercept of median best fitting bound	921.60		851.20	816.00	862.93
4: Optimal decision bound, $Y = 800$					
% of choices that were reinforced	73.9		80.5	79.4	77.9
% of choices that were optimal	74.5		81.5	80.0	78.7
% of choices accounted for by speed = 800	74.5		81.5	80.0	78.7
% of choices accounted for by direction = 785	51.8		50.8	53.3	52.0
% of choices accounted for by best fitting bound	75.6		85.4	81.3	80.8
best fitting speed only	74.8		85.4	80.9	80.4
best fitting direction only	57.5		60.3	54.4	57.4
Number of best fitting bounds	9		26	1	12.0
Slope of median best fitting bound	−1.02		0.84	−1.12	−0.43
Intercept of median best fitting bound	1,588.80		−16.81	1,733.03	1,101.67
5: Optimal decision bound, $Y = 1.87X - 669.52$					
% of choices that were reinforced	72.0		82.5	82.1	78.9
% of choices that were optimal	72.6		81.9	82.0	78.8
% of choices accounted for by speed = 800	72.3		80.0	81.4	77.9
% of choices accounted for by direction = 785	65.4		74.4	74.3	71.4
% of choices accounted for by best fitting bound	74.1		86.6	84.1	81.6
best fitting speed only	72.8		84.9	81.9	79.9
best fitting direction only	66.5		76.8	75.1	72.8
Number of best fitting bounds	19		7	40	22.0
Slope of median best fitting bound	2.78		1.85	1.09	1.91
Intercept of median best fitting bound	−1,244.44		−808.89	−318.26	790.52

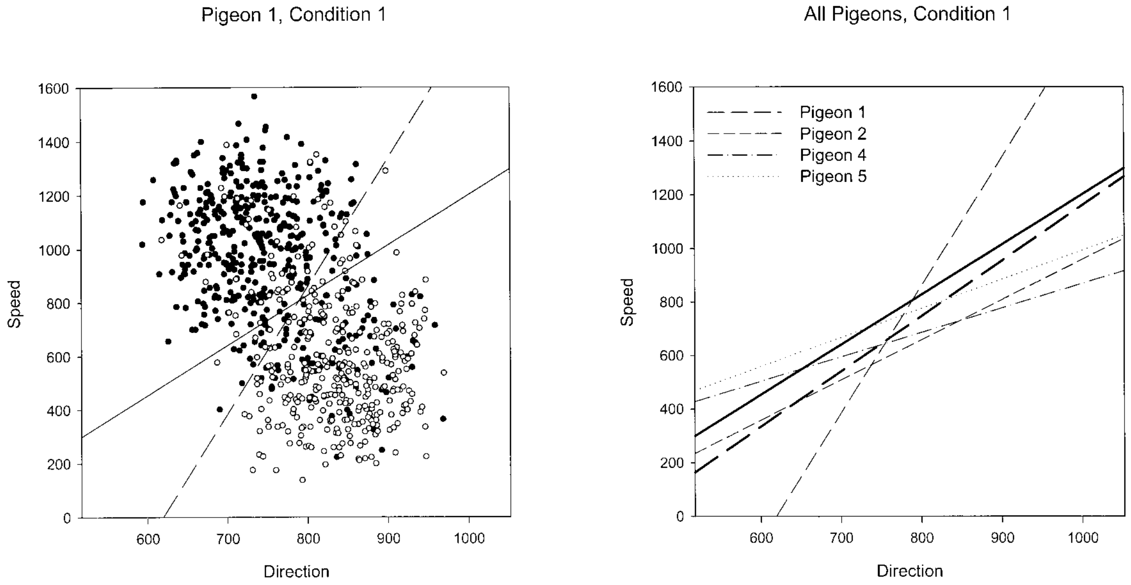

Fig. 6. Left: the obtained stimulus space for Pigeon 1 in Condition 1, with filled and open circles corresponding to individual responses categorizing stimuli as belonging to Category A or B, respectively, the dashed line showing the estimated decision bound for Pigeon 1, and the solid line showing the optimal bound. Right: all four individual-pigeon estimated decision bounds, the average decision bound (dashed line), and the optimal decision bound (solid line). Scale units are arbitrary numbers according to which smaller numbers refer to faster speeds and to movement to the right (see text for details).

pigeons were appropriately integrating information from both speed and direction.

Condition 2: Divided Attention Across Both Speed and Direction

Figure 7 shows the stimulus space and estimated decision bound for Pigeon 5, which was intermediate in terms of accuracy of categorizations. (Recall that Pigeon 2 died before the end of Condition 2.) All estimated slopes reversed sign from positive in Condition 1 to negative in Condition 2, in accord with the corresponding change in optimal decision bound slopes from 1.87 to −1.87 (Table 1). Individual slopes varied from −0.76 to −3.39, with the average of −1.78 closely corresponding to the optimal value of −1.87. Individual *y* intercepts varied from 1,166.41 to 3,026.44, with an average of 1,990.56 compared to the optimal 2,269.52. Like the slopes, the *y* intercepts changed drastically and thereby moved toward the corresponding value in the changed optimal bound. In general, the pigeons continued to integrate information from both dimensions, as required by the task, and also now appropriately associated movement to the left with Category A rather than with Category B.

Table 1 shows estimated best fitting speed-only and direction-only decision bounds. The best fitting integration bound fit better than either of these selective attention bounds for Pigeons 1 and 4, but for Pigeon 5, there was a best fitting speed-only bound that described the data better than the integration bound. For Pigeon 5, that is, there was a selective attention criterion in terms of speed, slightly different from the average speed, that led to a slightly better fit than did any estimated divided attention bound. Therefore, in this sense Pigeon 5 selectively attended to speed. Otherwise, Condition 2, like Condition 1, generally showed appropriate integration of information from both speed and direction.

Condition 3: Selective Attention to Direction, with Speed Irrelevant

Pigeon 5 was again intermediate in terms of accuracy so we again display, in Figure 8, that pigeon's stimulus space and median estimated decision bounds. All 3 pigeons produced decision bounds that approximated

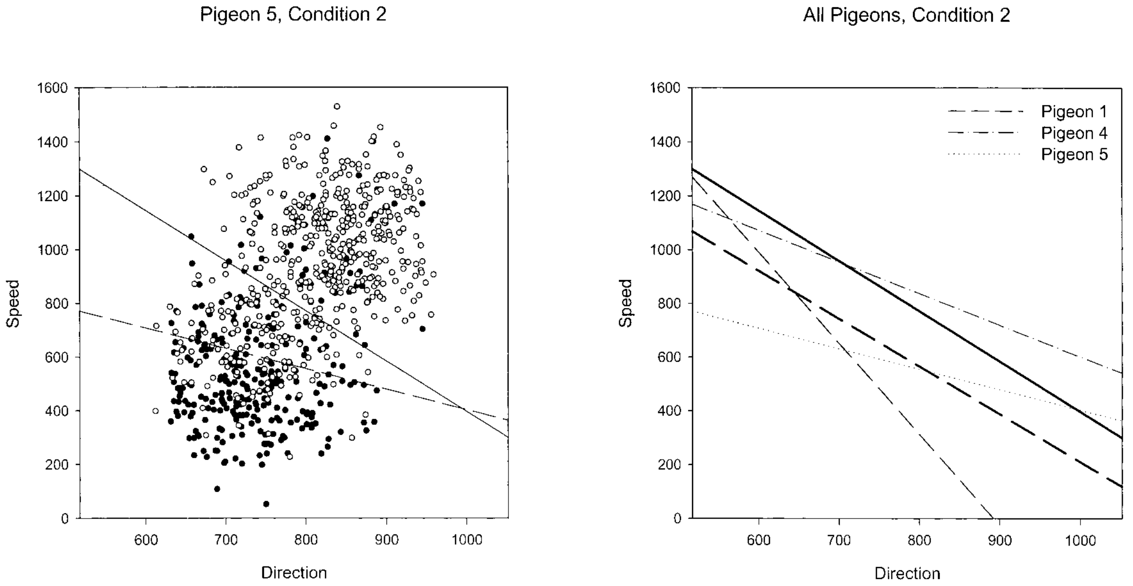

Fig. 7. Left: the obtained stimulus space for Pigeon 5 in Condition 2, with open and filled circles corresponding to individual responses categorizing stimuli as belonging to Category A or B, respectively, the dashed line showing the estimated decision bound for Pigeon 5, and the solid line showing the optimal bound. Right: all three individual-pigeon estimated decision bounds, the average decision bound (dashed line), and the optimal decision bound (solid line). Scale units are arbitrary numbers according to which smaller numbers refer to faster speeds and to movement to the right (see text for details).

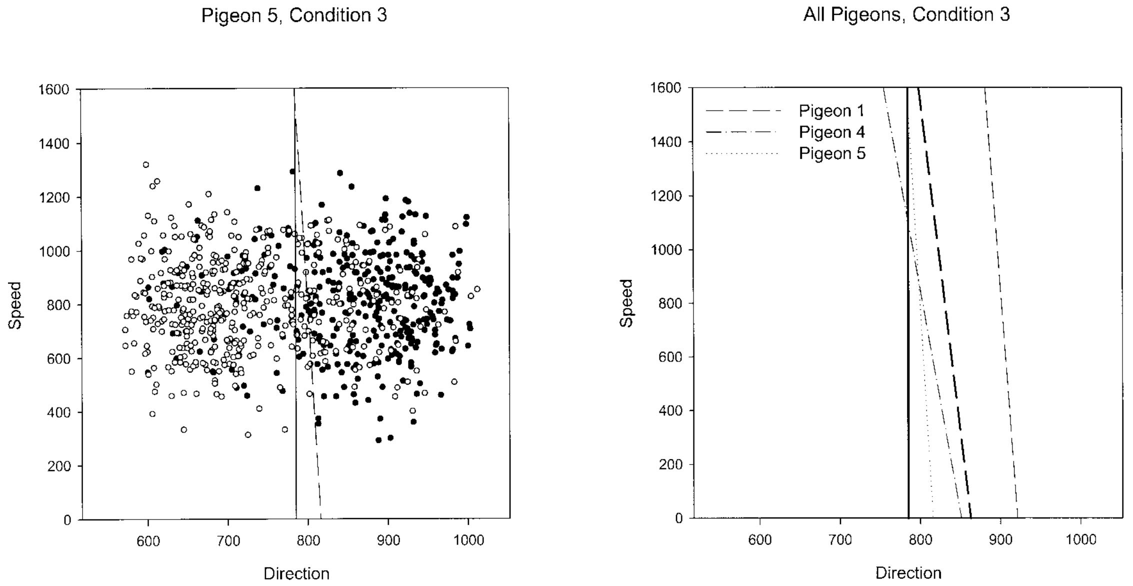

Fig. 8. Left: the obtained stimulus space for Pigeon 5 in Condition 3, with open and filled circles corresponding to individual responses categorizing stimuli as belonging to Category A or B, respectively, the dashed line showing the estimated decision bound for Pigeon 5, and the solid line showing the optimal bound. Right: all three individual-pigeon estimated decision bounds, the average decision bound, and the optimal decision bound. Scale units are arbitrary numbers according to which smaller numbers refer to faster speeds and to movement to the right (see text for details).

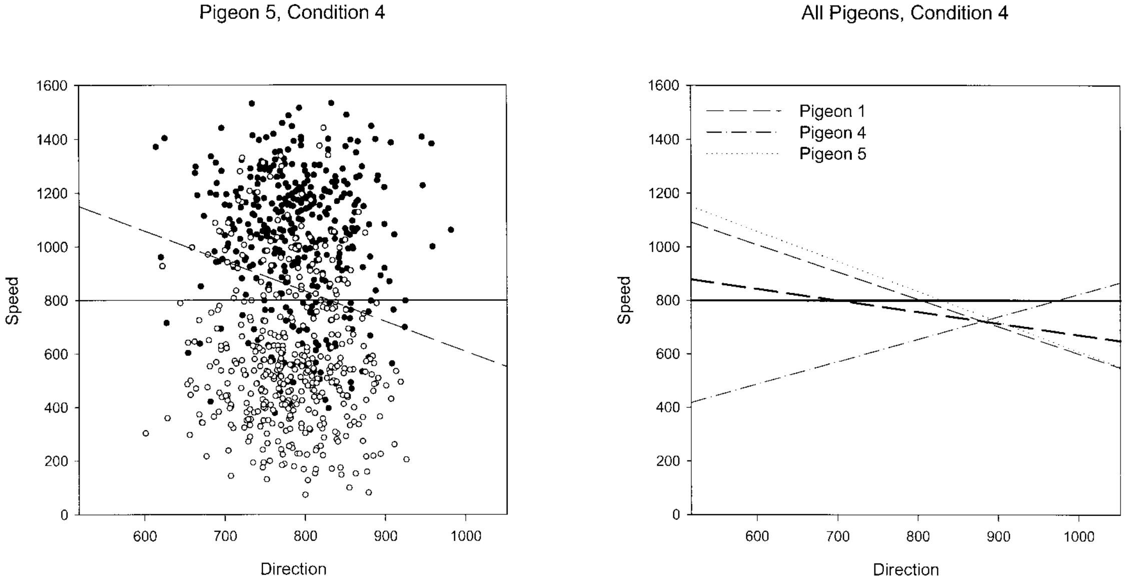

Fig. 9. Left: the obtained stimulus space for Pigeon 5 in Condition 4, with filled and open circles corresponding to individual responses categorizing stimuli as belonging to Category A or B, respectively, the dashed line showing the estimated decision bound for Pigeon 5, and the solid line showing the optimal bound. Right: all three individual-pigeon estimated decision bounds, the average decision bound, and the optimal decision bound. Scale units are arbitrary numbers according to which smaller numbers refer to faster speeds and to movement to the right (see text for details).

the vertical optimal bound (Table 1): In this sense, when the task demanded it, pigeons were more nearly able to attend exclusively to direction and to ignore speed. The group-average estimated slope of −0.04 compares favorably to the optimal 0, and the group-average estimated *y* intercept of 862.93 compares reasonably well to the optimal 785. (In this condition, we estimated speed as a function of direction to avoid the problem of an infinitely large slope.) It should be noted, however, that for none of the pigeons was the selective attention bound, even with direction free to vary, quite as good a fit as the estimated integration bound. Therefore, to some residual extent, one can see in this sense that all 3 pigeons did not completely selectively attend to direction. In this sense, Condition 3 was somewhat less successful in generating selective attention purely to direction than Conditions 1 and 2 were in generating divided attention to both dimensions.

Condition 4: Selective Attention to Speed, with Direction Irrelevant

Pigeon 5 was again intermediate in terms of accuracy, and we therefore again chose that pigeon's estimated decision bound as representative. Figure 9 shows a substantial change in estimated decision bound from that in Figure 8, corresponding to the change in tasks. The average slope changed from roughly vertical to roughly horizontal: The average slope of the individually estimated decision bounds was −0.43, which is quite close to the optimal value of 0. The average *y* intercept was 1,101.67, compared to the optimal 800.

In Condition 4, as in Condition 3, estimated decision bounds assuming divided attention between speed and direction fit categorizations as well as or better than the estimated decision bound based on selective attention to the relevant dimension, direction in Condition 3 and speed in Condition 4 (Table 1).

Condition 5: Replication of Integration Task of Condition 1

Comparisons of Figures 6 and 10 and entries in Table 1 for the results of Condition 1 and corresponding entries for the replication in Condition 5 show considerable consistency across pigeons in accuracy and estimated de-

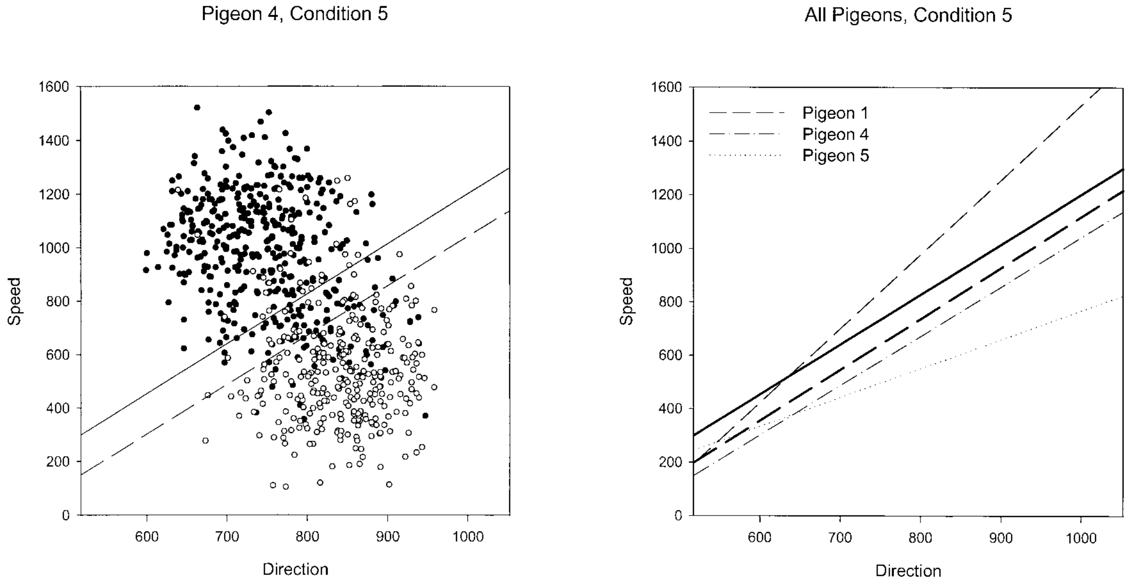

Fig. 10. Left: the obtained stimulus space for Pigeon 4 in Condition 5, with filled and open circles corresponding to individual responses categorizing stimuli as belonging to Category A or B, respectively, the dashed line showing the estimated decision bound for Pigeon 5, and the solid line showing the optimal bound. Right: all three individual-pigeon estimated decision bounds, the average decision bound, and the optimal decision bound. Condition 5 replicated Condition 1. Scale units are arbitrary numbers according to which smaller numbers refer to faster speeds and to movement to the right (see text for details).

cision bounds; the original integration task was well replicated. The pigeons, after reversing the relation between vectors and categories in Condition 2, and after selectively attending mostly to either speed or direction alone in Conditions 3 and 4, once again divided attention between both speed and direction as they did in Condition 1.

Pigeons in Condition 5 were particularly successful in integrating information from both dimensions, rather than selectively attending to just one dimension; in every case, the estimated integration bound fit better than any estimated selective attention bound (Table 1).

Overall Optimality

Figure 11 summarizes the degree to which average performance across the five selective and divided attention conditions conformed to the optimal decision bounds. Figure 11 shows the slope and *y* intercept of average estimated decision bounds as a function of the slope and intercept of the optimal decision bound, respectively. There was a remarkable correspondence between the optimal values and average performance. The close fit between obtained and optimal performance is remarkable because (a) the slopes and *y* intercepts of the optimal bounds were known before the experiment began (the optimal bound had no free estimated parameter) and (b) the estimated bounds were not obtained simply by varying a parameter within the same task, say, for example, by varying the base rate of one of the two categories within an experimental condition, but were obtained instead over tasks involving importantly different attentional mechanisms, divided or selective attention, and in one case (Condition 2) involved reversing the relation between vectors and categories. The data in Figure 11 therefore imply not only that pigeons, on the average, can be remarkably optimal in categorizing moving targets in terms of speed and direction, but that they can remain nearly optimal even when important attentional requirements of the categorization task change.

DISCUSSION

We asked if pigeons can categorize moving targets on the basis of movement, without any

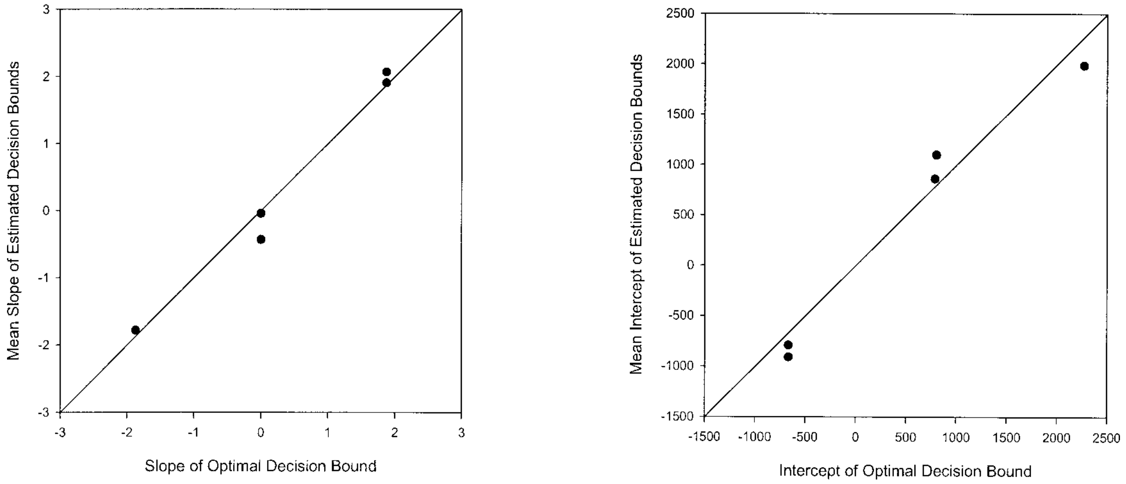

Fig. 11. The average of the slopes of the individually estimated decision bounds as a function of the optimal slope (left) and the average of the *y* intercepts of the individually estimated decision bounds as a function of the optimal *y* intercept (right).

other visual identifying characteristics of exemplars of two categories. Not only was the answer in this task affirmative, but in addition, pigeons categorized moving targets while attending to either speed or direction, or both, as the task demanded. In this task, pigeons switched among attentional strategies to a nearly optimal degree, by which we mean the following. Slopes and average *y* intercepts of linear decision bounds estimated for individual pigeons suggest that they adapt almost optimally, averaged across pigeons, to changing attentional demands when they categorize exemplars of two ill-defined two-dimensional categories involving the same target moving in different directions and at different speeds. When optimal performance demanded selective attention to a single dimension, either speed or direction, estimated decision bounds reflected correspondingly powerful control, although not always exclusive control, by the appropriate dimension, and when optimal performance demanded divided attention between both dimensions, estimated decision bounds reflected corresponding appropriate integration of information from both dimensions. Previous research with various types of static stimuli has shown that pigeons attend either to one or the other, or both, of two dimensions, such as color, line tilt, and tone frequency (Blough, 1972; Chase & Heinemann, 1972, 2001; Herbranson et al., 1999; Riley & Brown, 1991; Shimp et al., 2001). More particularly, Blough, Chase and Heinemann, and Herbranson et al. discussed theoretical decision bounds in two-dimensional stimulus spaces as a means of identifying control by individual dimensions or combined control by both. The present results extend these previous findings to show that pigeons similarly either selectively attend to just one of two features (speed or direction) of a moving stimulus or divide attention across both in a more holistic manner, depending on task demands.

Issues in the Analysis of Optimality

Few issues are more difficult or controversial than general claims to the effect that behavior is, in some sense, "optimal" (Gould & Lewontin, 1979; Herbranson et al., 1999). We therefore hasten to note that it would not yet be safe to assume that the present results, showing that average categorization tracked attentional demands to an almost optimal degree, will necessarily generalize to other experimental settings. Many experimental variables might affect categorization performance, some of which might improve performance and many of which might degrade it. The generality of the present results, therefore, will depend on the outcome of much additional research, giving careful attention to the issues described below.

First, although the present results show that pigeons changed how they attended to speed and direction as the task demanded, and although Figure 11 shows an almost astonishing degree of optimal categorization, on the average, it should be recalled that the two selective attention conditions (Conditions 3 and 4) also showed some evidence that pigeons continued to divide attention to some extent instead of attending exclusively to the relevant dimension. In general, estimated bounds fit the categorization data slightly better in divided attention tasks than in selective attention tasks. This difference is small, however, and obviously more research will be required, with speed and direction varied in many different ways, to determine the extent to which pigeons are better able to divide attention across speed and direction than to selectively attend to either speed or direction.

Second, the present task required pigeons to shift attention only across conditions lasting several days. This task therefore did not necessarily involve the dynamic shifts of attention that might occur when stimuli and attention interact in a real-time manner, as they did, for example, in Skinner (1960). How nearly optimally pigeons can shift attention in a more dynamic situation remains an open question.

Third, when pigeons peck, they often briefly close their eyes (Smith, 1974), so they might not observe the initial moments of trajectories of moving stimuli to which they are required to peck. The overall performance in the present experiment suggests any such effect here was negligible, but one can imagine other categories with much shorter stimulus durations or nonlinear trajectories for which consequences of the pigeon's natural pecking topography might prevent the high level of performance obtained here, provided a key peck is required to initiate a target's movement.

Fourth, categorization of a target's movement over some nontrivial period of time seems automatically to involve working memory for the target's recent trajectory, with a built-in retention interval for any given part of a target's trajectory equal to the remaining exposure duration preceding the categorization response. In the present experiment, because both target speed and direction within a trial were held constant, this might not have imposed as serious a problem as it might were speed and direction to vary in complex ways within a single observation period. Indeed, in our experiment, because both speed and direction were constant within a trial, longer viewing times presumably both degraded categorization, due to the greater memory load for earlier parts of longer trajectories, and facilitated categorization, because working memory performance generally improves with viewing time, as in delayed matching-to-sample tasks (Maki, Moe, & Bierley, 1977). In short, the present experiment involved only linear trajectories, and it is an open question for future research to determine what kinds of more complex trajectories can also serve as the basis for nearly optimal category learning (see Rilling & Neiworth, 1987, for additional discussion of relations between movement discrimination and short-term memory).

Fifth, consider the role of the initial spatial location of the target. In the present experiment, it seems unlikely that the pigeons used spatial locations on the monitor, rather than speed and direction, as cues upon which to base their categorizations. There are at least two reasons why this possibility seems unlikely: The target initially appeared on different trials in different locations on the monitor, and the target moved on different trials over many different regions of the screen, so that any given location or region would have been unlikely to have served as a useful discriminative cue. In general, however, literature on avian spatial attention (Shimp & Friedrich, 1993) and on attentional switches between local and global levels of perceptual analysis (Cavoto & Cook, 2000; Fremouw, Herbranson, & Shimp, 1998) suggest the way in which attention is directed in advance of target presentation to spatial regions and levels of analysis relevant to target observation may be expected to affect discrimination of moving targets. Thus, manipulations that increase or decrease spatial attention to a region of the screen in which a target is to appear might improve or degrade categorization, respectively.

Sixth, pigeons have two visual systems, a frontal system and a lateral system (Husband & Shimizu, 2001; Martinoya et al., 1983), with the frontal system more adapted to a pigeon's eating strategies, involving small, static stimuli, and the lateral system more adapted to stimuli that are peripheral and dynamic. It is unclear what roles these systems played in the present experiment. Given the random variations in initial target location, and given the variability in duration and length of the stimuli and the speed of the target, it seems unlikely that a pigeon was always capable of moving its head to optimize viewing. It is not unlikely that a pigeon might use different viewing strategies for different stimuli that appear in different locations and have different speeds and viewing times. It is an interesting question for future research to determine what roles the two systems play in the discrimination of different kinds of dynamic stimuli, and how pigeons use head movements to affect their discriminative capacities. It seems likely that how any given task encourages the use of different visual systems will affect accuracy of categorization of moving targets (Husband & Shimizu, 2001; Lea & Dittrich, 2001). Teuber (1960) noted that human motion thresholds ''obviously vary with size and pattern of moving stimulus, with pattern of surround, with illumination and with numerous other factors'' (p. 1642). Presumably, the kind of categorization required in the present experiment depends on all these variables; therefore, the conditions under which the nearly optimal categorization obtained here will be obtained remain to be determined.

Seventh, the ''oblique effect'' (e.g., Donis, 1999), according to which pigeons discriminate horizontal and vertical lines better than they do oblique lines, might affect categorization accuracy in experiments of the present type. That is, depending on whether frequently occurring stimuli involve trajectories on major axes or at oblique orientations, pigeons might perform more or less accurately.

Eighth, how fast a stimulus must move for a pigeon to be able to detect its motion is not yet known. Early evidence suggested that the pigeon's velocity threshold is relatively poor compared to the human's (Hodos et al., 1975; McKee, 1981), but more recent evidence suggests that the pigeon's threshold for movement may be better than originally estimated (Lea & Dittrich, 2001). It is also now known that the pigeon's movement thresholds may be different for frontal and lateral viewing fields (Lea & Dittrich). Because viewing times varied in the present experiment, and because we know only that the pigeons' heads were somewhat near the central region of the chamber while the target moved but know nothing of how a pigeon oriented its head toward the target while viewing it, estimating viewing angles or knowing whether or how a pigeon used different visual fields for different vectors is difficult. Whether attentional allocation would continue to approximate optimality, as in the present experiment, if target speeds were considerably faster or slower, or if a pigeon were required to use a particular visual field, is not known.

Ninth, presumably there are limitations imposed by context on a pigeon's ability to attend selectively to a nearly optimal degree. It should be interesting, for example, to determine further if a kind of ''intensive'' attentional effect discussed by Washburn and Putney (1998) in the context of research involving moving stimuli and nonhuman primates can be obtained in avians: Our experiment deals with the selective nature of attention to various features of a moving stimulus, but it leaves open the question of whether those features vary in terms of their ability to attract attention when a participant is also required to attend to other stimuli in a secondary task. Initial evidence from a simulated naturalistic foraging task developed by Dukas and Kamil (2000) suggests that blue jays in fact do not attend as effectively to a multidimensional central target if they are also required to attend to a peripheral target. To the degree to which the tasks of Washburn and Putney and Dukas and Kamil are analogous to the present situation, it seems unlikely that a pigeon could selectively attend in an almost optimal way to various features of a target moving in the distance if at the same time it were foraging for food on the ground.

These issues raise questions about how well the present results characterize the general categorization of moving targets. The present results, nevertheless, allow us to state that one task has been identified in which pigeons allocate attention to a moving target in ways that are, on average, nearly optimal.

Does Categorization of Moving Targets Involve Abstract Visual Concepts?

Dittrich and Lea (1993) and Lea and Dittrich (2001) examined relations between avian motion discrimination and the idea of a general concept. Motion is, in at least a primitive way, inherently conceptual, because by definition it involves integration of different stimuli across time (see also Cook & Katz, 1999, p. 195; Emmerton, 1986). Perhaps in the present experiment, categorization was necessarily conceptual in the specific sense that categorization logically required some kind of many-to-one unification of diverse images that appeared over successive moments. Whether this logical unification and construction of coherence are in terms of perceptual processes, memory processes, perceptual interactions, or in other terms, is, as far as we are aware, unclear not only in the nonhuman animal literature but in the analogous human literature as well (see Berthoz, 2000, for an interesting discussion of this issue). The possibility discussed by Emmerton, Cook and Katz, and Lea and Dittrich is that such unification takes place, whatever the underlying processes. On the other hand, it must be acknowledged that from the perspective of behavioral neuroscience, it might seem increasingly likely that such integration might be possible at a fairly low level of neural processing, because much evidence suggests individual striatal neurons of monkeys respond to movement and direction (see Goldstein, 1996, for a review). Single-cell recording in pigeons also has identified cells sensitive to motion and direction, and these cells are not in brain regions usually viewed in humans as related to abstract thought (Frost et al., 1994). It therefore remains to be determined whether apparent unification of successive images required for the perception of movement involves high-level abstractions or can be explained by low-level motion and direction detectors.

There is a second way in which perception of movement may be necessarily conceptual. Customarily, with static naturalistic stimuli, one says a pigeon has acquired the visual concept of a fish if it generalizes training to novel exemplars (Herrnstein & Loveland, 1964; Huber, 2001; Wright, 2001). In the present experiment, even though pigeons saw many different exemplars of both categories, many exemplars were nevertheless novel because they were selected from an immense pool of possible exemplars numbering in the hundreds of thousands (see Herbranson et al., 1999). By the customary definition, the present performances were therefore automatically conceptual. However, just as there was ambiguity in whether movement is encoded in terms of abstractions or lower level sensory events, there is also ambiguity in the nature of the kind of generalization needed to establish a learned behavior as involving conceptual learning. For instance, would the present performances have generalized if the target were changed? Specifically, if the target were changed from a moving white circle to a moving object of changing shape and color, or to an expanding two-dimensional projection of a peregrine falcon seeming to loom ever closer, would the pigeons have categorized movement in the same way? We do not know, but we tend to agree with Dittrich and Lea (1993) that there is more to naturalistic motion perception than motion vector perception.

Our position on the question of whether the present performances were conceptual is therefore somewhat agnostic. Badly needed, in our opinion, is an adequate theory in terms of which the basic nature of categorization would be described and explained (Shimp, 1984). Contemporary theories of categorization deal with static prototypes and static specific exemplars (Ashby & Maddox, 1998; Estes, 1994), however, and therefore do not as yet deal with the implications for categorization of real-time processing of moving stimuli. Quantitative control of behavior by dynamic stimuli by its very nature raises important questions about categorization behavior, including the conventional distinction drawn between the concrete, in the form of individual memories of specific exemplars, and the abstract, in the form of memories of prototypes or rules.

Implications for Current Theories

One might be forgiven for assuming that the ability of a theory to deal with performances in naturalistic conditions is one reasonable criterion for evaluating the generality and overall significance of the theory. Few contemporary theories of learning, memory, and conditioning, however, are rigorously held up to that criterion. By that criterion, most current theory, when applied to performances involving moving stimuli, looks much weaker than it customarily does. Although it is true that research on nonhuman animal learning and cognition presently includes many tasks that explicitly address time, including delayed matching-to-sample tasks with which to study memory (Maki et al., 1977; Wright, 2001) and many tasks with which to study timing itself (Church & Kirkpatrick, 2001; Gallistel & Gibbon, 2000), it is nevertheless the case that, as Skinner (1976/1996) so poignantly lamented, theoretical analyses of behavior often do not attempt to describe or explain the real-time processes that are presumably responsible for behavioral outcomes averaged over time. Relatively few theories of nonhuman animal behavior, that is, predict real-time behavior. Correspondingly, few theories of nonhuman animal behavior address discrimination of, generalization over, memory for, attention to, or categorization of dynamic visual stimuli. A problem is that there is no clear solution to the problem of how to represent an animal's real-time "knowledge" of a moving visual stimulus theoretically. It is not entirely clear, at least not to us, how well-known theories of Pavlovian conditioning (Rescorla & Wagner, 1972), choice behavior (Davison & McCarthy, 1988; Herrnstein, 1997), short-term memory (Wright, 2001), or timing (Gallistel & Gibbon, 2000) can address this question. We suspect considerable progress will result from research in nonhuman animal timing, visual search, memory, categorization, and choice that addresses the exciting challenge of determining the implications of dynamic stimuli.

The virtual absence from research on nonhuman animal behavior of such a striking feature of the natural world as movement is surely due in part to technological limitations. Until recently, few researchers have had the interest or resources Skinner (1960) had when he worked on the *Pigeons in a Pelican* project. He designed, constructed, and tested technology with which to present moving stimuli and even employed a servo mechanism by which moving stimuli were made to depend on a pigeon's behavior. Modern computer technology now makes it relatively simple to arrange such tasks. This rapid change in technology may not necessarily produce, however, a correspondingly rapid change in its use, because there are now established empirical and intellectual traditions and conventions in terms of which dynamic stimuli, let alone real-time interactions between dynamic stimuli and behavior, are not a part (Shimp, 2001). We therefore might be facing a moment in the development of research on animal behavior when unusual strides forward might be made by paying increasing attention to dynamic issues. We may have a rare opportunity to increase generalizability of data and theory by extending conventional methods and theory to more naturalistically valid cases involving moving stimuli. Perhaps the generality of contemporary theory for learning and cognition might be improved if evaluative criteria for such theories included issues of stimulus dynamics, the continuous behavior stream, or how motion can improve discrimination of stimuli, recognition of objects, and detection of predators and prey (Cook & Katz, 1999; Jitsumori, Natori, & Okuyama, 1999; Kirkpatrick-Steger, Wasserman, & Biederman, 1998; Lea & Dittrich, 2001).

REFERENCES

Ashby, F. G., & Gott, R. E. (1988). Decision rules in the perception and categorization of multidimensional stimuli. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 14,* 33–53.

Ashby, F. G., & Maddox, W. T. (1998). Stimulus categorization. In M. H. Birnbaum (Ed.), *Measurement, judgment, and decision making: Handbook of perception and cognition* (pp. 251–301). San Diego: Academic Press.

Berthoz, A. (2000). *The brain's sense of movement* (G. Weiss, Trans.). Cambridge, MA: Harvard University Press.

Blough, D. S. (1972). Recognition by the pigeon of stimuli varying in two dimensions. *Journal of the Experimental Analysis of Behavior, 18,* 345–367.

Cavoto, K. K., & Cook, R. G. (2000). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 27,* 3–16.

Chase, S., & Heinemann, E. G. (1972). Choices based on redundant information: An analysis of two-dimensional stimulus control. *Journal of Experimental Psychology, 92,* 161–175.

Chase, S., & Heinemann, E. G. (2001). Exemplar memory and discrimination. In R. G. Cook (Ed.), *Avian visual cognition.* Retrieved September 6, 2002, from http://www.pigeon.psy.tufts.edu/avc/

Church, R. M., & Kirkpatrick, B. (2001). Theories of conditioning and timing. In R. R. Mowrer & S. B. Klein (Eds.), *Handbook of contemporary learning theories* (pp. 211–253). Mahwah, NJ: Erlbaum.

Cook, R. G., & Katz, J. S. (1999). Dynamic object perception by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 25,* 194–210.

Davison, M., & McCarthy, D. (1988). *The matching law.* Hillsdale, NJ: Erlbaum.

Dittrich, W. H., & Lea, S. E. G. (1993). Motion as a natural category for pigeons: Generalization and a feature-positive effect. *Journal of the Experimental Analysis of Behavior, 59,* 115–129.

Dittrich, W. H., Lea, S. E. G., Barrett, J., & Gurr, P. R. (1998). Categorization of natural movements by pigeons: Visual concept discrimination and biological motion. *Journal of the Experimental Analysis of Behavior, 70,* 281–299.

Donis, F. J. (1999). The oblique effect in pigeons (*Columba livia*). *Journal of Comparative Psychology, 113,* 107–115.

Dukas, R., & Kamil, A. C. (2000). The cost of limited attention in blue jays. *Behavioral Ecology, 11,* 502–506.

Emmerton, J. (1986). The pigeon's discrimination of movement patterns (Lissajous figures) and contour-dependent rotational invariance. *Perception, 15,* 573–588.

Emmerton, J. (1990). Pigeons' perception of complex movement patterns. In M. L. Commons, R. J. Herrnstein, S. M. Kosslyn, & D. B. Mumford (Eds.), *Quantitative analyses of behavior: Vol. 8. Behavioral approaches to pattern recognition and concept formation* (pp. 67–87). Hillsdale, NJ: Erlbaum.

Estes, W. K. (1994). *Classification and cognition.* New York: Oxford University Press.

Fremouw, T., Herbranson, W. T., & Shimp, C. P. (1998). Priming of attention to local or global levels of visual analysis. *Journal of Experimental Psychology: Animal Behavior Processes, 24,* 278–290.

Frost, B. J., Wylie, D. R., & Wang, Y. C. (1994). The analysis of motion in the visual systems of pigeons. In M. N. O. Davies & P. R. Green (Eds.), *Perception and motor control in pigeons* (pp. 248–269). Berlin: Springer-Verlag.

Gallistel, C. R., & Gibbon, J. (2000). Time, rate, and conditioning. *Psychological Review, 107,* 289–344.

Goldstein, E. B. (1996). *Sensation and perception* (4th ed.). Pacific Grove, CA: Brooks/Cole.

Gould, S. J., & Lewontin, R. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society, B205,* 581–598.

Herbranson, W. T., Fremouw, T., & Shimp, C. P. (1999). The randomization procedure in the study of categorization of multidimensional stimuli by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 25,* 113–135.

Herrnstein, R. J. (1997). *The matching law: Papers in psychology and economics.* Cambridge, MA: Harvard University Press.

Herrnstein, R. J., & Loveland, D. H. (1964). Complex visual concepts in the pigeon. *Science, 146,* 549–551.

Hodos, W., Smith, L., & Bonbright, J. C., Jr. (1975). Detection of the velocity of movement of visual stimuli by pigeons. *Journal of the Experimental Analysis of Behavior, 25,* 143–156.

Huber, L. (2001). Visual categorization in pigeons. In R. G. Cook (Ed.), *Avian visual cognition.* Retrieved September 6, 2002, from http://www.pigeon.psy.tufts.edu/avc/

Husband, S., & Shimizu, T. (2001). Evolution of the avian visual system. In R. G. Cook (Ed.), *Avian visual cognition.* Retrieved September 6, 2002, from http://www.pigeon.psy.tufts.edu/avc/

Jitsumori, M., Natori, M., & Okuyama, K. (1999). Recognition of moving video images of conspecifics by pigeons: Effects of individuals, static and dynamic motion cues, and movement. *Animal Learning & Behavior, 27,* 303–315.

Kirkpatrick-Steger, K., Wasserman, E. A., & Biederman, I. (1998). Effects of geon deletion, scrambling, and movement on picture recognition in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 24,* 34–46.

Lea, S. G., & Dittrich, W. H. (2001). Motion discrimination and recognition. In R. G. Cook (Ed.), *Avian visual cognition.* Retrieved September 6, 2002, from http://www.pigeon.psy.tufts.edu/avc

Maki, W. S., Moe, J. C., & Bierley, C. M. (1977). Short-term memory for stimuli, responses, and reinforcers. *Journal of Experimental Psychology: Animal Behavior Processes, 3,* 156–177.

Malloy, T. E., Jensen, G. C., Song, T., Herbranson, W. T., Fremouw, T., & Shimp, C. P. (1991). Interactive demonstration of avian categorization. Retrieved June 18, 2002, from http://www.psych.utah.edu/shimp/Avian_Categorization.htm

Martinoya, C., Rivaud, S., & Bloch, S. (1983). Comparing frontal and lateral viewing in the pigeon: II. Velocity thresholds for movement discrimination. *Behavioral Brain Research, 8,* 375–385.

McKee, S. P. (1981). A local mechanism for differential velocity detection. *Vision Research, 21,* 491–500.

McVean, A., & Davieson, R. (1989). Ability of the pigeon (*Columba livia*) to intercept moving targets. *Journal of Comparative Psychology, 103,* 95–99.

Neiworth, J. J., & Rilling, M. E. (1987). A method for studying imagery in animals. *Journal of Experimental Psychology: Animal Behavior Processes, 13,* 203–214.

Potts, W. (1984). The chorus-line hypothesis of manoeuvre coordination in avian flocks. *Nature, 309,* 344–345.

Rescorla, R., & Wagner, A. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning: Vol 2. Current research and theory* (pp. 64–99). New York: Appleton-Century-Crofts.

Riley, D. A., & Brown, M. F. (1991). Representation of multidimensional stimuli in pigeons. In G. R. Lockhead & J. R. Pomerantz (Eds.), *The perception of structure* (pp. 227–245). Washington, DC: American Psychological Association.

Rilling, M. E., & LeClair, T. L. (1989). Visually guided catching and tracking skills in pigeons: A preliminary analysis. *Journal of the Experimental Analysis of Behavior, 52,* 377–385.

Rilling, M., LeClair, L., & Warner, M. (1993). A comparative, hierarchical theory for object recognition and action. In T. R. Zentall (Ed.), *Animal cognition: A tribute to Donald A. Riley. Comparative cognition and neuroscience* (pp. 313–333). Hillsdale, NJ: Erlbaum.

Rilling, M. E., & Neiworth, J. J. (1987). Theoretical and methodological considerations for the study of imagery in animals. *Learning and Motivation, 18,* 57–79.

Rosch, E., & Mervis, C. B. (1975). Family resemblance: Studies in the internal structure of categories. *Cognitive Psychology, 7,* 573–605.

Sekuler, R. (1975). Visual motion perception. In E. C. Carterette & M. P. Friedman (Eds.), *Handbook of perception* (Vol. 5, pp. 387–424). New York: Academic Press.

Shimp, C. P. (1973). Probabilistic discrimination learning in the pigeon. *Journal of Experimental Psychology, 97,* 292–304.

Shimp, C. P. (1984). The question: Not *shall* it be, but *which* shall it be? Commentary on ''Are theories of learning necessary?'' by B. F. Skinner. *Behavioral and Brain Sciences, 7,* 536–537.

Shimp, C. P. (2001). Behavior as a social construction. *Behavioural Processes, 54,* 11–32.

Shimp, C. P., & Friedrich, F. J. (1993). Behavioral and computational models of spatial attention. *Journal of Experimental Psychology: Animal Behavior Processes, 19,* 26–37.

Shimp, C. P., Herbranson, W. T., & Fremouw, T. (2001). Avian visual attention: Laboratory and cultural perspectives. In R. G. Cook (Ed.), *Avian visual cognition.* Retrieved September 6, 2002, from http://www.pigeon.psy.tufts.edu/avc/

Skinner, B. F. (1960). Pigeons in a pelican. *American Psychologist, 16,* 28–37.

Skinner, B. F. (1996). Farewell, my lovely. In A. C. Catania & P. H. Hineline (Eds.), *Variations and selections: An anthology of reviews from the Journal of the Experimental Analysis of Behavior* (p. 230). Bloomington, IN: Society for the Experimental Analysis of Behavior. (original work published 1976)

Smith, R. F. (1974). Topography of the food-reinforced key peck and the source of 30-millisecond interresponse times. *Journal of the Experimental Analysis of Behavior, 21,* 541–551.

Teuber, H.-L. (1960). Perception. In *Handbook of physiology* (Vol 3., pp. 1595–1668). Washington, DC: American Physiological Society.

Walls, G. (1942). *The vertebrate eye and adaptive radiation.* Bloomfield Hills, MI: Cranbrooke.

Washburn, D. A., & Putney, R. T. (1998). Stimulus movement and the intensity of attention. *The Psychological Record, 48,* 555–570.

Watanabe, S. (1991). Effects of ectostriatal lesions on natural concept, pseudoconcept, and artificial pattern discrimination in pigeons. *Visual Neuroscience, 6,* 497–506.

Wright, A. A. (2001). Learning strategies in matching-to-sample. In R. G. Cook (Ed.), *Avian visual cognition.* Retrieved September 6, 2002, from http://www.pigeon.psy.tufts.edu/avc/

Received October 22, 2001
Final acceptance June 24, 2002